

## CHAPTER I

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# Questions in Animal Behavior

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**I**MAGINE AN ANIMAL THAT DOES NOT BEHAVE. Then try to imagine being interested in an animal that does not behave. Without doubt, there are aspects of an animal's biology—its morphology, brain, and genes, its ecology and evolutionary history—that spark the interest of many scientists. But it is the animal's *behavior* that often focuses the attention of scientists and nonscientists, children and adults. One cannot imagine the success of the plethora of wildlife documentaries flooding the public airways if the animals in them did not behave.

Animal behavior is the fulcrum between the processes internal to the individual—its genetics, neurobiology, and physiology—and all that is external to it, including the environment, its social surroundings, and the other species it eats or is eaten by. Details of an animal's behavior have been shaped by millennia of selection molding them within the constraints imposed by the details of the animal's biology and endowing the animal with the capacity to respond flexibly to its surroundings in a manner that can sometimes be both exquisite and enigmatic. These factors make animal behavior one of the most integrative endeavors in biology: It encompasses both proximate and ultimate questions, how the behavior works, and why it has come to work as it does.

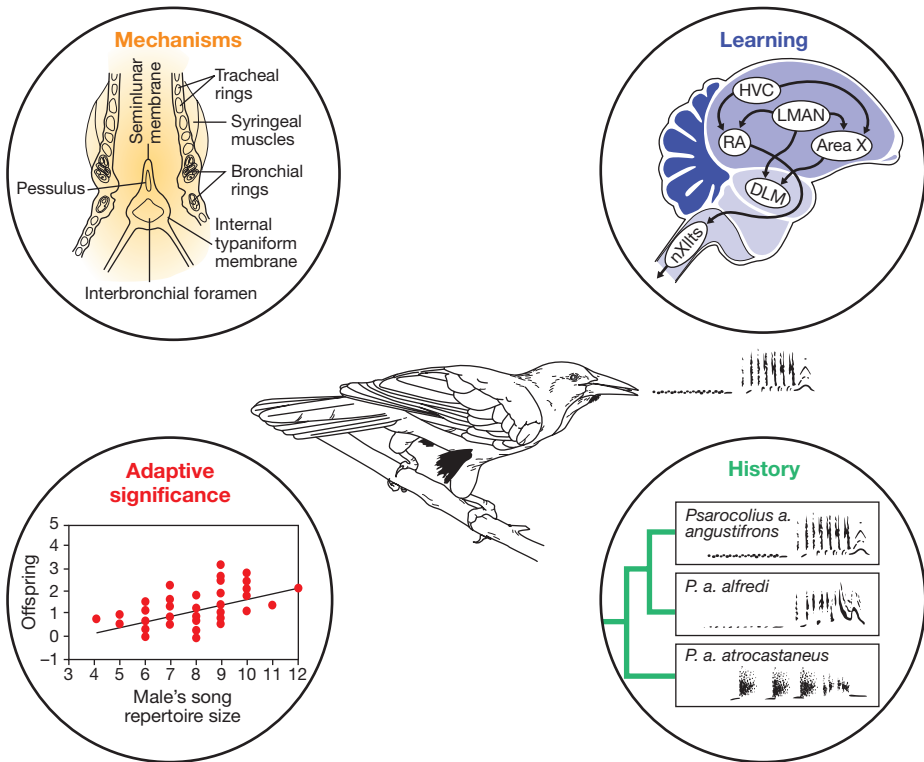
### TINBERGEN'S FOUR QUESTIONS

In 1973 Niko Tinbergen was awarded the Nobel Prize in Physiology or Medicine, along with Karl von Frisch and Konrad Lorenz, as one of the founders of ethology, the study of animal behavior in its natural environment. In an attempt to organize this new endeavor, he codified the study of behavior in a 1963 paper, "On aims and methods of ethology," by proposing four general questions: causation, ontogeny, survival value, and evolution. Today we know these as mechanisms, acquisition,

adaptive significance, and evolutionary history. The first two questions address proximate causes and the latter two ultimate causes.

All four questions can address the same behavior. We can illustrate this by considering a male songbird perched on a treetop vigorously singing its complex song in a feat of acoustic acrobatics. How can we explain this behavior? It depends on what question we ask and what we mean when we ask it (Fig. 1.1).

Why does a bird produce the complex acoustic patterns we know as song? This question can be rephrased to ask, how does he make the song? The mechanism of singing involves accessing a neural code in the brain that drives the respiratory patterns



**Figure 1.1.** A deep understanding of animal behavior requires answers to all of Tinbergen's four questions. One example is, "Why do birds sing?" Here we represent a singing male oropendola, a member of the New World blackbird family, and (clockwise from *top, left*) the morphology of the syrinx that enables complex song production, the brain circuitry involved in song learning, a phylogeny of some oropendola taxa and sonograms of the song they produce, and a hypothetical relationship between male song repertoire size and the number of offspring sired. (HVC) High vocal center; (nXIIIts) hypoglossal nucleus; (DLM) dorsolateral anterior thalamic nucleus; (LMAN) lateral magnocellular nucleus or the nidopallium; (RA) robust nucleus of the arcopallium.

and muscles of the bird's vocal organ, the syrinx, to produce a pattern of sound pressure fluctuations that can be interpreted by a receiver. The mechanism also involves the biomechanical details of the syrinx, which functions similarly to our larynx. There are some elegant characteristics of the songbird syrinx that endow these birds with the ability to make two separate songs at once, the "two-voiced" song, which results in some of the most complicated vocal repertoires in the animal kingdom.

