

Principles of Early Ethology

Perhaps the single most famous paper in the history of ethology is that of Lorenz and Tinbergen on the egg-rolling response of the greylag goose. It combines for the first time the concepts of releasers, "motor programs," and drives, which together allow us to make sense of so much of animal behavior. Egg-rolling behavior is striking: when an incubating goose notices an egg near the nest, its attention is suddenly riveted. It fixates on the egg, slowly rises, extends its neck over the egg, and with the bottom of its bill painstakingly rolls the egg back up into the nest (Fig. 3-1). With the egg safely back in the nest, the goose nestles down to incubate.

At first sight this looks like a thoughtful and intelligent piece of behavior on the part of the bird: the goose has perceived the problem and solved it. Lorenz and Tinbergen, however, were struck by the stereotyped nature of the whole sequence—the goose performed as if it were a machine. They wondered if the rolling might be some sort of program which, once triggered, would inevitably run to completion. To test this notion, they tried removing the egg once the goose had begun its neck extension. Perversely, the animal went through the rest of the behavior, gingerly rolling in and settling down on the nonexistent egg.



Fig. 3-1 The egg-rolling response of the greylag goose. The behavior begins when the brooding goose notices an egg outside the nest (A) and fixates on it. The goose rises, extending its neck to touch the egg (B). The goose places its bill carefully over the egg (C) and gently rolls it back into the nest (D).

RELEASERS AND MOTOR PROGRAMS

Lorenz and Tinbergen termed the goose's remarkable behavior a "fixed-action pattern" (FAP). The distinguishing characteristics of the behavior are the innate and stereotyped coordination and patterning of several muscle movements which, when released, proceed to completion without requiring further sensory input. In terms of its almost total independence of feedback, the fixed-action pattern represents an extreme class of prewired behavioral performances which have come to be known as "motor programs."

Tinbergen went on to discover a phenomenon more remarkable still: an incubating goose can be stimulated to perform egg rolling by a wide variety of only marginally egg-like objects—beer cans and baseballs, for example. From further experiments it became clear that the egg-rolling behavior could be triggered by virtually any large, nearby convex object with smooth rounded edges—objects some of which, once in the nest, clearly felt wrong to the goose, and which upon investigation were disdainfully discarded as obviously not goose eggs. Lorenz and Tinbergen realized that geese must possess an innate and highly schematic filter which, when stimulated by anything satisfying its crude criteria for "eggness," releases the fixed-action pattern. They called the filter-trigger complex an "innate releasing mechanism" (IRM) while the features of the stimulus essential to triggering it were termed "releasers" or, because the geese responded only to one aspect of the stimulus object, "sign stimuli." In nature, of course, the simple but diagnostic criteria

of the IRM are sufficient to exclude almost everything the goose is likely to encounter which is not an egg.

The egg rolling then is a behavioral unit. It has a specific trigger which is satisfied by an egg (among other things), and a specific response, curiously independent of feedback, which results in the recovery of the egg. As we shall see in Chapter 12, this entire unit is turned on and off by another class of circuitry known popularly as "drive" or "motivation," which ensures that eggs are rolled only from the onset of incubation until hatching is due to begin. The recognition of foreign objects in the nest which results in the discarding of a beer can which the goose has just gone to great pains to acquire is a separate program or behavioral unit with its own special cues and motor responses.

In fact, there is yet a third program for dealing with eggs, this one aimed specifically at ridding the nest of broken eggs and getting the shells several meters away. After showing that broken-egg removal depends on sign stimuli for brokenness (sharply defined or jagged edges and concavity; see Fig. 3-2), Tinbergen began to wonder why the black-headed gulls he was studying would *want* to remove broken eggs in the first place. Observation indicated to him that the cause was unlikely to be danger of injury or disease, since the cliff-dwelling kittiwake gull should face the same problems and yet is indifferent to its own empty eggshells. Tinbergen then guessed that predation

