Konrad Lorenz 1958

The Evolution of Behavior

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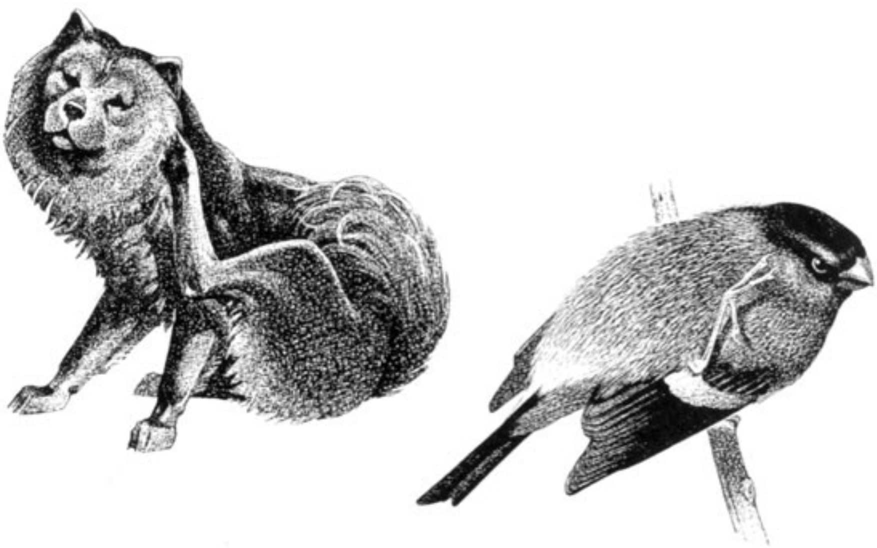
The Evolution of Behavior

Beneath the varying behavior which animals learn lie unvarying motor patterns which they inherit. These behavior traits are as much a characteristic of a species as bodily structure and form

A whale's flipper, a bat's wing and a man's arm are as different from one another in outward appearance as they are in the functions they serve. But the bones of these structures reveal an essential similarity of design. The zoologist concludes that whale, bat and man evolved from a common ancestor. Even if there were no other evidence, the comparison of the skeletons of these creatures would suffice to establish that conclusion. The similarity of skeletons shows that a basic structure may persist over geologic periods in spite of a wide divergence of function.

Following the example of zoologists, who have long exploited the comparative method, students of animal behavior have now begun to ask a penetrating question. We all know how greatly the behavior of animals can vary, especially under the influence of the learning process. Psychologists have mostly observed and experimented with the behavior of individual animals; few have considered the behavior of species. But is it not possible that beneath all the variations of individual behavior there lies an inner structure of inherited behavior which characterizes all the members of a given species, genus or larger taxonomic group — just as the skeleton of a primordial ancestor characterizes the form and structure of all mammals today?

Yes, it is possible! Let me give an example which, while seemingly trivial, has a bearing on this question. Anyone who has watched a dog scratch its jaw or a bird preen its head feathers can attest to the fact that they do so in the same wav. The dog props itself on the tripod formed by its haunches and two forelegs and reaches a hindleg forward in front of its shoulder. Now the odd fact is that most birds (as well as virtually



SCRATCHING BEHAVIOR of a dog and a European bullfinch is part of their genetic heritage and is not changed by training. The widespread habit of scratching with a hindlimb crossed over a fore-limb is common to most Amniota (birds, reptiles and mammals).

DISPLAY BEHAVIOR of seagulls shows how behavior traits inherent in all gulls have adapted to the needs of an aberrant species. At top is a typical gull, the herring gull, which breeds on the shore. It is shown in the "choking" posture which advertises its nest site. In middle the herring gull is shown in the "oblique" and "long call" postures, used to defend its territory. At bottom is the aberrant kittiwake, which unlike other gulls breeds on narrow ledges and has no territory other than its nest site. The kittiwake does not use the "oblique" or "long call" postures, but employs the "choking" stance for both advertisement and defense.

all mammals and reptiles) scratch with precisely the same motion! A bird also scratches with a hindlimb (that is, its claw), and in doing so it lowers its wing and reaches its claw forward in front of its shoulder. One might think that it would be simpler for the bird to move its claw directly to its head without moving its wing, which lies folded out of the way on its back. I do not see how to explain this clumsy action unless we admit that it is inborn. Before the bird can scratch, it must reconstruct the old spatial relationship of the limbs of the four-legged common ancestor which it shares with mammals.

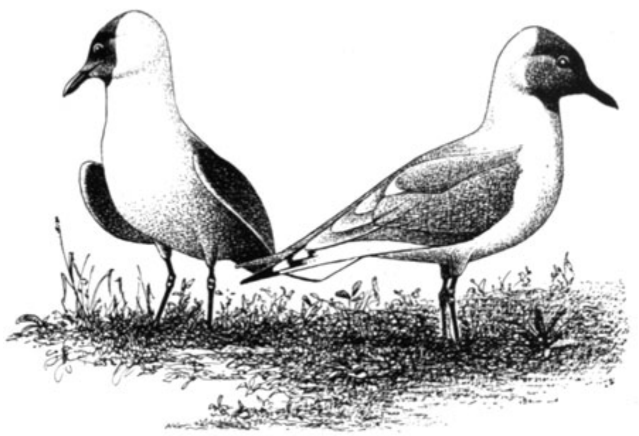
In retrospect it seems peculiar that psychologists have been so slow to pursue such clues to hereditary behavior. It is nearly 100 years since T. H. Huxley, upon making his first acquaintance with Charles Darwin's concept of natural selection, exclaimed: "How stupid of me, not to have thought of that!" Darwinian evolution quickly fired the imagination of biologists. Indeed, it swept through the scientific world with the speed characteristic of all long-overdue ideas. But somehow the new approach stopped short at the borders of psychology. The psychologists did not draw on Darwin's comparative method, or on his sense of the species as the protagonist of the evolutionary process.