We can answer this same question another way: How does he know how to make the song? We know that songbirds acquire their song through learning. To produce these complex acoustic patterns, they must be exposed to songs of another member of their species, a "conspecific," during a sensitive period early in their life. These two answers to the same question both concern proximate issues in behavior, the underlying mechanisms governing the behavior, and how the behavior is acquired.

We can also ask why the bird sings—that is, what is the function of song? Questions about the function of behavior address its adaptive significance and ask how a behavior influences the fitness of the animal producing it. Male songs have multiple functions. These songs are used to interact acoustically with other males and as courtship signals to females. Variation in song among males is under evolutionary selection because it influences a male's reproductive success. In many species, for example, females prefer males with larger song repertoires, so it seems that large repertoire size could have evolved under selection generated by female mate choice. This is a functional explanation of why birds sing complex songs, and it is rooted in understanding the potential adaptive significance of the behavior.

We can ask again: Why does the bird sing a complex song? A seemingly simple answer is: Because it is a songbird. This answer is not as glib as it might first appear; it is an informed response motivated by concerns about the past. Not all birds have complex songs. Thus, we can ask about the evolutionary history of the trait. Complex song does not occur randomly among birds. Instead, the occurrence of complex song shows a strong historical pattern. Complex song is common within one phylogenetic group of birds, the oscines or "songbirds," and is not common in other groups. This group of birds is also among the few that learn song and that have an anatomically complex syrinx. Questions about evolutionary history ask where a behavior came from. Questions of function and history are usually considered ultimate questions.

It is important to understand what questions are being asked of an animal's behavior. "Why does a bird sing complex song?" has at least four answers: because it has a complex syrinx, because it learned the song of an adult, because selection favors complex songs, and because it is a songbird. The field of animal behavior has been replete with disagreements because different researchers were asking different questions, not just because they were arriving at different answers. Tinbergen's four questions were meant to resolve some of these problems.

## TINBERGEN'S ONE QUESTION

In the same 1963 paper, Tinbergen proposed a more general question that concerns all animal behaviorists: Why do animals behave the way that they do? He suggested one had to address each of his four questions to arrive at a complete understanding of animal behavior (i.e., to answer his one question). This will be a subtext running throughout this book.

Animal behavior encompasses research disciplines that sometimes have little overlap. Mechanisms of behavior are traditionally the domain of neurobiologists and physiologists, whereas studies of the acquisition of behavior are often conducted by comparative psychologists who study learning or geneticists interested in behavioral genetics. Behavioral ecologists have been at the forefront of understanding the adaptive significance of behavior, whereas studies of the history of behavior have been conducted by those with a background in phylogenetics. These are fields of science that often have little interaction, publish in different journals, and embrace different research traditions. Yet none of this makes any difference to the behavior being studied. The fact that a neurobiologist has never been in the field does not negate the importance of natural selection in shaping the neural circuit being studied; nor does the ignorance of a field biologist about the “black box” controlling behavior exclude the critical importance of this mechanism for the animal’s survival.

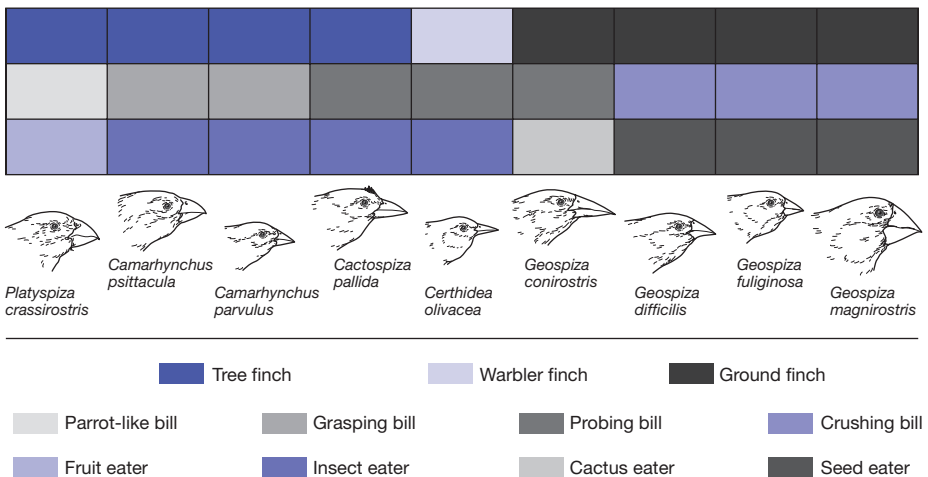
We hope to demonstrate throughout this text that an integrative analysis of animal behavior attempts to obtain a deep and complete understanding of behavior by addressing each of Tinbergen’s four questions. There are two reasons to strive for such integration. Because there are different aspects to behavior, we must address all of them to truly answer Tinbergen’s one question about why animals behave the way that they do. But another important reason is that answers to questions at one level of analysis can inform answers at other levels. We can briefly illustrate this point by developing the issue of birdsong further.