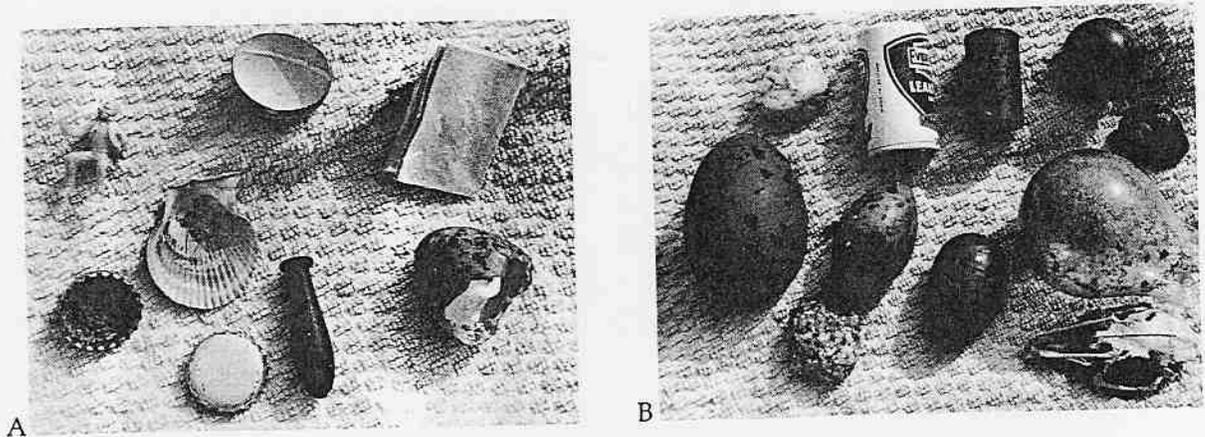


Fig. 3-2 A. Objects shown by Tinbergen to trigger the eggshell-removal program generally have sharp edges and flat or concave contours. B. Objects which are convex and lack sharp edges (as long as they are small enough to be comfortable) are tolerated in the nest and dutifully incubated. The dropper and skull are intriguing anomalies.

might represent a strong selective pressure for ground-nesting birds, and that the bright-white interiors of the eggs, when exposed, destroyed the camouflaging effect of the speckled, earth-toned exteriors. Hence, a broken egg would be likely to attract the attention of sharp-eyed predators, and lead them to a nest of eggs and chicks.

Tinbergen tested this hypothesis by setting out an array of both normal gull eggs and gull eggs painted white. Crows and even other species of gulls began to prey on the eggs almost immediately, even though they were set out well away from the nesting area. The predators took more than 60 percent of the white eggs, but found fewer than 20 percent of the normal ones. That evolution does a superb job of camouflaging eggs and wiring predators to spot them was indicated by the ability of predators to find the hand-colored mimics of gull eggs that Tinbergen set out in another experiment almost as well as the white ones. Trying the same experiment with only real, unpainted eggs, with and without broken eggshells 5 cm away, confirmed Tinbergen's guess (Table 3-1). Two-thirds of the intact eggs which were near broken ones were taken, while predators found only one-fifth of the other eggs. Of course in a real colony where there are adults to defend against predation, losses would be lower, but a three-to-one improvement in the rate of loss to predation is far more than is needed to drive evolution and lead to eggshell removal. Even the distance to which broken eggs are removed is important: the farther away, up to 2 m, the better. Hence, the removal behavior is almost certainly a product of predation pressures.

TABLE 3-1 *Survival Value
of Eggshell Removal*

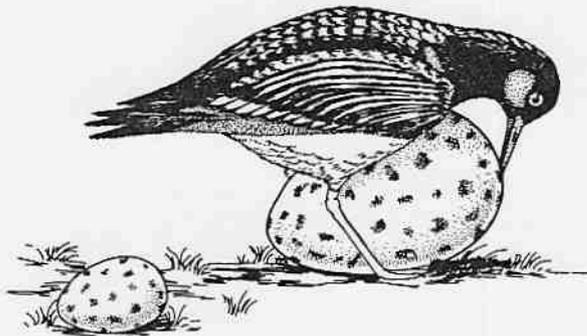
<i>Distance from egg to eggshell (cm)</i>	<i>% eggs taken by predators</i>
5	65
15	42
100	32
200	21
no eggshell	22

Source: N. Tinbergen et al., "Egg Shell Removal by the Black-headed Gull," *Behaviour* 19 (1963): 74-117.

SUPERNORMAL STIMULI

Tinbergen's insistence that evolutionary guesses must be put to the test brought to ethology that essential rigor which separates modern science from the armchair speculations of its Aristotelian and medieval precursors. Moreover, his informed and restrained experimentation uncovered phenomena of sweeping significance which Lorenz's purely observational approach, though powerful in its own way, could never hope to have touched. For example, in the process of asking just how unegg-like an object of human manufacture could be and still trigger the egg-rolling releasing mechanism, Tinbergen found that incubating geese would even attempt to roll volleyballs into their nests. This observation led immediately to one of Tinbergen's classic choice experiments. Allowed to decide between a goose egg and a volleyball, geese inveterately chose to recover the volleyball. In some way volleyballs seemed to be better stimuli for the goose's IRM than real eggs. In other words, there are "supernormal stimuli" (Fig. 3-3).

Fig. 3-3 A supernormal stimulus. Given a choice between its own egg (*left*) and a giant egg, a brooding oyster catcher chooses the larger of the two.