Perhaps, with their heritage from philosophy, they were too engrossed in purely doctrinal dissension. For exactly opposite reasons the "behaviorists" and the "purposivists" were convinced that behavior was much too variable to permit its reduction to a set of traits characteristic of a species. The purposivist school of psychology argued for the existence of instincts; the behaviorists argued against them. The purposivists believed that instincts set the goals of animal behavior, but left to the individual animal a boundless variety of means to reach these goals. The behaviorists held that the capacity to learn endowed the individual with unlimited plasticity of behavior. The debate over instinct versus learning kept both schools from perceiving consistent, inherited patterns in behavior, and led each to preoccupation with external influences on behavior.

If any psychologist stood apart from the sterile contention of the two schools, it was Jakob von Uexküll. He sought tirelessly for the causes of animal behavior, and was not blind to structure. But he too was caught in a philosophical trap. Uexküll was a vitalist, and he denounced Darwinism as gross materialism. He believed that the regularities he observed in the behavior of species were manifestations of nature's unchanging and unchangeable "ground plan," a notion akin to the mystical "idea" of Plato.

The Phylogeny of Behavior

But even as the psychologists debated, evolutionary thought was entering the realm of behavior studies by two back doors. At Woods Hole, Mass., Charles Otis Whitman, a founder of the Marine Biological Laboratory, was working out the family tree of pigeons, which he had bred as a hobby since early childhood. Simultaneously, but unknown to Whitman, Oskar Heinroth of the Berlin Aquarium was studying the phylogeny of waterfowl. Heinroth, too, was an amateur aviculturist who had spent a lifetime observing his own pet ducks. What a queer misnomer is the word "amateur"! How unjust that a term which means the "lover" of a subject should come to connote a superficial dabbler! As a result of their "dabbling," Whitman and Heinroth acquired an incomparably detailed knowledge of pigeon and duck behavior.



"HEAD-FLAGGING" is another form of display in which the kittiwake has adapted its behavioral birthright to meet unusual needs. Most gulls — like this pair of black-faced gulls — use this stance in courtship (by averting its menacing facial and bill coloration, the bird "appeases" the aggressive instinct of its mate). Kittiwakes alone evince this posture not only in mating adults but in ledge-bound nestlings, which use it to "appease" invaders.

As phylogenists, Whitman and Heinroth both sought to develop in detail the relationship between families and species of birds. To define a given group they had to find its "homologous" traits: the resemblances between species which bespeak a common origin. The success or failure of their detective work hinged on the number of homologous traits they could find. As practical bird-fanciers, Whitman and Heinroth came to know bird behavior as well as bird morphology, and each independently reached an important discovery: Behavior, as well as body form and structure, displays homologous traits. As Whitman phrased it just 60 years ago: "Instincts and organs are to be studied from the common viewpoint of phyletic descent."

Sometimes these traits of behavior are common to groups larger than ducks or pigeons. The scratching habit, which I have already mentioned, is an example of a behavior pattern that is shared by a very large taxonomic group, in this case the Amniota: the reptiles, birds and mammals (all of whose embryos grow within the thin membrane of the amniotic sac). This widespread motor pattern was discovered by Heinroth, who described it in a brief essay in 1930. It is noteworthy that Heinroth observed the extreme resistance of such inborn habits to changes wrought by learning. He noticed that while most bird species maintain their incongruous over-the-shoulder scratching technique, some have lost this behavior trait. Among these are the larger parrots, which feed with their claws and use the same motion — under the wing — for scratching. Parakeets, however, scratch in the unreconstructed style, reaching around the lowered wing, and do not pick up food in their claws. There are a few exceptions to this rule. The Australian broadtailed parakeet has learned to eat with its claw. When eating, it raises its claw directly to its bill. But when scratching, it still reaches its claw around its lowered wing! This oddity is evidence in itself of the obstinacy of the old scratching habit. So far no one has been able to teach a parakeet to scratch without lowering its wing or to train a parrot to scratch around a lowered wing.