One function of birdsong is to provide information about species identity. Thus, the divergence of song between populations can contribute to speciation. Although the songbird’s “two-voiced” syrinx is primarily responsible for the acoustic features of the song, the morphology of the bird’s beak can also influence what the song sounds like, specifically its trill rate and frequency range. But the beak not only influences what comes out of the bird but also what goes into it. Beak morphology is critical for feeding, and nowhere is this shown more clearly than in the Galápagos finches.

Many popular accounts of the voyage of the *Beagle* credit the adaptive radiation of Galápagos finches as providing Charles Darwin with insights that were critical to development of his theory of natural selection, although it did not happen until Darwin returned to England and the ornithologist John Gould drew his attention back to these birds. Although these finch species are very similar in size and color, they differ quite profoundly in the variety of their beak morphologies. Divergence

in these finches was driven by diet, and their beaks evolved to complement and enable the diet. "It is very remarkable that a nearly perfect gradation of structure in this one group can be traced in the form of the beak, from one exceeding in dimensions that of the largest gros-beak, to another differing but little from that of a warbler," as Darwin stated in *The Voyage of the Beagle*. These birds evolved large, parrot-like beaks for eating fruit, grasping and probing beaks for hunting insects, and crushing beaks for crushing seeds—larger beaks for larger seeds and smaller beaks for smaller seeds (Fig. 1.2). Jeffrey Podos showed that not only does the beak's form vary with diet, but it also varies with song; males with larger beaks that eat large seeds have a slower pulse rate and more restricted frequency range than Galápagos finches with smaller beaks. Thus, selection that results in the evolution of beaks to promote feeding efficiency incidentally causes evolution of song differences among birds with different diets. It has been suggested that divergence of songs contributes to speciation between populations that not only eat different things but also sound different.

The above example uncovers a relationship between feeding ecology, song behavior, and speciation. The critical insights were how beaks influenced song and diet and how song functioned in mate recognition. We will investigate a few additional examples of such synergisms between different levels of analysis.



**Figure 1.2.** In Darwin's finches, bill morphology is closely related to diet. The *middle* of the figure shows species of all of the finches included in the analysis. Each finch (from *left to right*) corresponds to each column, from *left to right*, in the diagram above. The diagram at the *top* of the figure has three rows. The *top* row illustrates the ecological group to which each finch belongs, the *middle* row the type of bill, and across the *bottom* row a description of their diet. Each of these rows corresponds to the color-coded legend at the *bottom* of the figure. For example, the finch *Platyspiza crassirostris* is a "tree finch" (*top* row, blue) with a parrot-like bill (*middle* row, light gray) who eats fruit (*bottom* row, light blue).

## SYNERGISMS BETWEEN DIFFERENT LEVELS OF ANALYSIS

### Evolutionary History Informs Function

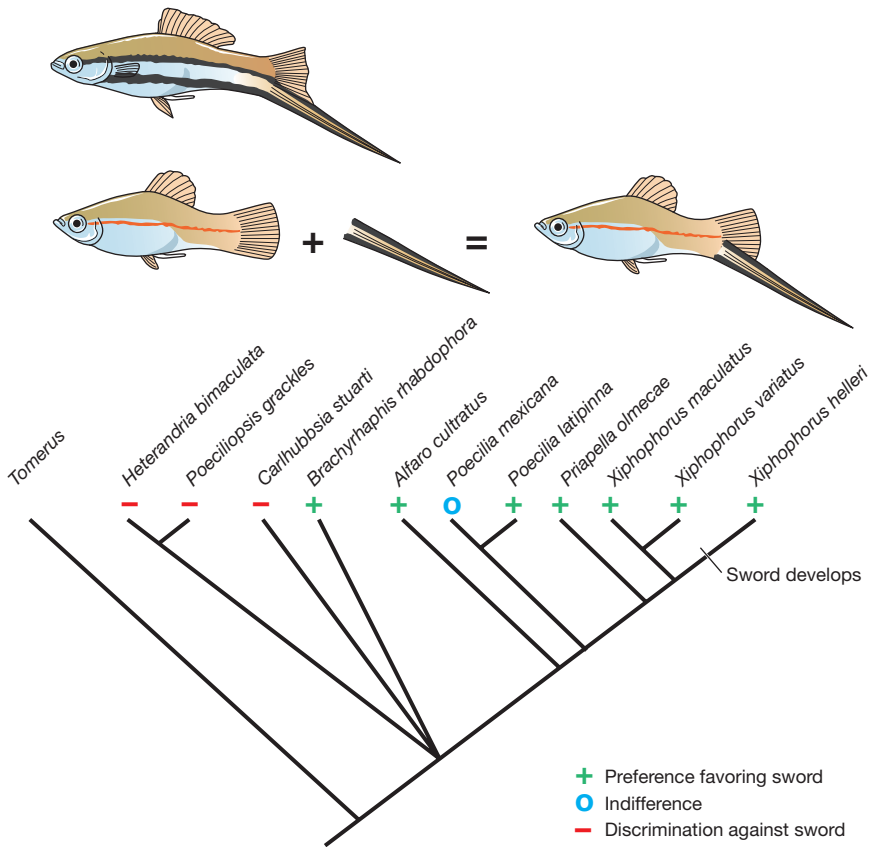
Female mate choice has been a major topic within behavioral ecology for many years. As Darwin pointed out in his theory of sexual selection, this behavior is responsible for the evolution of some of the most bizarre morphologies and behaviors in the animal kingdom. One controversial aspect of Darwin's proposal was why females should prefer certain male traits. The search for this answer usually assumes that male traits provide information to the female about the male's physical or genetic quality. However, studies of mate choice in swordtails reveal another possibility.