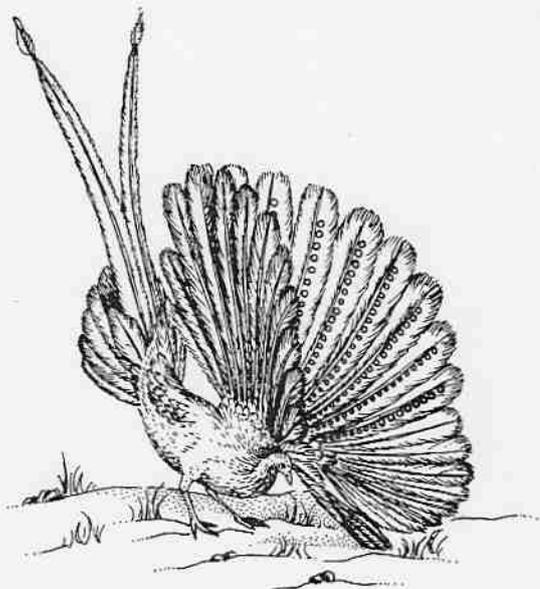
Supernormal stimuli, although inherently unnatural, provide a crucial clue to the process of natural selection. It is clear that the natural releaser, the goose's egg in this case, is only one of many stimuli which could satisfy the animal's simple criterion and release egg rolling. Since variation exists in nature, and since changes in some stimulus features like the egg's size can result in an increased ability to trigger the response, selection should favor the genes leading to more potent releasers. In other words, goose eggs should eventually become the size of volleyballs.

Of course, evolution must balance conflicting demands. The goose's egg, for example, must represent a balance between the goose's physiology—how large an egg it *could* lay and incubate—the pressure of sharp-eyed predators, the optimum number of offspring, and so on. The most dramatic examples of this balance are found in sexual selection. Although there are rarely two eggs outside the nest for an incubating goose to choose between, animals quite often have several members of the opposite sex to compare. Species recognition usually involves releasers, and the role of the releaser can be quite complex. Animals frequently must compete for the opportunity to pass on their genes by mating. It is a fact of life that an animal which does poorly in sexual competition leaves no offspring, and so its genes are not perpetuated. Animals whose genes code for features which most stimulate the opposite sex, on the other hand, will leave disproportionately more offspring. As a result, sexual sign stimuli should become increasingly supernormal, though again under the restrictions imposed by the natural world.

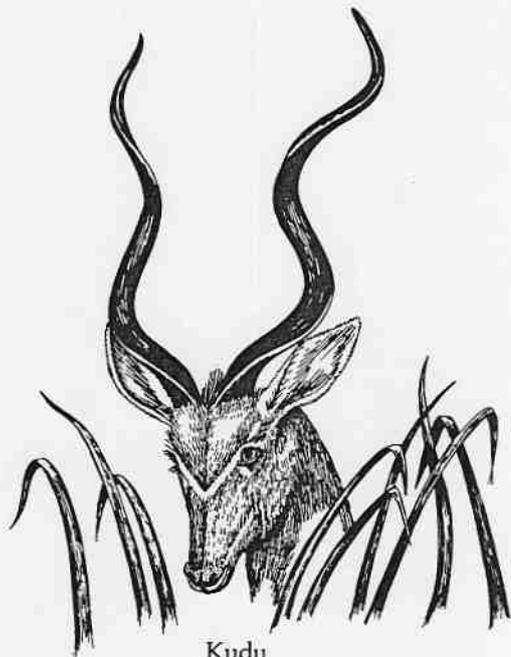
Because mating is so crucial, sexual selection can have bizarre results. Darwin, in his *Descent of Man*, gathered together a long list of examples of species in which the males possess some dramatic sexual dimorphism, a structure whose existence seems exclusively the product of sexual competition among males, and whose metabolic cost, attractiveness to predators, and general unwieldiness must be a substantial burden (Fig. 3-4). Fiddler crabs are a compelling example of this system. Male fiddler crabs spend most of their time "beckoning" to females with their one oversized claw (Fig. 3-5). The claw-waving display is a simple, species-specific sexual releaser. The pattern of waving is a code which is unique to, and therefore an indicator of, the species; and as such is used by female fiddler crabs to sort out which males are which. Once male fiddler crabs had the temporal pattern of the display pretty well perfected, the conspicuousness of the waving must have become very important in attracting the attention of females in the presence of other waving males. Natural selection—which is to say, the female fiddler crab—has favored ever larger and more conspicuous claws. The enormous claws of modern fiddler crab males are useless for feeding or for digging burrows, and are known by predators to contain a very tasty meal; furthermore, they pose a great impediment to movement and escape. Clearly the morphological arms race has gotten out of hand, but the IRMs of the females