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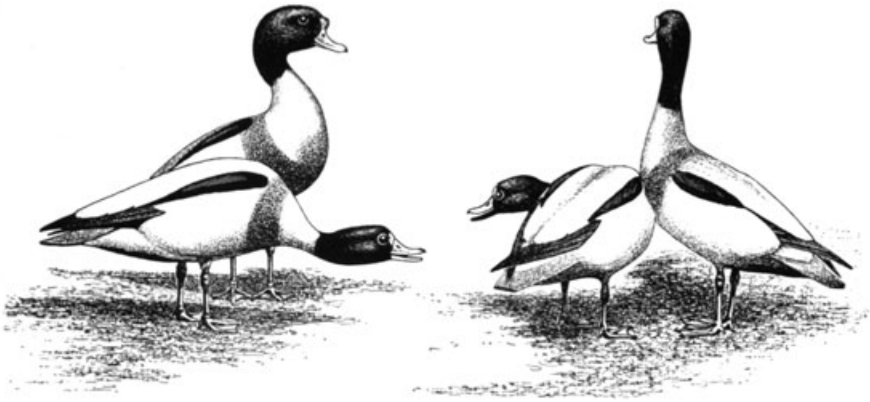
Today a growing school of investigators is working in the field opened up by Whitman and Heinroth. They have set themselves the task of discovering inherited patterns of behavior and tracing them from species to species. Many of these patterns have proved to be reliable clues to the origin and relationship of large groups of animals. There is no longer any doubt that animals in general do inherit certain deep-seated behavioral traits. In the higher animals such traits tend to be masked by learned behavior, but in such creatures as fishes and birds they reveal themselves with great clarity. These patterns of behavior must somehow be rooted in the common physiological inheritance of the species that display them. Whatever their physiological cause, they undoubtedly form a natural unit of heredity. The majority of them change but slowly with evolution in the species and stubbornly resist learning in the individual; they have a peculiar spontaneity and a considerable independence of immediate sensory stimuli. Because of their stability, they rank with the more slowly evolving skeletal structure of animals as ideal subjects for the comparative studies which aim to unravel the history of species.

I am quite aware that biologists today (especially young ones) tend to think of the comparative method as stuffy and old-fashioned — at best a branch of research that has already yielded its treasures, and like a spent gold mine no longer pays the working. I believe that this is untrue, and so I shall pause to say a few words in behalf of comparative morphology as such. Every time a biologist seeks to know *why* an organism looks and acts as it does, he must resort to the comparative method. Why does the ear have its peculiar conformation? Why is it mounted behind the jaw? To know the answer the investigator must compare the mammalian frame with that of other vertebrates. Then he will discover that the ear was once a gill slit. When the first air-breathing, four-legged vertebrates came out of the sea, they lost all but one pair of gill slits, each of which happened to lie conveniently near the



"INCITING" is a threatening movement used by the female duck to signal her mate to attack invaders of their territory. At left a female of the European sheldrake *(with head lowered)* incites her mate against an enemy that she sees directly before her. The female at right *(with head turned)* has seen an enemy to one side. Each female watches her enemy regardless of her own body orientation.

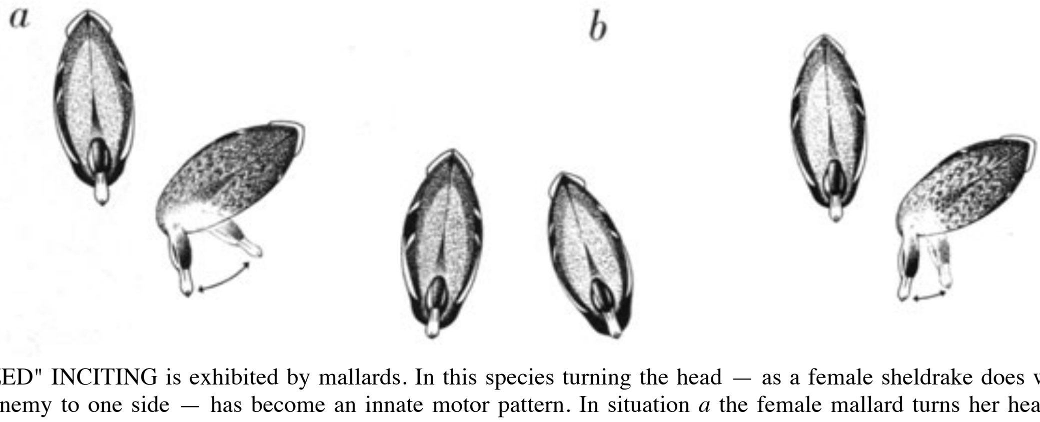
labyrinth of the inner ear. The water canal which opened into it became filled with air and adapted itself to conducting sound waves. Thus was born the ear.

This kind of thinking is 100 years old in zoology, but in the study of behavior it is only now coming into its own. The first studies leading to a true morphology of behavior have concentrated largely on those innate motor patterns that have the function of expression or communication within a species. It is easy to see why this should be so. Whether the mode of communication is aural, as in the case of bird songs, or visual, as in the "display" movements of courtship, many of these motor patterns have evolved under the pressure of natural selection to serve as sharply defined stimuli influencing the social behavior of fellow-members of a species. The patterns are usually striking and unambiguous. These qualities, so essential to the natural function of the behavior patterns, also catch the eye of the human observer.

Gulls, Terns and Kittiwakes

For some years N. Tinbergen of the University of Oxford has intensively studied the innate behavior of gulls and terns: the genus *Laridae*. He has organized an international group of his students and co-workers to conduct a worldwide study of the behavior traits of gulls and terns. They are careful to observe the behavior of their subjects in the larger context of their diverse life histories and in relationship to their different environments. It is gratifying that this ambitious project has begun to meet with the success which the enthusiasm of its participants so richly deserves.

