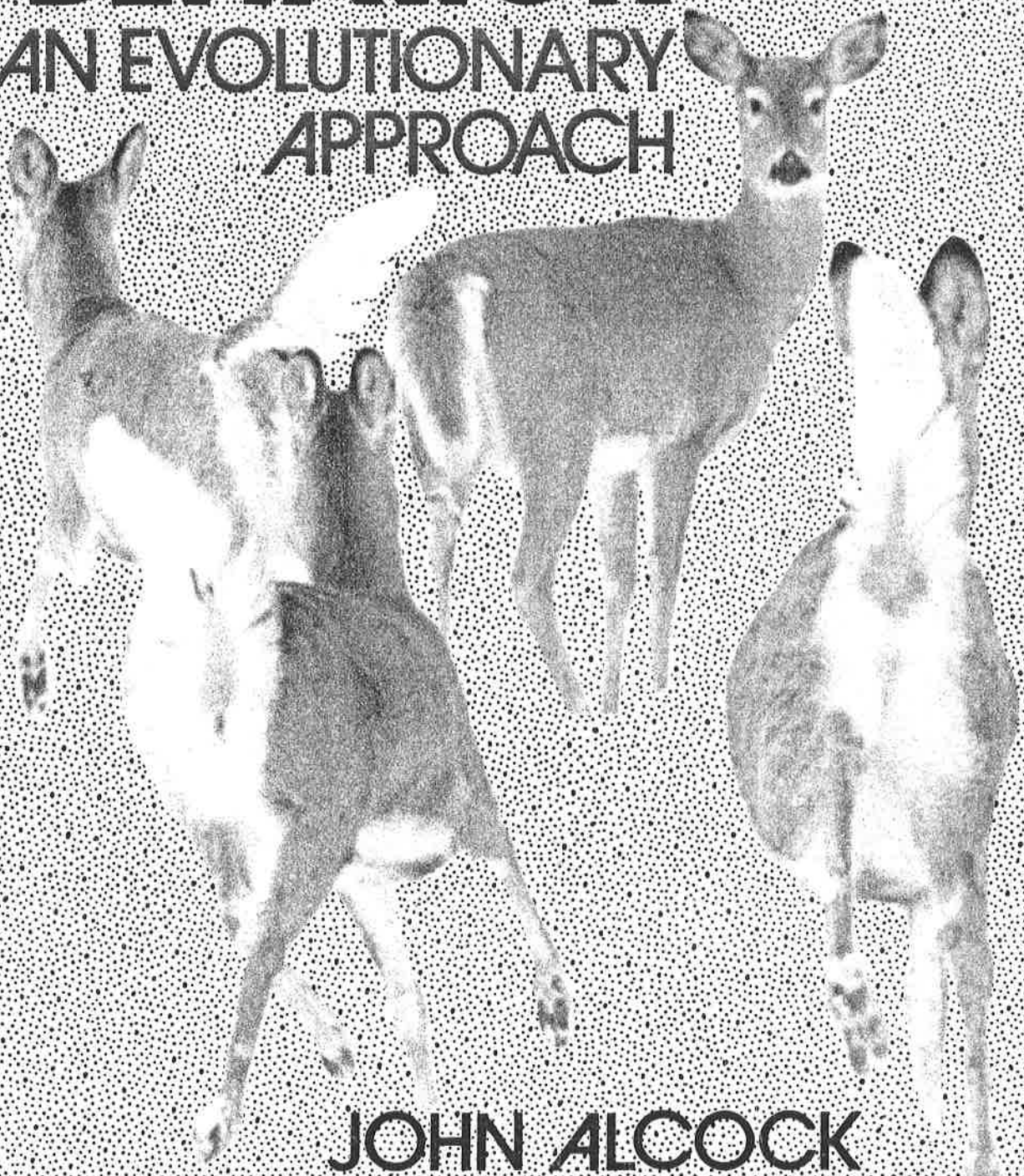
THIRD EDITION

ANIMAL BEHAVIOR

AN EVOLUTIONARY APPROACH



JOHN ALCOCK

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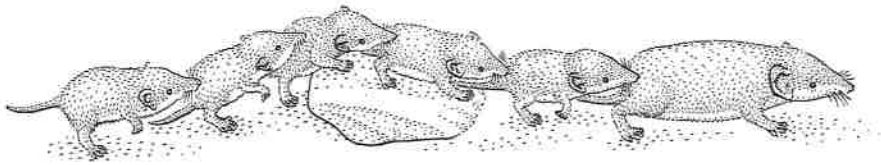