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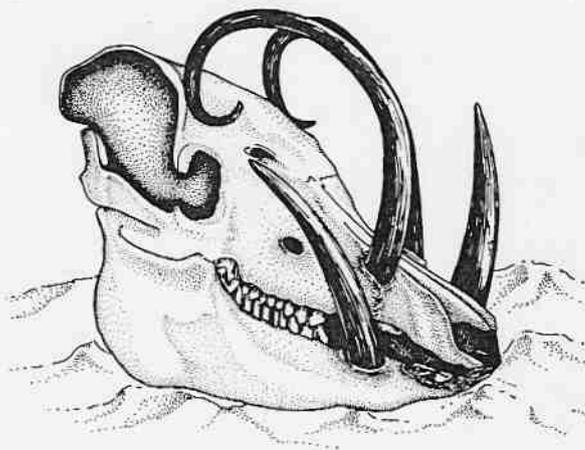
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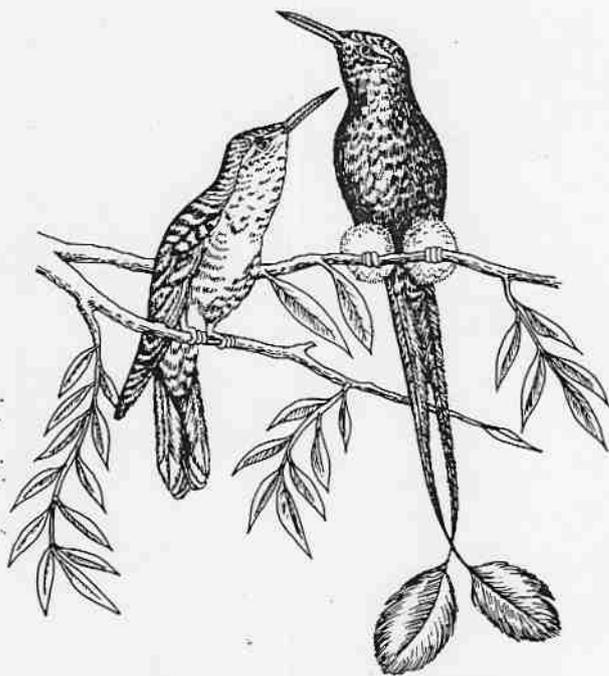
side view of male Argus pheasant,
while displaying before the female



Kudu



skull of Babirusa pig



Tropical hummingbird, male and female

Fig. 3-4 Examples of sexual dimorphisms used by Darwin to illustrate sexual selection.

make disarmament out of the question. Evolution seems here to have operated like a ratchet with its one-way movement, and the sexual advantage of even larger claws is almost certainly still there, awaiting perhaps only a reduction in predator pressure to remove the present constraints. Only extinction or the establishment of some selective advantage for females without this releaser circuitry could bring an end to the supernormal claw of male fiddler crabs.

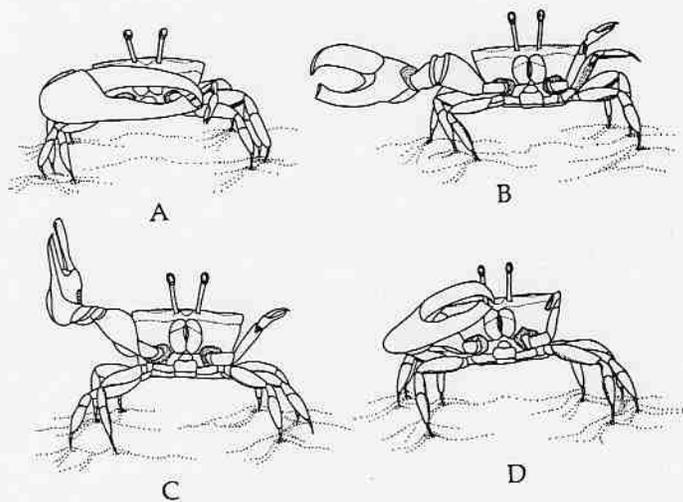


Fig. 3-5 The claw-waving display of a male of one species of fiddler crab.

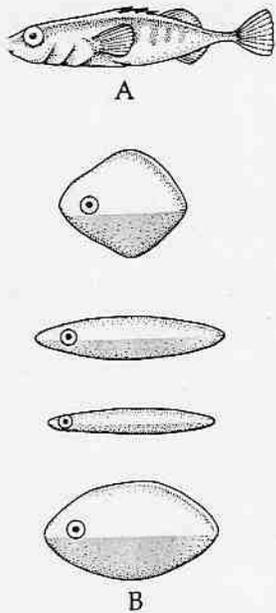


Fig. 3-6 Stickleback models. An accurate model of a stickleback without any real coloration (A) fails to elicit attacks from territorial males, while any of a variety of unfishlike models with red undersides (B) effectively release attack behavior.

