

## A REVIEW OF SOME ASPECTS OF AVIAN FIELD ETHOLOGY<sup>1</sup>

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THE last 30 years have seen the development of a new approach to the study of behavior, which has increasingly interested ornithologists as they have attempted to understand avian biology fully. This new approach is now known as ethology. Both amateur and professional ornithologists have contributed to its progress from the beginning.

A basic tenet of ethology is that all behavior of animals can eventually be understood. The ethologist attempts to explain behavior functionally (what does it do for the animal?), causally (what are the internal and external factors responsible for each given behavior?), and evolutionarily (what is the probable phylogeny of the behavior, how does it contribute to the survival of the species, and what are the selective pressures acting upon it?) (see Tinbergen, 1951, 1959; Hinde, 1959*b*).

Some basic procedures are essential in an ethological study (Hinde, 1959*b*: 564). The first step is to describe and classify all the behavior of an animal, at the same time, if possible, dividing the behavior into logical units which can be dealt with further in other disciplines—particularly physiology and ecology (see Russell *et al.*, 1954). Although studies often begin qualitatively, they eventually should be quantified. Generalizations, which are to be valid for many species, must be based on work using closely related species first, and more distantly related ones later. The animal is studied as an integrated whole. Some workers, notably Konrad Lorenz, keep and breed animals in captivity under close scrutiny.

Most of this paper deals with communication of birds. We have stressed particularly the analysis of displays, their evolution, and their relation to taxonomy—topics of great interest to systematic ornithologists as well as to ethologists. In addition, we discuss certain maintenance activities.

### LITERATURE OF ETHOLOGY

Much of the early ethological literature appeared in European publications, but it is now also appearing in this country frequently. The principal journals are: *Animal Behaviour* (formerly *British Journal of Animal Behaviour*), *Symposium of the Zoological Society of London*, *Journal of Comparative and Physiological Psychology*, *Zeitschrift für Tierpsychologie*, and *Behaviour* (with monographs appearing as supplements in the last two). Papers on avian ethology also appear frequently in the major ornithological journals. Standard reference books on ethology are *The study of instinct* (Tinbergen, 1951), *Learning and instinct in animals* (Thorpe, 1963), and *Social behavior and organization among vertebrates* (Etkin, 1964).

Recent monographs on individual species include those by Marler (1956*a*) on the Chaffinch (*Fringilla coelebs*); Hinde (1952), Great Tit (*Parus major*); Tinbergen

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(1953), Herring Gull (*Larus argentatus*); Moynihan (1955*b*), Black-headed Gull (*L. ridibundus*); Curio (1959*a*), Pied Flycatcher (*Muscicapa hypoleuca*); Simmons (1955), Great Crested Grebe (*Podiceps cristatus*); and Immelmann (1959), Zebra Finch (*Taeniopygia castanotis*).

Some outstanding examples of comparative ethological studies are those by Lorenz (1952) on dabbling ducks, Meyerriechs (1960) on herons, Tinbergen (1959) and Moynihan (1955*b*, 1956, 1958*a, b*, 1959, 1962) on gulls, Andrew (1957*a, b*) on emberizine finches and (1961*a*) other passerines, Hinde (1955–1956) on carduelines, Dilger (1960) on parrots (*Agapornis*), McKinney (1961) on eiders (*Somateria*), Curio (1959*b*) on flycatchers (*Muscicapa*), and Löhrl (1960–1961) on nuthatches (*Sitta*).

#### ETHOLOGICAL CONCEPTS

Since there are several recent reviews of ethology (Emlen, 1955; Thorpe, 1963; Hinde, 1959*b*, 1961; Eibl-Eibesfeldt and Kramer, 1958), we shall discuss only a few critical concepts and terms of particular interest to field students. Many of the theoretical concepts are still controversial and will undoubtedly be modified substantially in the future. The glossaries of Verplanck (1957) and Thorpe (1951) contain many definitions of ethological terms.

Some actions of animals are variable, others more stereotyped, and the two kinds often occur together in a behavioral sequence. "The variable introductory phase of an instinctive behaviour pattern or sequence" is called *appetitive behavior* and the act terminating a behavior pattern or sequence is the *consummatory act* (Thorpe, 1951). Tinbergen (1951: 106) gives an example of a sequence in which a Peregrine Falcon (*Falco peregrinus*) searching for food begins by randomly roaming over its hunting territory. This appetitive behavior continues until a stimulus situation is encountered (e.g., a flock of teal executing flight maneuvers). Such situations may cause the falcon to abandon its random searching, but what follows is still appetitive behavior of a more specialized kind—the flock of teal may release sham attacks by the falcon, resulting in the isolation of a member of the flock. The final stoop, capture, kill, plucking, and eating form a relatively simple and stereotyped "chain of consummatory acts."