Esther Cullen, one of Tinbergen's students, has been studying an eccentric



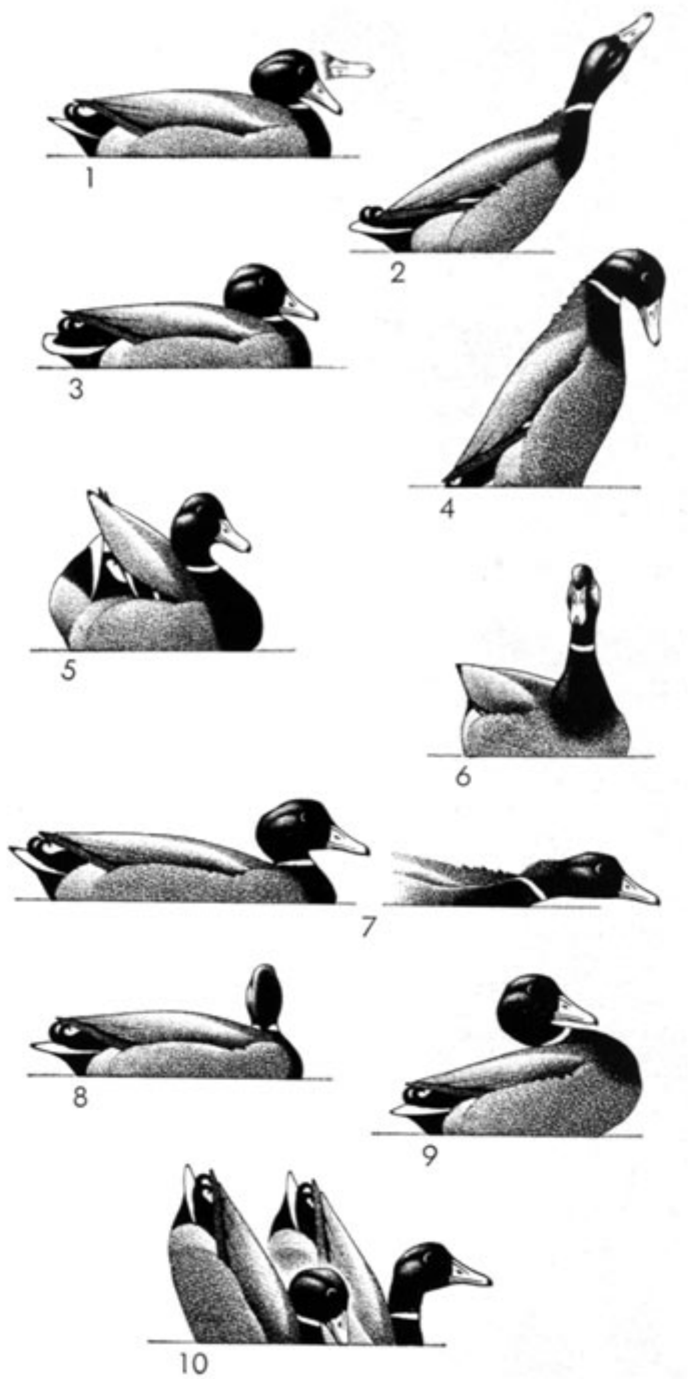
"RITUALIZED" INCITING is exhibited by mallards. In this species turning the head — as a female sheldrake does when inciting against an enemy to one side — has become an innate motor pattern. In situation *a* the female mallard turns her head toward the enemy. In *b*, with the enemy in front of her, she still turns her head even though this results in her turning it away from the enemy.

among the seagulls — the kittiwake. Most gulls are beachcombers and nest on the ground, and it is safe to assume that this was the original mode of life of the gull family. The kittiwake, however, is different. Except when it is breeding, it lives over the open sea. Its breeding ground is not a flat shore but the steepest of cliffs, where it nests on tiny ledges.

Mrs. Cullen has listed 33 points, both behavioral and anatomical, in which the kittiwake has come to differ from its sister species as a result of its atypical style of life. Just as the whale's flipper is a recognizable mammalian forelimb, so many of the kittiwake's habits are recognizably gull-like. But the kittiwake, like the whale, is a specialist; it has given its own twist to many of the behavior patterns that are the heritage of the *Laridae*.

For example, the male of most gull species stakes its claim to nesting territory by uttering the "long call" and striking the "oblique posture," its tail up and head down. To advertise its actual nesting site, it performs the "choking" movement. In the kittiwake the inherited patterns of behavior have been modified in accord with the habitat. On the kittiwake's tiny ledge, territory and nest sites are identical. So the kittiwake has lost the oblique posture and long call, and uses choking alone for display purposes.

Another example is the kittiwake gesture which Tinbergen calls "head-flagging." In other gull species a young gull which is not fully able to fly will run for cover when it is frightened by an adult bird. But its cliffside perch provides no cover for the young kittiwake. When it is frightened, the little kittiwake averts its head as a sign of appeasement. Such head-flagging does not occur in the young of other gulls, although it appears in the behavior of many adult gulls as the appeasement posture in a fight and in the rite of courtship. The kittiwake species has thus met an environmental demand by accelerating, in its young, the development of a standard motor habit of adult gulls.



TEN COURTSHIP POSES which belong to the common genetic heritage of surface-feeding ducks are here shown as exemplified in the mallard: (1) initial bill-shake, (2) head-flick, (3) tail-shake, (4) grunt-whistle, (5) head-up—tail-up, (6) turn toward the female, (7) nod-swimming, (8) turning the back of the head, (9) bridling, (10) down-up. How the mallard and two other species form sequences of these poses is illustrated on pages 72 through 76.