Perhaps the most famous example of an IRM other than the egg rolling of geese is the territorial and mating behavior of the three-spined stickleback mentioned in Chapter 2. The males of this versatile species of fish divide their world into territories which they guard jealously. During this territorial phase the underside of each male becomes bright red, and the approach of a neighboring male in territorial garb releases an aggressive display or even an attack at the invisible boundary between the two males' territories. From the first Tinbergen suspected that the red belly was the releaser for this behavior. When a passing red postal truck elicited attacks from the males, there was little doubt that the sign stimulus was the color, and not the body shape or odor of other males. In typically Tinbergenian fashion, a series of increasingly unfishlike models were presented to territorial males (Fig. 3-6), and the red stripe emerged as the one necessary criterion. In fact, the red stripe conveys a double

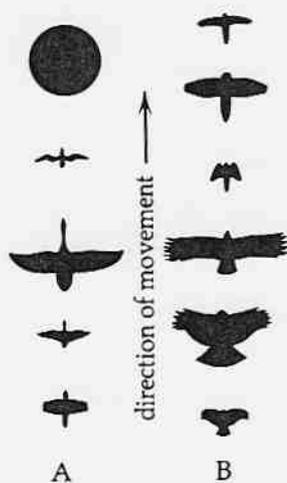
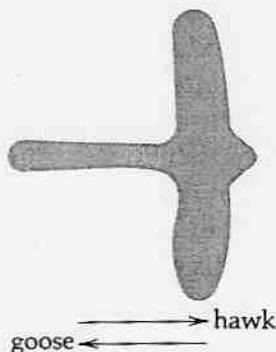
DEVELOPMENT OF
ETHOLOGY

Fig. 3-7 Some bird silhouettes evoke escape responses (B) in naïve chicks, while others do not (A). "Hawkness" to birds seems to be mostly a matter of relative neck and tail length.



message: when the male is swimming in its normal, horizontal orientation, it indicates a fish in full aggressive mood; but when the loser in an encounter adopts a vertical posture, it signals submission and an intention to retreat. That evolution can get away with such a simple sign stimulus as a red bar can be taken as pretty good evidence that there is a dearth of red objects in the natural world of the stickleback.

Almost the same story may be told of European robins: the red feathers on the breasts of territorial males are the sign stimulus for aggressive interactions. Just as with the sticklebacks, a red object of almost any shape is sufficient to release aggressive behavior—a tuft of red feathers on a wire, for example. And again, as with sticklebacks, we must suppose that the trees of spring contain little else that is red.

A famous releaser reported by Spalding, rediscovered by Lorenz, and systematically investigated by Tinbergen, involves the escape response of naïve chicks when they are shown the silhouette of a flying hawk. After numerous model experiments, it now seems clear that a short head and a long or broad tail are the features necessary to trigger the escape behavior (Fig. 3-7). The most elegant test utilized the silhouette of a flying goose. Presented normally the model had no effect, but when flown in reverse so that the broad, short tail became the head, and the long neck and head became the tail, the escape response was triggered (Fig. 3-8). The adaptive value of this behavioral unit is clear: it is crucial that young birds "know" to hide from hawks from the first, and the simple but diagnostic requirements of the IRM should be satisfactory for even the most myopic chick.

The same adaptive value for an IRM holds true for snake-eating birds: in many species, the sight of the deadly coral snake releases alarm behavior. Like predatory birds, the various species of coral snakes share only a few features, and it is from these that natural selection has fashioned the IRM. Birds which had never before seen a snake were presented rods painted with various patterns. Stripes running lengthwise, regardless of

Fig. 3-8 The same bird silhouette has very different meanings to naïve chicks depending on its direction of travel. When "flown" to the right with the short neck leading it releases escape behavior, but when flown to the left with the long neck leading it is ignored.

color, never upset the birds. Rods with alternating blue and green rings were likewise ignored. But a clumsy, hand-held wooden rod with just a pair of red and blue rings at one end—quite obviously a dowel and not a snake—inevitably elicited alarm from the hatchlings. Clearly a bird which does not recognize and avoid coral snakes from the outset may not survive the experience of learning.

INTERLOCKING RELEASERS

Very often, particularly in courtship, IRMs and FAPs are arranged in serial fashion. For example, in butterfly courtship a behavior on the part of the female releases a behavior in the male, which then elicits the next behavior in the female, and so on until mating is achieved. The first releaser is the flight pattern of the female. Tinbergen showed through the usual model experiments that three factors trigger pursuit by males: the contrast between the dark female and her lighter background, the "bobbling" flight pattern, and the rapid alteration of her apparent size which is a consequence of her wing flapping. Tinbergen demonstrated that neither the details of the elaborate wing patterns nor even the butterfly shape are important. On the other hand, higher rates of wing flapping—presumably impossible for physiological or aerodynamic reasons—are more attractive to males than the natural rate.