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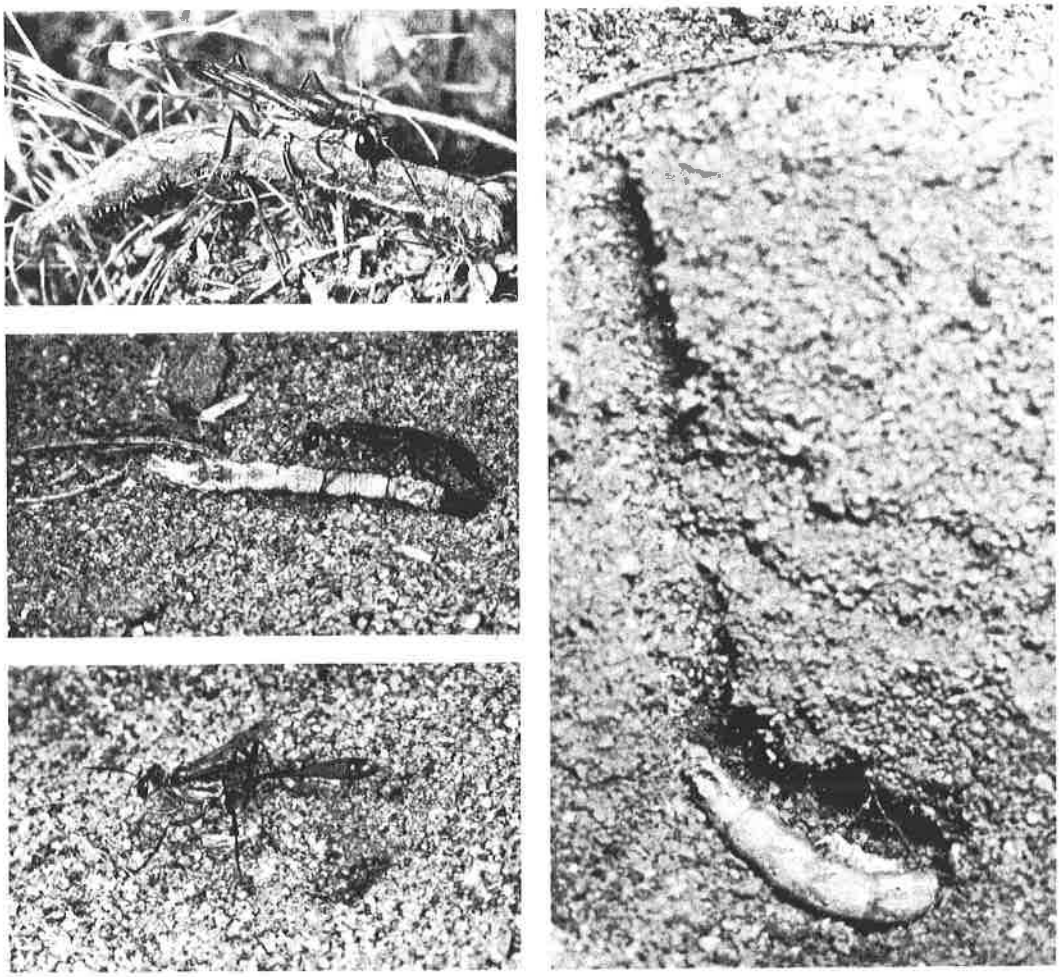
CHAPTER 1

An Evolutionary Approach to Animal Behavior

Curiosity About Behavior

Imagine that you are in southern Arizona wandering about a sandy area in May when you notice a long, thin, reddish wasp carrying a large green caterpillar beneath its body. Unbeknownst to you, the wasp is a female of the species *Ammophila novita*. As you peer at the wasp, she crawls onto a tuft of grass and deposits the caterpillar at the top (Figure 1). She then leaves the immobile grub and flies off low over the ground for some distance before alighting. After walking about for a while, the female begins to gnaw at the soil with her mandibles. She picks up a load of loosened material with her forelegs, presses the load beneath her "chin," and flies up a short distance before releasing the earth, scattering it over the ground. The wasp then returns to her digging site and repeats the process. Soon she has constructed a vertical shaft that can accommodate her body and more. After about 20–30 minutes of excavation, the wasp makes a final flight with a load of sand and then flies back to the spot where she had left the caterpillar. She grasps it with her jaws and drags the prey to the burrow. Depositing the larva near the entrance, she enters the shaft, turns around, grabs the head of her victim and pulls it down into the tunnel. After several minutes, she reemerges and begins to kick sand and pebbles into the burrow (Figure 1), not stopping until the shaft is completely filled. The wasp then flies away.

If you were suitably bewildered by this puzzling series of activities you would probably want to excavate the burrow to find out what had been done to the caterpillar. Having thoughtfully carried a garden trowel, an old spoon, and a wire probe on your walk, you could cautiously cut away the sand, using the probe to push out the new fill in the vertical shaft bit by bit. After following the tunnel down a few inches, you find that it turns to travel horizontally a short way; and very soon the caterpillar appears, resting on its side (Figure 1). On its flank you will find a small white translucent egg. Your work has revealed the answers to some of the questions you had while watching the animal at work. The burrow is an underground nest with a brood chamber that contains a prey placed there for the wasp's offspring. Additional observation and excavations would show that an *Ammophila* larva emerges from the egg and consumes the cater-



1 Digger wasp nesting behavior. A female wasp is storing a caterpillar, which she has paralyzed, on a tuft of grass (*top left*). After digging a nest, the wasp has retrieved her prey and is about to drag it into the burrow (*center left*). The wasp has laid an egg on the prey and is now kicking sand into the nest to fill the burrow (*bottom left*). The excavated nest contains the caterpillar coiled in the brood cell (*right*). Photographs by the author.

pillar, after which it metamorphoses into a pupa and finally becomes an adult wasp.