#### *Mate Choice in Swordtails*

Swordtails are live-bearing fishes in which the lower rays of the caudal fin are extended into a sword-like appendage. Swordtails are close relatives of platyfish, which are in the same genus (*Xiphophorus*), although platyfish usually lack these sword-like appendages. Mate choice experiments in *Xiphophorus helleri* show that females prefer males with longer swords (Fig. 1.3). Most behavioral ecology studies would stop there and speculate about what sword length tells the female about the male's health or genes. But in a series of studies by Alexandra Basolo, the focus of preference for swords shifted to a species without swords, the platyfish *Xiphophorus maculatus*. When a plastic sword was appended to a male platyfish, the females preferred the male with the artificial sword. Experiments with other platyfish and even other live-bearing fish yielded similar results. How can one interpret these results, with females preferring a male trait that does not exist in nature?

Although the phylogenetic relationships within *Xiphophorus* are not fully resolved, it appears that swordtails are all each other's closest relatives, and they inherited swords from a common ancestor after they diverged from the platyfish. However, as both swordtails and platyfish prefer males with swords, we assume that the preference was inherited from a common ancestor that would have existed before the swordtails and platyfish diverged. This historical logic suggests that the preference for the sword predated the evolution of the sword. If this interpretation is correct, it suggests that the sword was already favored by females when it evolved, as opposed to the alternative, that the sword evolved first as a signal of male quality and females then evolved a preference for it. Of course, female preferences for the trait and the traits themselves can both evolve further once the interaction of trait and preference is established.

There is more, however, to the sword's tale. In many species of live-bearing fish, females prefer larger males. It has been suggested that the sword is an energetically cheap way to make the male larger. In experiments by Gil Rosenthal and Christopher Evans using video animations, females compared two males of the same total body length (measured from the tip of the snout to the base of the tail), but one male had a sword, whereas the other male was lacking a sword. Actually, because these



**Figure 1.3.** Fishes in the genus *Xiphophorus* are either swordtails or platyfish. Swordtails have elongated caudal rays that form the sword, which are lacking in platyfish. Alexandra Basolo showed that female swordtails prefer normal males with swords to males in which the sword is surgically removed, and that female platyfish prefer males with swords that are surgically added to normal swordless males. The same is true for some close relatives that lack swords. The preference for the sword therefore evolved before the sword itself. The conclusion is that males evolved traits that exploit preexisting female preferences.

were animations, the two males had the same body and the same courtship behavior. Female *X. helleri* preferred the male with the sword to the one without a sword. But when size was manipulated such that the swordless male was as long as the male with the sword, the females did not show a preference. Thus, female *X. helleri* prefer longer males whether or not a sword adds to their length. It appears that males evolved swords to exploit a preexisting female bias for larger males. These studies on the swords of swordtails provide an excellent example of how information on the evolutionary history of the behavior can inform us about how it evolved.

## Mechanism Informs Function

Few natural scenes are as stunning and breathtaking as the fall foliage in northeastern North America. The trees are ablaze in riotous reds, yellows, and oranges as they prepare to drop their leaves for the winter. Plant physiologists have offered several explanations for this autumnal explosion of color. Some of the colors, such as yellow, are by-products of disintegration; as the green chlorophyll disappears, the underlying colors are revealed. But certain products (red anthocyanins) are produced only in the fall, and these products have several functions. They are antioxidants, they might function as sinks for harmful metals, and they also might warm the leaves and protect them against ultraviolet (UV) light.