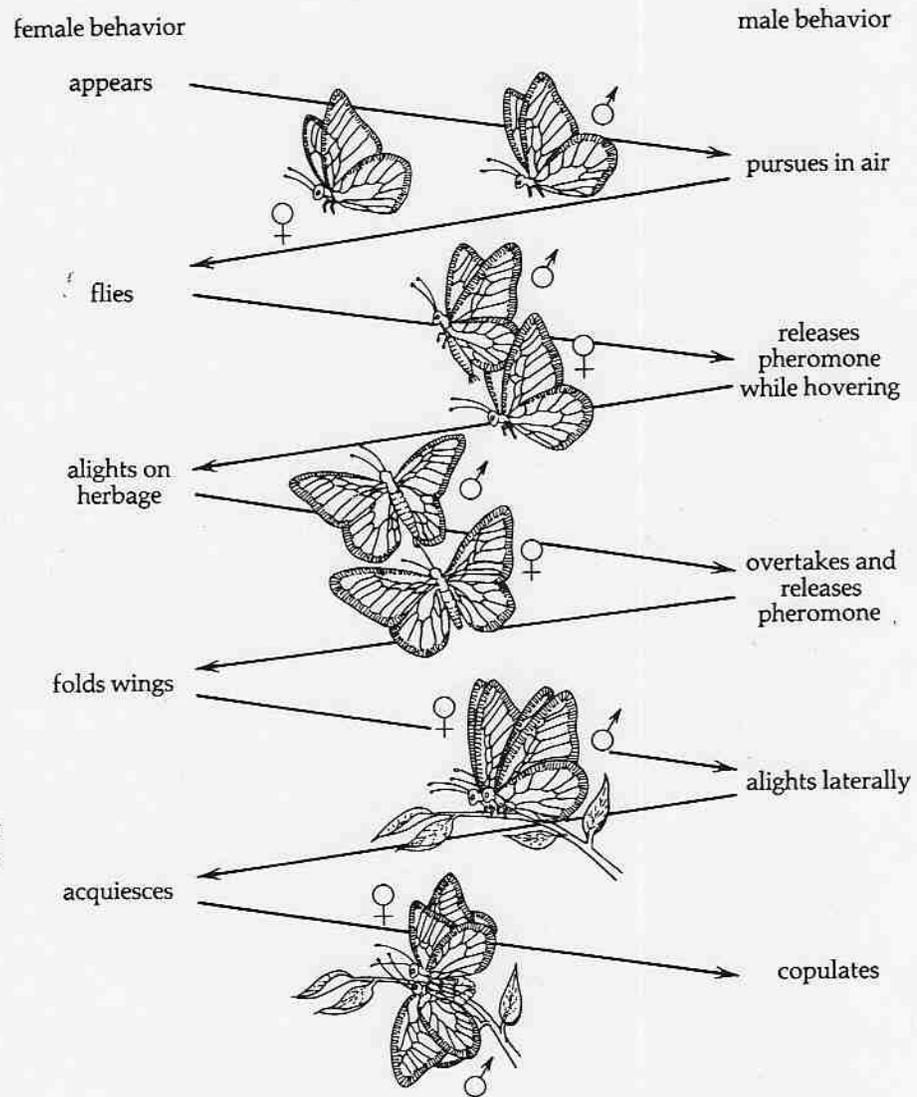
Males of the queen butterfly respond to these sign stimuli through pursuit, followed by an elaborate behavior known as "hair penciling." The males possess fine brush-like structures at the tips of their abdomens which they extrude and wave in front of the flying females. These hair pencils release a special odor which the females detect with their antennae.

Females respond to the male odor by alighting with wings spread. The male responds by hovering in front of the female, sweeping his hair pencils across her antennae until she responds by closing her wings. This is the signal which causes the male to alight next to her, where he begins drumming her antennae with his own until copulation begins.

The elaborate series of releasers in butterfly courtship serves to ensure that mating occurs only between members of the opposite sex of the same species, both of whom are physiologi-

cally ready to mate (Fig. 3-9). The flight-pattern releaser informs the male of neither the sex, the species, nor the physiological readiness to mate of his intended partner. The hair penciling of the male, on the other hand, informs the female of all three. If the courted butterfly lands and folds its wings, the male can afford to proceed in the certainty that the species, sex, and readiness are all appropriate.

Fig. 3-9 Courtship sequence of queen butterflies. The female's flight pattern releases pursuit and hair penciling by the male. The hair-pencil odor releases settling by the female. This causes the male to hover and sweep his hair pencils across her antennae. The female responds by folding her wings, the signal which causes the male to alight and begin mating. This interlocking sequence of releasers assures that only queen butterflies in reproductive condition and of opposite sex actually mate.



THE "DO-LOOP"

One of the most frustrating things about working with computers is their consummate stupidity. The slightest error on our part, even so much as a misplaced comma or extraneous space which leaves the meaning of the instruction clear to us, confounds these simple-minded computational giants completely. This inflexibility is one crucial feature which distinguishes man from even the most complex of the machines he creates—at least from the ones that work. The computer lacks even any rudimentary insight or imagination, and so must be told not only what the problem is that it is going to be called upon to solve, but exactly how to go about solving it—and even that in agonizing mechanical detail.