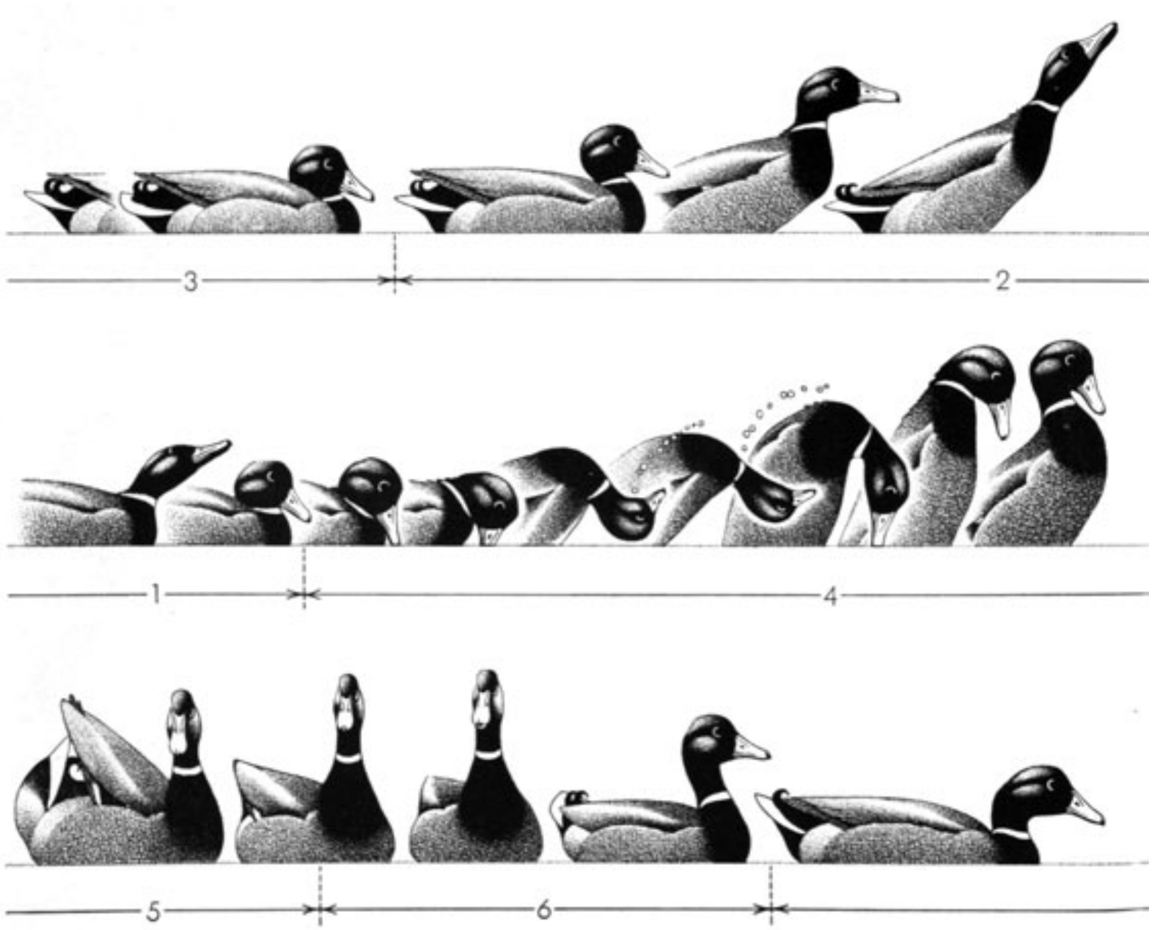
Recently Wolfgang Wickler, one of my associates at the Max Planck Institute for Comparative Ethology, has found a similar case of adaptation by acceleration among the river-dwelling cichlid fishes. Most cichlids dig into the river bottom only at spawning time, when they excavate their nest pits. But there is an eccentric species *(Steatocranus),* a resident of the rapids of the Congo River, which lives from infancy in river-bottom burrows. In this cichlid the maturation of the digging urge of the mating fish is accelerated, appearing in the infant of the species. It is not hard to conceive how selection pressure could have led to this result.

The work of the Tinbergen school has had the important result of placing innate motor habits in their proper setting. He and his co-workers have shown that these traits are highly resistant to evolutionary change, and that they often retain their original form even when their function has diverged considerably. These findings amply justify the metaphor that describes innate patterns as the skeleton of behavior. More work of the Tinbergen kind is badly needed. There is great value in his synthetic approach, uniting the study of the physical nature and environment of animals with study of their behavior. Any such project is of course a tall order. It requires concerted field work by investigators at widely separated points on the globe.

Behavior in the Laboratory

Fortunately it is quite feasible to approach the innate motor patterns as an isolated topic for examination in the laboratory. Thanks to their stability they are not masked in the behavior of the captive animal. If only we do not forget the existence of the many other physiological mechanisms that affect behavior, including that of learning, it is legitimate for us to begin with these innate behavior traits. The least variable part of a system is always the best one to examine first; in the complex interaction of all parts, it must appear most frequently as a cause and least frequently as an effect.