### *Autumn Leaves and Aphid Vision*

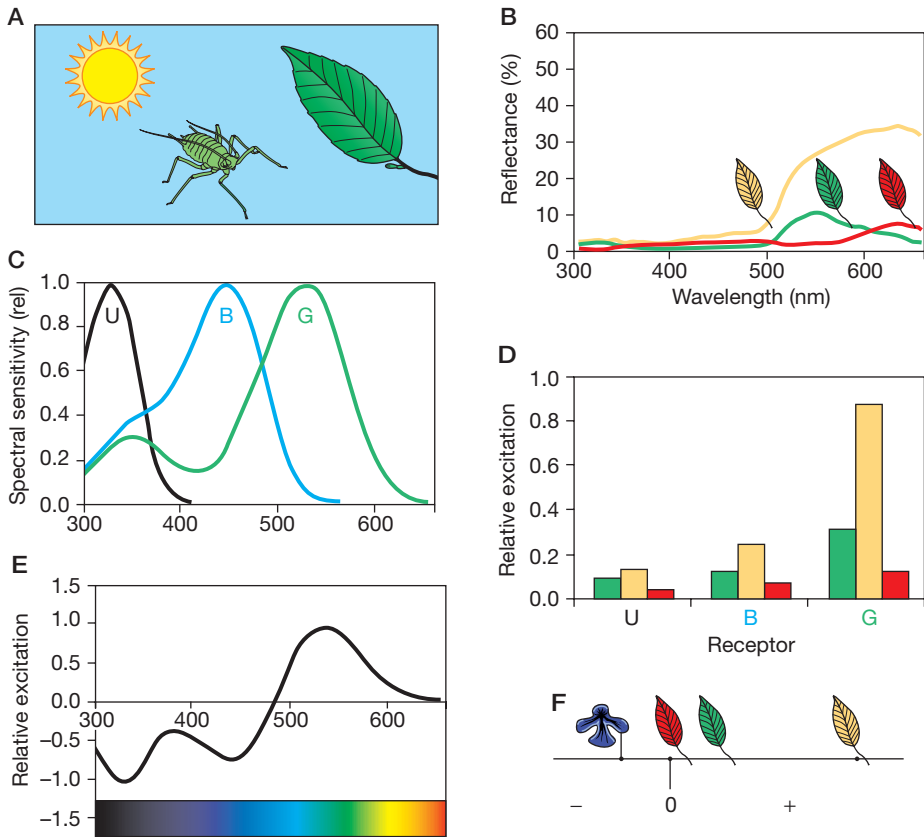
A strikingly different explanation for fall colors was offered by the evolutionary biologist W.D. Hamilton, one of the great thinkers of biology in the 20th century, and published posthumously in 2001. He posited that these are warning colors that the trees use to signal herbivores, such as aphids, to stay away. This should be an “honest” signal, that is, a reliable indicator of the signaler’s quality, in that the brighter the leaves, the more toxic they are to the herbivore. The more “yellow” the leaves of a species of tree, the more likely it is to be colonized by aphids. Thus, it was suggested that these species need to invest more in warning signals to repel aphids, an argument that was independently proposed and addressed with a game theory model by Marco Archetti.

A basic assumption of the warning color argument is that the insects perceive the difference between red and yellow. The mind-bending question we ask ourselves at this point is, “When two people say they see an object they report is colored blue, how can we be sure they are really experiencing the same color as we are?” We cannot. But we can be sure that other species do not necessarily have the same experience of color that we have. An animal’s sensation of color can be determined if we know the spectrum of sunlight that strikes an object, the spectrum of light reflected by that object, the spectral sensitivities of the receiver’s photopigments, and the interaction of different photopigment classes in the color perception system.

Does the aphid see the same explosion of brilliance in the fall foliage that triggered such gifted poetry from Robert Frost? Hardly, according to Lars Chittka and Thomas Döring. Aphids, like all other herbivorous insects studied to date, lack a long-wavelength or “red”-sensitive cone. Their three classes of cones are sensitive to wavelengths in the very short (“ultraviolet”), short (“blue”), and medium (“green”) wavelengths (Fig. 1.4). In Figure 1.4D we see how green, yellow, and red leaves from a bird-cherry tree, whose reflectances are illustrated in Figure 1.4B, would excite each of the three classes of aphid photoreceptors.

Most animals that perceive true color, or hue, do so with a color opponency system that compares the output from pairs of different cone classes. Behavioral





**Figure 1.4.** An analysis of how aphids perceive colored leaves. (A) A leaf reflects light from the sun and is seen by an aphid with green (G), blue (B), and ultraviolet (U) photoreceptors. (B) The reflectance spectra of three different colored leaves from the bird-cherry tree, *Prunus padus*. To humans, these leaves appear green, red, and yellow. (C) The wavelengths perceived by the green peach aphid is influenced by the spectral sensitivities of its UV, blue, and green photoreceptors; the tentative spectra are shown here. (D) The degree to which each of these three classes of photoreceptors are excited by the three different leaf colors varies considerably. (E) This figure shows the summed excitation of the photoreceptors. The integration of the photoreceptors is based on an opponency system with positive input from the green photoreceptor and negative input from the other two receptors. Based on behavioral data, a mechanism of this kind is presumably what many insect herbivores use as a “greenness detector.” (F) The summed excitation of the color opponency system by the three bird-cherry leaves and a blue-purple flower (*Ajuga genevensis*) is illustrated on a one-dimensional scale. We see that the yellow leaf produces an even more positive signal from the “greenness detector” than the green leaf, which contradicts the behavior hypothesis that green and yellow should be perceived quite differently.