Suppose, for example, we ask our computer to calculate something so simple as the number of doublings necessary to generate a million offspring. That problem requires fewer than a dozen English words to state, but for the computer the problem must be put more explicitly:

Step #	Instruction
1	Let $A = 1$
2	Let $N = 0$
3	Do steps 4 through 6 until A is greater than or equal to 1,000,000; then go to step 7
4	Let $A = 2 \times A$
5	Let $N = N + 1$
6	Return to step 3
7	Print N , the number of doublings
8	Stop

Obviously, this program requires that the grammar, the functions (addition and multiplication), and the complex conditional cycling instruction of step 3 be "hardwired" or already stored in the machine by some previous programmer. Step 3 is known to users of FORTRAN (one of the most widespread of the computer "languages") as a "do-loop": the machine cycles mindlessly through the steps until the contingency ($A \geq 10^6$) is met. Typical programming errors might include requiring A to *equal* 10^6 , which, as the calculation leaps from 524,288 to 1,048,576 in one step, never happens; or to mistype " A " as " S " which, as far as the machine knows, is nonexistent, and so cannot reach 10^6 . The result in either case is that the computer, slavishly following its instructions, gets hung up in an endless loop of perfectly exact but pointless calculations. Such errors of programming, when they occur, must be painstakingly culled out by the wary programmer through trial and error in a process known as "debugging."

We might say that evolution, the wiliest of programmers, has been

elaborating and debugging its programs for millions of years. One of its most intriguing debugging solutions for keeping its creatures from getting hung up in do-loops is the phenomenon of habituation or, more familiarly, boredom (see Chapter 5). Nevertheless, some behavioral programs, never having gone awry under the orderly auspices of nature, have never needed to have this safeguard built in. These cases, more plainly than any others, illustrate the machine-like nature of animal behavior.

Take, for example, the species of wasp which builds those familiar tunnel-like mud chambers on the sides of houses. The wasp carefully seals the bottom of each chamber and drops prey she has paralyzed in from the top. Then she lays an egg, closes the top, and begins another nest. This seems reasonably clever at first sight. However, if we cut off the bottom of the nest so that it is open at both ends, the wasp becomes caught in a do-loop. She captures prey and drops them in from the top, but they fall out the bottom. The wasp may even explore the nest and emerge from the open bottom without repairing it. Instead, she continues to try to stock the chamber. It seems that the only contingency which nature has programmed in to instruct her to "exit the loop" is a full chamber.

Apparently wasps in general are remarkably resistant to boredom. One species of digger wasp which, as we know, builds its nests in the ground, preys on crickets. This wasp typically returns from its hunt to the burrow, sets the cricket down about an inch from the entrance, goes briefly into the nest (apparently to check on things), and then returns to the surface and takes the paralyzed cricket back down. Again this seems sensible enough. If, however, we move the cricket away from its original spot even a bit, the wasp must search a moment for it. Then she moves the cricket back to the exact spot on which she had placed it before, and reexamines the nest. As you can guess by now, this sets up a loop. As long as we keep moving the cricket, the wasp cannot go on to the next step, and will replace the cricket and reinspect the nest at least as many times as human patience can endure. J. H. Fabre, the eminent French naturalist, tried forty times before throwing up his hands in exasperation.

These examples illustrate not only the machine-like nature of some behavior, but also how we can go about understanding the programming instructions the genes have generated. The essential element in these cases was the lack either of some contingency plan—boredom, for example—to terminate the loop, or of one of the "backup routines" so obvious in animal navigation (see Chapters 13 and 14) to which the whole problem may be referred when the first-order routine fails to generate an answer. In examining other cases we should be looking for simple manipulations for which evolution could not have prepared the animal, and which ought to affect the presumptive program in revealing ways. In Chapter 13, for example, we will see how merely closing a beehive for two hours at midday causes the bees' superficially complex sun-movement

compensation behavior to fall apart or, in Chapter 14, how attaching a magnet to a pigeon on a cloudy day destroys its mysterious ability to get home. Nature never performs such irrational experiments, so the animals' programming is confounded in revealing ways.

WHY RELEASERS?