Comparative study of innate motor patterns represents an important part of the research program at the Max Planck Institute for Comparative Ethology. Our



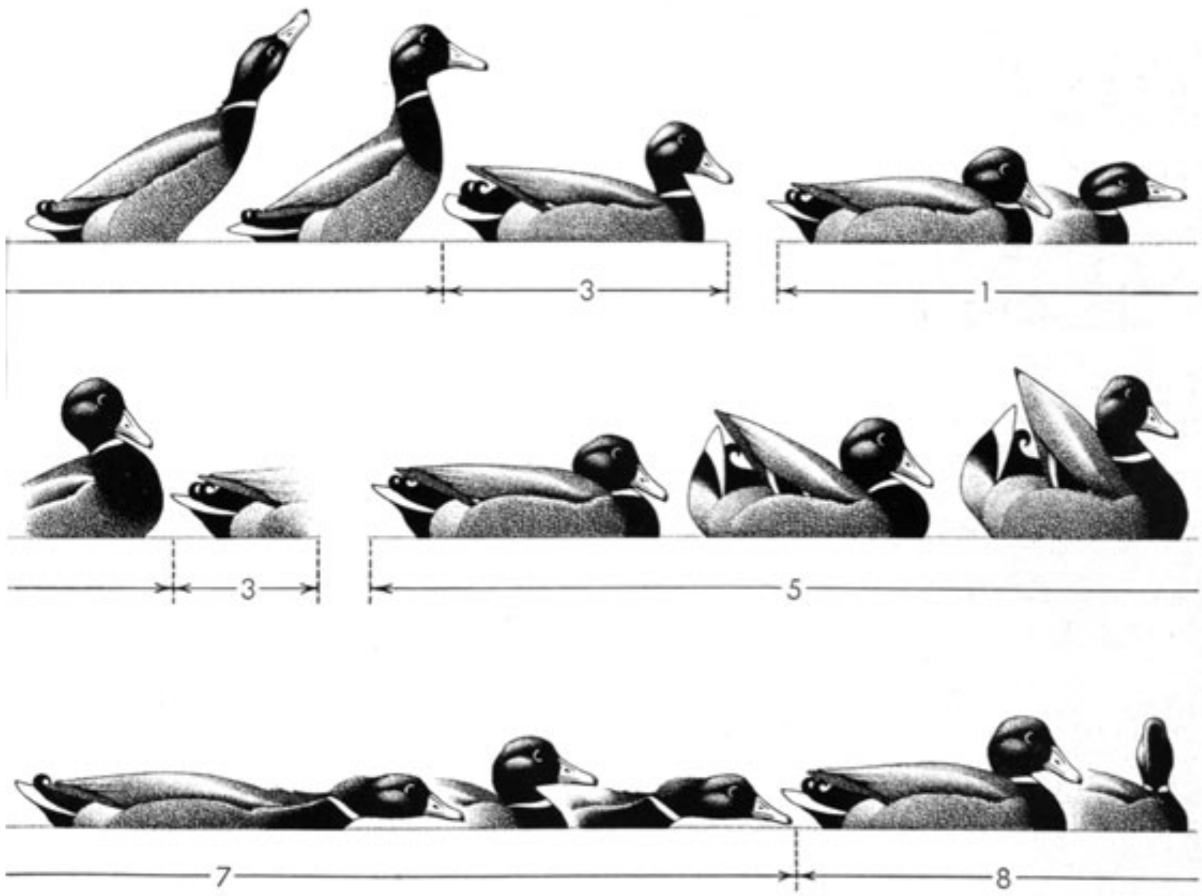
COURTSHIP SEQUENCES OF MALLARD are shown in this series of drawings, based on motion pictures made by the author at his laboratory in Seewiesen, Germany. Each sequence combines in fixed order several of the 10 innate courtship poses, illustrated on [see next page]

subjects are the various species of dabbling, or surface-feeding, ducks. By observing minute variations of behavior traits between species on the one hand and their hybrids on the other we hope to arrive at a phylogenetics of behavior.

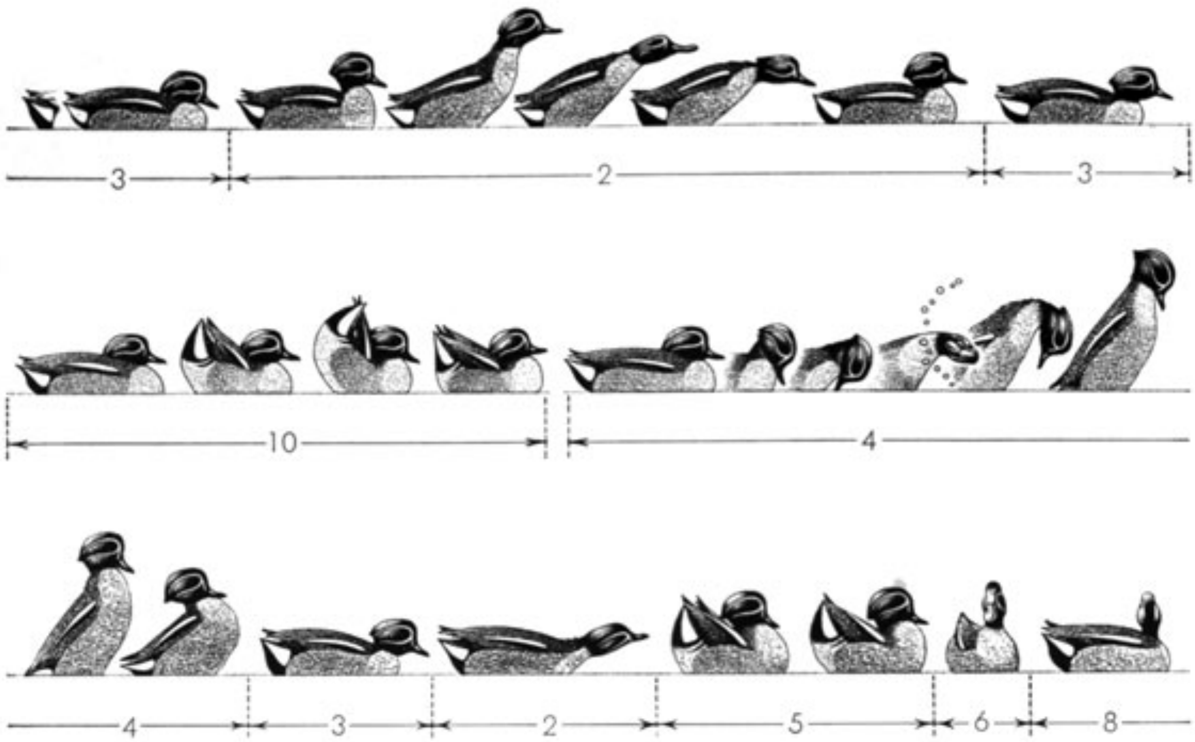
Our comparative studies have developed sufficient information about the behavior traits of existing species to permit us to observe the transmission, suppression and combination of these traits in hybrid offspring. Ordinarily it is difficult to find species which differ markedly with respect to a particular characteristic and which yet will produce fertile hybrids. This is true especially with respect to behavioral traits, because these tend to be highly conservative. Species which differ sufficiently in behavior seldom produce offspring of unlimited fertility. However, closely related species which differ markedly in their patterns of sexual display are often capable of producing fertile hybrids. These motor patterns serve not only to bring about mating within a species but to prevent mating between closely allied species. Selection pressure sets in to make these patterns as different as possible as quickly as possible. As a result species will diverge markedly in sexual display behavior and yet retain the capacity to interbreed. This has turned out to be the case with dabbling ducks.