Despite your research, you would probably have many other questions about *Ammophila* behavior. How does the wasp manage to capture a caterpillar? How does it find its way back to its prey after having deposited it on a grassy mound or twig? Why does it scatter the dirt that it excavates from the burrow? Why does this species provision its nests with a single

large caterpillar whereas other *Ammophila* provide many small prey to their offspring? Further reflection (it would be best if this were done somewhere in the shade) would reveal that these questions could be placed into two basic groups.

In fact, all questions about behavior are either "how questions" about its PROXIMATE CAUSES or "why questions" about its ULTIMATE CAUSES [549]. How questions ask how an individual manages to carry out an activity; they ask how mechanisms *within* the animal operate to make behavioral responses possible. Why questions ask why the animal has evolved the proximate mechanisms that enable it to do certain things. It is useful and necessary to make a careful distinction between the proximate and ultimate causes of biological phenomena. Otherwise confusion and misunderstanding about possible explanations will result.

For example, imagine an argument between two people on why humans eat so much candy and drink so many soft drinks. One person could claim this happens because these foods taste sweet. Because the sensation of sweetness is rewarding, people learn to consume foods that provide this pleasant experience. The other person might reply that this was entirely wrong. People eat sugary foods because they provide a rich source of calories to fuel the human body's metabolic machinery.

A dispute of this sort is the sterile outcome of a failure to recognize different levels of explanation in biology. The first hypothesis is couched in proximate terms as it deals with the psychological mechanisms within an individual and how they might cause a person to behave in certain ways. The second (ultimate) hypothesis focuses on why humans may have evolved these internal reinforcement mechanisms in the first place. Both ideas could be correct because proximate and ultimate answers complement rather than compete with one another. This point can be amplified through an examination of the proximate and ultimate aspects of digger wasp behavior.

How Questions

How does an *Ammophila* wasp find and catch a caterpillar that is larger than itself? To answer this question, we would have to learn how the wasp's nervous system enables the insect to maneuver in the air and detect the visual or olfactory cues of its prey. There is a physiological foundation for the wasp's behavior, a set of proximate causes based on the operation of its neural networks, muscles, wings, legs, and sense organs. How does the wasp manage to remember where it left a paralyzed prey when it went off to build its nest many meters away? Perhaps, like some other digger wasps [705, 732], it can store information about the visual landmarks along its route, information that it uses to navigate back to a prey storage site.

But how did the wasp get the kind of nervous system, muscles, wings, and legs that enable it to capture its victim and learn about the landmark features of its environment? The *Ammophila* female did not spring from thin air through spontaneous generation. She had a father and a mother

and developed from a fertilized egg, which contained genetic instructions donated by each parent. These instructions regulated the way in which development occurred, channeling the proliferation and specialization of cells along pathways that produced a nervous system with special features. Thus, there are genetic-developmental causes, as well as physiological-psychological mechanisms, that account for the distinctive behavior of *Ammophila* wasps.

As is true for the vast majority of animal species, we know little about the proximate causes of the behavior of *Ammophila novita*. Just how the nervous system of a navigating wasp operates is totally mysterious, nor is anything known about the genetic-developmental basis of any wasp's nervous system.

Why Questions

But let's say that you were provided with or that you personally discovered everything there was to know about the proximate causes of *Ammophila novita* behavior. You should not be wholly satisfied. You should still want to know *why* the wasp possesses its special kind of genetic mechanisms, why its brain works the way it does, and why the wasp has some behavioral abilities but not others.

Why questions deal with the evolutionary or *ultimate* reasons why an animal does something. Why does the female wasp hunt for and capture moth larvae? As we have seen, this behavior has a *function*; it provides food for the wasp's offspring, which consume the paralyzed caterpillars and eventually develop into adults. At the appropriate time, they will gnaw their way up to the surface and start a new reproductive cycle, if all goes well.

Each aspect of the wasp's behavior can be examined to determine why behaving that way may help the animal cope with its environment. For example, why does the wasp store the paralyzed caterpillar in a shaded, elevated cache site? Perhaps this prevents the dessication of the prey and hides the larva from various thieves and parasites (such as ants or other hunting wasps), which might more easily locate the caterpillar if it were lying on the ground near the conspicuously digging female. Why does she go to the trouble of flying up with soil from her excavation and scattering the sand widely? Perhaps this prevents the buildup of a mound of earth by the nest entrance and so removes a cue that nest robbers might use to find the burrow and its contents [223].

But why does a female of *A. novita* adopt "functional" responses to its environment? Because of the history of the species to which it belongs. In ancestral populations there were individuals that had slightly different genes and therefore slightly different developmental instructions, physiological systems, and behavioral abilities. Some individuals happened to have genes that helped them develop the kinds of nervous systems and muscles that were the foundation for effective responses to environmental problems. These wasps acquired prey more efficiently, escaped their ene-