experiments suggest that aphids perceive color by an opponency system with medium versus short wavelength components, with an excitation spectrum as in Figure 1.4E. Insect herbivores generally use such a mechanism as a “greenness” detector, with positive input through the green photoreceptor and negative ones through the short wavelength receptors. Modeling this color opponency mechanism, the aphid’s perception of the bird-cherry leaves and a blue flower can be represented in one-dimensional “greenness” (Fig. 1.4F). As expected, the green elicits a more positive response than red. Whereas yellow and red both appear bright to humans, red appears dull to aphids. Interestingly, insects that rely on such a color opponency system are stimulated even more strongly by yellow than by green. Hence yellow has been referred to as a “super-normal foliage-type stimulus.” If this is true, then aphids should find yellow attractive and not repellent; in fact, it should be even more attractive than green. This is what was reported as data supporting the original signaling hypothesis: Tree species with more yellow had more aphids.

The suggestion that trees use bright colors as warning signals to insects was an insightful and logically consistent hypothesis about the function and adaptive significance of fall foliage. This hypothesis predicts, however, that red and yellow should be less attractive to aphids than green. But the details of the aphid’s color vision suggest the opposite. The Chittka and Döring paper also notes that there are aphid species that prefer green to yellow, indicating the possibility of species differences. Nevertheless, knowledge of the mechanisms of insect color perception leads us to dismiss the hypothesis of foliage as an honest signal to herbivores.

### Acquisition Informs Evolutionary History

Tinbergen’s question of “evolution” asks about the contribution of evolutionary history to current behavior. In many cases, the behavioral similarities between siblings, parents, and offspring, as well as the similarities between different species, result from shared genes that influence the same behavior. The sucking and the grasping reflexes in human neonates, which are shared with all mammals and all primates, respectively, are good examples. Patterns of shared behaviors throughout a family’s or a species’ history often result from genomic transmission across generations.

Not all patterns of behavioral inheritance or similarity result from genomic transmission. Behaviors can be culturally transmitted across generations. Song learning in oscines is a good example. Populations of conspecific birds can have distinctively different versions of the same conspecific song—dialects. These dialects are not encoded in the genes but result from the combination of song learning and cultural drift due to different copying errors among populations.

Similarities in personality in humans, such as the extrovert–introvert continuum, can have a substantial genetic component as shown by studies of monozygotic twins. When this is the case, the evolution of the behavior in question can be analyzed using standard population genetic approaches. Whenever there are genetic contributions

to behavior, however, there is sure to also be an environmental component. These gene-by-environment interactions have made the old nurture–nature debate something of an anachronism. It is even more complex when the environmental effect is personified in cultural transmission from mother to offspring.

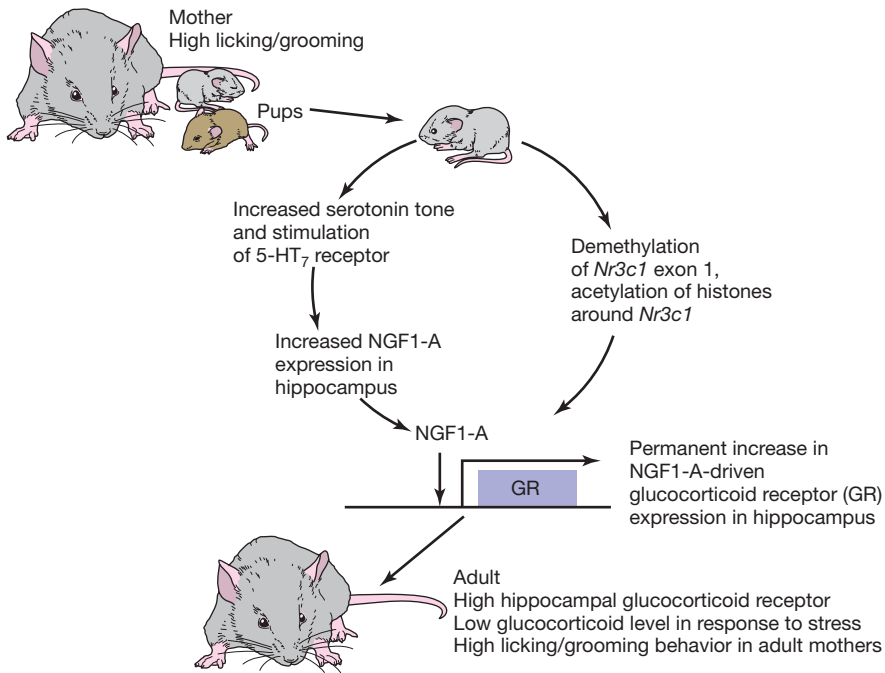
### *Cross-Generational Transmission of Stress by Maternal Behavior*