The first thing we wanted to know was how the courtship patterns of ducks become fixed. Credit is due to Sir Julian Huxley, who as long ago as 1914 had observed this process, which he called "ritualization." We see it clearly in the so-called "inciting" movement of female dabbling ducks, diving ducks, perching ducks and sheldrakes.

To see "inciting" in its original un-ritualized form, let us watch the female



page 71. The numbers under the ducks refer to these poses. Shown here are the following obligatory sequences: tail-shake, head flick, tail-shake; bill-shake, grunt-whistle, tail-shake; head-up tail-up, turn toward female, nod-swimming, turning back of the head.



COURTSHIP OF EUROPEAN TEAL - another species of surface-feeding duck — includes tail-shake, head-flick, tail-shake (as in the mallard); down-up; grunt-whistle, tail-shake, head-flick, head-up-tail-up, turned toward the female, turning back of the head.

of the common sheldrake as she and her mate encounter another pair of sheldrakes at close quarters. Being far more excitable than her placid companion, the female attacks the "enemy" couple, that is, she adopts a threatening attitude and runs toward them at full tilt. It happens, however, that her escape reaction is quite as strong as her aggressive one. She has only to come within a certain distance of the enemy for the escape stimulus to overpower her, whereupon she turns tail and flees to the protection of her mate. When she has run a safe distance, she experiences a renewal of the aggressive impulse. Perhaps by this time she has retreated behind her mate. In that case she struts up beside him, and, as they both face the enemy, she makes threatening gestures toward them. But more likely she has not yet reached her mate when the aggressive impulse returns. In that case she may stop in her tracks. With her body still oriented toward her mate, she will turn her head and threaten the enemy over her shoulder. In this stance she is said to "incite" an aggressive attitude in her partner.

Now the incitement posture of the female sheldrake does not constitute an innate behavior trait. It is the entirely plastic resultant of the pressure of two independent variables: her impulse to attack and her impulse to flee. The orientation of her head and body reflects the geometry of her position with respect to her mate and the enemy.