Releasers, then, and the accompanying physiological arrangements which produce the IRM and the associated motor program, represent the single most general strategy in animal behavior from protozoa to primates. The concept of releasers dramatically illustrates the innate, programmed nature of much of behavior. At the same time, a releasing mechanism is not an explanation but rather another ultimately divisible component of behavior, and one which has proved especially troublesome. It was not easy for early ethologists to account for the selective advantage of releasers. They proposed that IRMs might have evolved before animals developed the intellectual capacity to "reason" for themselves, and have been preserved by that most pragmatic and conservative force, evolution. It is undoubtedly the case that IRMs enable animals to react more quickly in a variety of situations and moods, without interference from the time-consuming and error-prone process of thinking. Perhaps they serve to focus an animal's attention, allowing it to ignore irrelevant and confusing stimuli in situations that are particularly important to its genes. They may enable animals to perform perfectly some crucial piece of behavior when there is no room for learning because even a small mistake may be fatal. Or just as often IRMs might show an otherwise distracted animal exactly what information it needs to acquire. It might be, too, that IRMs simply began as a way to compensate for relatively crude sense organs—eyes and the like—and have proved useful despite the enormous technical refinements evolution has accomplished along the way.

Against all these alleged advantages stand two very obvious objections: IRMs occasionally trigger responses to cues which are obviously inappropriate, responses which are maladaptive and which, with only a slight increase in IRM specificity, might have been avoided; and IRMs in sexual selection can force species such as fiddler crabs (and perhaps the sabre-toothed

tiger and the giant elk before it) down evolutionary paths which are potentially debilitating or even fatal. As we shall see in Chapter 4, one of the most impressive consequences of the discoveries which led to modern ethology is a convincing, mechanistic explanation of the evolution of IRMs.

IMPRINTING AND PROGRAMMED LEARNING

In addition to releasers, motor programs, and drives, the early ethologists discovered one more dramatic and controversial example of behavioral programming: imprinting. Originally thought of as a remarkable curiosity, imprinting has become the classic example of programmed learning, a widespread phenomenon whose sweeping importance makes it one of the cornerstones of modern ethology. Lorenz, following up an earlier observation by Oskar Heinroth, found that orphaned baby geese and ducks would begin to follow him as they would a parent of their own species as long as he "adopted" them before they were two days old. Later, they would ignore members of their own species, evidently having accepted Lorenz as their model of the perfect parent (see Fig. 2-6). Still later, the geese would court humans instead of other geese. Young geese isolated until two days of age, however, failed to imprint on anything. Lorenz referred to this age of susceptibility as a "critical period" (known more commonly now as the "sensitive period"). He concluded that the birds would imprint on anything, that imprinting etched indelibly a general species configuration in the birds as well as enabling them to identify their particular parents, and that the process was irreversible.

But as with releasers, motor programs, and drives, the early ethologists had two sorts of problems with imprinting. The first, far more severe with imprinting than with the other three, was that it was hard to repeat Lorenz's observations under controlled conditions. Chicks simply did not imprint well for other people, partly because these other scientists used the wrong techniques (Lorenz had failed to report many of the essential details, the importance of which even he was mostly unaware) and partly because certain of Lorenz's untested interpretations were wrong. The other problem is more familiar: imprinting, like releasing mechanisms, seems curiously unselective and maladaptive. Mistakes seem inevitable, mistakes fatal for the chick

which must identify its parents correctly to receive their protection and care, and which must later select an individual of the proper species with whom to mate, on the basis of a "follow-whatever-moves" program. Where is the decisive selective advantage of this remarkable behavior?

As with IRMs, one of the triumphs of modern ethology has been the unraveling of this conundrum. As we shall see, the mechanistic and evolutionary insights which have resulted help explain nearly the whole realm of adaptively flexible behavior in animals as simple as bees or as complex as birds, primates, and perhaps even ourselves.

SUMMARY

Animals come neurally wired to recognize important stimuli in their environments on the basis of one or two simple but diagnostic features. These "sign" stimuli are then used to trigger appropriate behavioral responses. The most obvious of such behavioral reactions are motor programs—self-contained neural circuits which in the most dramatic cases produce a coordinated muscle performance (a fixed-action pattern) wholly independent of feedback. Two other much more subtle but equally critical reactions to releasers are learning and changes in drive. Drive or motivation controls an animal's responsiveness to releasers and other stimuli, while programmed learning as exemplified by imprinting directs an animal to acquire particular information at an appropriate time and from a correct source. Together, these four classic phenomena form the basis of modern ethology.

STUDY QUESTION

Look back at the hunting sequence of Tinbergen's digger wasps (Chapter 2) and interpret it in terms of releasers and motor programs. How does it compare with butterfly mating? Why should the wasp, having caught an insect to sting, care whether it is actually a honey bee or not?

FURTHER READING

Lorenz, Konrad, and Tinbergen, Niko. "Taxis and Instinct in the Egg-Rolling Response of the Greylag Goose." In vol. 1 Lorenz's *Studies in Animal and Human Behavior* (Cambridge, Mass.; Harvard University Press, 1970), pp. 328-42.

Tinbergen, Niko. "The Curious Behavior of Sticklebacks." *Scientific American* 187, no. 6 (1952): 22-26.