A remarkable study of nongenomic transmission of personality-like behavioral traits occurs in rats. There is natural variation in maternal behavior in rats including maternal licking-grooming and arched-back nursing (LG-ABN). The quantity of these maternal behaviors shown by the mother predicts the degree to which these same behaviors will be exhibited by her daughters when they later become mothers. Thus, these maternal behaviors are transmitted across generations. This transmission is not genomic, however. Cross-fostering experiments show that high-LG-ABN females reared daughters who later exhibit high LG-ABN, even though their biological mothers were low-LG-ABN females. Similarly, a pup whose biological mother was high LG-ABN but was raised by a low-LG-ABN mother later matured into a low-LG-ABN mother herself. Thus, mothering style is predicted by a pup's adopted, not its biological mother.

There is also a correlation between maternal behavior and how offspring behave. Offspring of high-LG-ABN mothers are less fearful as adults and show a more modest hypothalamic–pituitary–adrenal response in stressful situations. Cross-fostering experiments also show that the correlation between these traits is not a genetic one. Behavioral manipulation can bring about the same effect. Handling of pups increases maternal behavior toward the pups and decreases the pups' response to stress.

The influence of maternal behavior on their offspring in adulthood can also be elucidated at the genomic level. Stress reactivity is modulated by expression of genes in brain areas known to regulate the stress response. In comparison to offspring of low-LG-ABN mothers, the offspring of high-LG-ABN mothers exhibit increased serotonin expression in the hippocampus, which eventually results in the expression of a transcription factor nerve growth factor-inducible protein A (NGFI-A) (Fig. 1.5). NGFI-A then binds to a glucocorticoid receptor gene, which results in increased expression of the hormone receptor in offspring raised by high-LG-ABN mothers. Why is this not a genetic trait?

Not all inherited changes in phenotypes are due to changes in DNA sequences. "Epigenetics" refers to the class of mechanisms responsible for nongenomic inherited changes, and DNA methylation is one of these mechanisms. It plays an important role in gene expression as it can silence a gene without changing its DNA sequence. Demethylation leads to a marked expression of the gene's proteins and is a critical component of the epigenetic code. The differences in gene expression associated with stress reactivity between adult rats subjected to high versus low levels of maternal



**Figure 1.5.** An illustration of how maternal behavior in rats is transferred epigenetically across generations. A series of traits in adult rats can be traced back to the maternal behavior that they received as pups. High maternal behavior is characterized by high levels of licking and grooming. This natal experience increases the levels of serotonin in the hippocampus, which, in turn, leads to the increased expression of the transcription factor NGF1-A. In addition, there is demethylation of the first exon of the glucocorticoid receptor (GR) gene in the hippocampus, whereas the surrounding histones are acetylated. This creates a glucocorticoid receptor gene that is permanently more open to transcriptional activation by NGF1-A, which eventually results in more glucocorticoid receptors in the hippocampus of the adult rat. It is this difference in the number of receptors that accounts for the differences between endocrine and behavioral features of adult rats that received high versus low levels of maternal behavior when they were pups.

care (LG-ABN) appear to be linked to differences in DNA methylation. These differences were shown to emerge in the first week of life, and, like the behavioral traits, they persist into adulthood and can be reversed with cross-fostering. Exposure to a high-LG-ABN mother causes demethylation of the NGF1-A binding site; however, methylation is not reversed when pups are exposed to low-LG-ABN mothers. This provides the mechanism that allows a long-term effect of NGF1-A gene expression.

These results show that maternal behavior, fear response, gene expression, and DNA methylation can all be nongenomically transmitted across generations. If the correlations between these traits within a population were examined using standard breeding value analysis based on mother–daughter correlations, or these suites of

traits among species were compared using standard phylogenetic character analyses, these patterns of behavioral variation would mistakenly be characterized as having a strong genetic component, whereas in reality these patterns are evidence of cultural evolution through epigenetics and not genetic evolution.

### Function Informs Mechanisms

Just as knowledge about mechanisms can inform us about function, the function of behavior can often result in the discovery of mechanisms previously unknown. Two classic examples are echolocation in bats and magnetic orientation in pigeons.