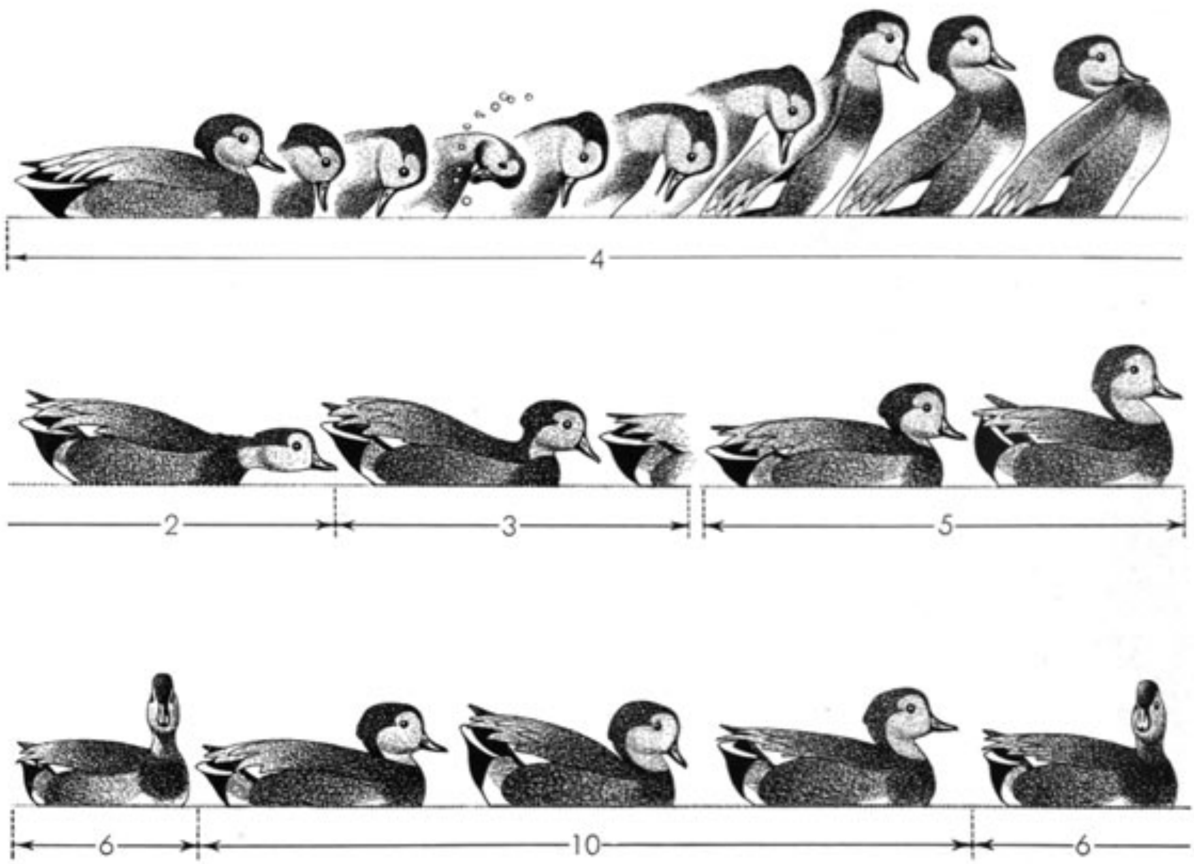
The same incitement posture in mallards, on the other hand, is distinctly ritualized. In striking her pose the female mallard is governed by an inherited motor pattern. She cannot help thrusting her head backward over her shoulder. She does this even if it means she must point her bill away from the enemy! In the sheldrake this posture is the resultant of the creature's display of two conflicting impulses. In the mallard it has become a fixed motor pattern.

No doubt this motor pattern evolved fairly recently. It is interesting to note that while the female mallard is impelled to look over her shoulder when inciting, the older urge to look at the enemy is still there. Her head travels much farther backward when the enemy is behind her. If you observe closely, it is plain that her eyes are fixed on the enemy, no matter which way her head is turned.

Occasionally a female, impelled by the awkwardness of watching the enemy from the ritualized posture, will swing about and face them directly. In that case one may say that her old and new motor patterns are simultaneously active. Like the sheldrake, the mallard must once have faced the enemy during incitement. Overlying this instinct is a new one — to move her head backward over her shoulder regardless of the location of the enemy. The old orienting response survives in part. It usually displays itself at low levels of excitement. Especially at the beginning of a response, the female mallard may stretch her neck straight forward. As her excitement mounts, however, the new motor pattern irresistibly draws her head around. This is one of many instances in which the mounting intensity of a stimulus increases the fixity of the motor coordination.

What has happened is that two independent movements have been welded together to form a new and fixed motor pattern. It is possible that all new patterns are formed by such a welding process. Sometimes two patterns remain rigidly welded. Sometimes they weld only under great excitement.

Recently we have been studying



GADWALL COURTSHIP includes the grunt-whistle, always followed by the tail-shake, head-flick, tail-shake sequence also found in the other species illustrated. The head-up-tail-up (5) and the down-up (10) are always followed by a turn toward the female (6). During the most intense excitement of the courtship display, these pairs themselves become welded into the invariable sequence 5-6-10-6.

behavior complexes in which more than two patterns are welded. In their courtship behavior our surface-feeding ducks display some 20 elementary innate motor patterns. We have made a special study of three species which have 10 motor patterns in common but display them welded into different combinations. As shown in the illustration on page 71, these patterns are (1) initial bill-shake, (2) head-flick, (3) tail-shake, (4) grunt-whistle, (5) head-up—tail-up, (6) turn toward the female, (7) nod-swimming, (8) turning the back of the head, (9) bridling, (10) down-up movement. Some of the combinations in which these motor patterns are displayed are shown on pages 72 through 76. In some species certain of the patterns occur independently *(e.g.,* 1 and 10 in the mallard). Some simple combinations have wide distribution in other species as well (e.g., 4, 3 and 5, 6 in all the species). Main combinations are more complicated, as the illustrations show.

What happens when these ducks are crossbred? By deliberate breeding we have produced new combinations of motor patterns, often combining traits of both parents, sometimes suppressing the traits of one or the other parent and sometimes exhibiting traits not apparent in either. We have even reproduced some of the behavior-pattern combinations which occur in natural species other than the parents of the hybrid. Study of our first-generation hybrids indicates that many differences in courtship patterns among our duck species may also be due to secondary loss, that is, to suppression of an inherited trait. Crosses between the Chiloe teal and the Bahama pintail regularly perform the head-up—tail-up, although neither parent is capable of this. The only possible conclusion is that one parent species is latently in possession of this behavioral trait, and that its expression in a given species is prevented by some inhibiting factor. So far our only second-generation hybrids are crosses between the Chiloe pintail and the Bahama pintail. The results look promising. The drakes of this generation differ greatly from each other and display hitherto unheard-of combinations of courtship patterns. One has even fused the down-up movement with the grunt-whistle!

Thus we have shown that the differences in innate motor patterns which distinguish species from one another can be duplicated by hybridization. This suggests that motor patterns are dependent on comparatively simple constellations of genetic factors.