#### *Bats Listening in the Dark*

Bats have long had a place in myth and lore because of their nocturnal wanderings. This same behavior has generated curiosity from naturalists who for centuries have asked how bats can fly at such low light levels. A series of very clever experiments by Lazzaro Spallanzani and his colleagues in the 18th century in which bats were deprived of various senses demonstrated quite clearly that bats used neither vision nor odor to navigate. Spallanzani first concluded that bats must have a sixth sense that we will never understand, but later experiments by Swiss naturalist Charles Jurine suggested that they use their hearing. The famous French anatomist Georges Cuvier, however, disagreed. With apparent hubris and without the constraints of data, he declared that the patterns of air currents the bat's wings generate during flapping would be disrupted by nearby objects. The touch sensors in the bat's wings, he suggested, could then detect these disturbances and use this information for navigation. According to his theory, bats did not reckon by sight or sound, but by touch. The acceptance of this theory seemed to be based only on Cuvier's sterling reputation as an anatomist, and some of his acolytes mocked Spallanzani's hearing hypothesis with disdain, asking, "If bats see with their ears, do they hear with their eyes?"

Final resolution of this conundrum had to wait until the middle of the 20th century. Donald Griffin and Robert Galambos, novice graduate students at Harvard University at the time, made use of then recently available techniques to once again ask the question that had preoccupied Spallanzani for so long. They showed that the bat's ear was sensitive to ultrasonics (frequencies above the upper human limit of hearing, 20 kHz), that only deaf and silenced bats were unable to navigate an obstacle course, and that successful avoidance was correlated with the bat's production of echolocation signals. There seems to be little question that it was the behavior of nocturnal flight that drove scientists to finally uncover the mechanism of echolocation, which almost seems like the sixth sense that Spallanzani once attributed to bats.

Recent research by John Zook has suggested that Cuvier might have been partially correct in his assertion that bats see with their wings. Zook showed that the bats' wings

are, in fact, endowed with touch sensors that contribute to navigation. Merkel cells are common mammalian touch receptors, and bat wings have Merkel-like cells with the addition of a tiny hair protruding from the center. Electrophysiological studies showed that these cells are responsive to air flowing over their surfaces. These cells can be desensitized pharmacologically. Under these conditions, bats were capable of straight-line flight but fumbled badly when confronted with an object they needed to avoid. The philosopher Thomas Nagel asked, “What is it like to be a bat,” pointing out that although we might be able to understand the mechanisms of echolocation, we could never experience it—we could never really know what it is like to be a bat. Our imaginations now are further challenged in trying to conceive what it would be like to navigate with our skin.

In the discovery of echolocation in bats, scientists were motivated by what the animals could do. In the discovery of magnetic orientation in pigeons, they were motivated by what animals could not do.

### *Pigeons Flying in the Fog*

Pigeons are well known for their abilities to home over long distances, which is why carrier pigeons have been used to carry messages for at least 3000 years since their skill was first tapped by the Egyptians and Persians. Understanding how they do this has been the subject of many scientific careers. It was known that pigeons use the sun as an orientation cue. But pigeons can also home successfully on cloudy days. One of the preeminent researchers in this field was William Keeton of Cornell University in Ithaca, New York. Ithaca is characterized by a wealth of overcast days, which allowed Keeton ample opportunity to study homing without the sun. In a typical experiment, pigeons were driven some distance from the loft and released, and their vanishing direction at the release site was noted, as was the time that they returned to the home loft.

Although many birds use the position of the sun as an orientation cue, Keeton’s pigeons usually returned to the home loft on cloudy as well as sunny days, suggesting that there must be another backup navigation system that could guide the birds home-ward when the sun was not visible. There was an exception, however. If the pigeons were transported and released by one particular research assistant, the birds tended to vanish. This person drove an old Volkswagen Beetle with the motor in the back. When the cage of birds was placed in the car’s back seat, the birds were adjacent to the motor. Keeton surmised that the motor’s generator might be disrupting the magnetic field in the vicinity, and he decided to determine if the pigeons were using the earth’s magnetic field in their orientation. He placed small bar magnets on the heads of some pigeons and non-magnetic bars on the heads of others. On sunny days the pigeons were able to return successfully but not on cloudy days. Thus Keeton concluded, and many subsequent studies have confirmed, that pigeons use magnetic cues as a backup system to their use of solar cues.

These studies of behavioral mechanisms led to a cascade of studies addressing how animals gain access to the geomagnetic field. Where is their compass and how does it work? A recent summary by Henrik Mouritsen and Thorsten Ritz points out that many birds have two sources for detecting magnetic fields. One is based on light-dependent processes in the eyes, where there are putative magnetosensory molecules, “cryptochromes.” The other relies on putative magnetosensory clusters of magnetite in the upper beaks of some birds. We will return to a discussion of these mechanisms in Chapter 5.

In studies of both bat echolocation and birds, we have stellar examples of how studies of a behavior’s function often inevitably lead to further questions about the behavior’s underlying mechanisms.

## CONCLUSIONS

Animal behavior is a phenomenon that transcends the typical categories that partition the biological sciences. To facilitate understanding between those working at different levels of analysis, Tinbergen codified the study of animal behavior with his four questions: mechanisms, acquisition, function, evolution. Tinbergen also indicated that a complete understanding of animal behavior would need to address each question. In some cases, it appears that a correct understanding of any one question depends on knowledge of the others. It is in that spirit that we offer our view of an integrative analysis of animal behavior.

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