Stereotyped movements, many of which serve as consummatory acts, have been termed *fixed patterns* or *fixed action patterns* (Thorpe, 1956). Investigation of such patterns led to the modern concepts of instinctual behavior. *Instinct* as exemplified by these actions is a stereotyped pattern of behavior which is inherited and specific (Hinde, 1959*b*).

In addition, instinctual behavior may be characterized by the accumulation of *reaction specific energy* (now often referred to as *specific action potential* or S.A.P.) which is defined by Thorpe (1951) as "the state of the animal responsible for its readiness to perform the behaviour patterns

of one instinct in preference to all other behaviour patterns." He points out that this specific readiness "diminishes or disappears when the consummatory act of the charged instinct has been performed." However, if the action is not released, the S.A.P. accumulates. The threshold for release of the particular act is then lowered and the action may occur without any external stimulus. Such action is often called a *vacuum activity*, overflow activity, or "Leerlaufreaktion" (Lorenz, 1950; Thorpe, 1956). Lorenz observed this in a captive Starling (*Sturnus vulgaris*) which repeatedly performed all the behavior patterns of insect hunting, catching, killing, and swallowing, without any discernible stimulus (Tinbergen, 1951: 61). Lorenz postulated a mechanism which would prevent the occurrence of an act before the animal encountered the specific environmental stimuli. This "block" has been termed the *innate releasing mechanism* (I.R.M. or, more recently, R.M.) (Lorenz, 1950; Thorpe, 1956). The I.R.M. is "selectively responsive to a special stimulus situation" (Tinbergen and Perdeck, 1951: 2). This concept was introduced to account for the facts that animals often respond to a particular stimulus situation with specific responses even though they have never encountered the situation before, and that, in such cases, the animal often responds to only a very limited part of the total stimulus situation.

*Releasers* are structures or actions that emanate *sign stimuli* which are perceived by an animal. Releasers often reach a high degree of specialization, and their evolution may parallel that of the associated specific response (Lorenz, 1935). Tinbergen (1953: 197), using models, showed that in Herring Gulls the red spot on the parent's bill is the primary releaser of the pecking response of the chick. Neither the background color of the bill or head color are releasers; in fact, the presence of the head is not even necessary. Although most of the examples of releasers and their sign stimuli are derived from experimental studies of visual stimuli, the concepts are also applicable to olfactory, auditory, and tactile ones (see Lorenz, 1950). *Supernormal stimuli* are those that are even more effective than the natural stimuli; for example, Tinbergen (1951: 45) found that oystercatchers prefer a clutch of five eggs to a natural clutch of three and an abnormally large egg to one of their own.

*Drive* has been defined by Thorpe (1951) as "the complex of internal and external states and stimuli leading to a given behaviour." Thus, this term may include the stimuli, specific action potential, and innate releasing mechanisms involved in a given behavioral act. Because of the difficulties of determining internal states without experimentation, the term *tendency* has been used recently to indicate "the readiness to show a particular type of behaviour as observed under natural conditions" (Hinde, 1955-1956, as given by Marler, 1956a: 5). Causal factors include both

external and internal stimuli leading to a given behavior (Tinbergen, 1959: 29) and thus causation is approximately synonymous with the term drive or motivation.

*Displacement activity* has been used in two ways. It sometimes means behavior which is thought to have been activated by one or more drives which are not the drives normally associated with it. In other use it refers to the performance of a behavior pattern out of the context of behavior with which it is normally related (Thorpe, 1951). The first definition is highly controversial (see Iersel and Bol, 1958; Rowell, 1961; Sevenster, 1961); the second is more useful for the field observer. One example of displacement activity is that of fighting Great Tits which "may suddenly start to peck at a bud or pick up leaves and then throw them over their shoulders—activities normally used in feeding" (Hinde, 1959*b*). Some displacement activities, however, are not entirely irrelevant. They are seen frequently when an animal seemingly has tendencies to behave in two different ways or when one strong tendency is prevented from expression. For example, song in birds which have just escaped a dangerous situation is probably a manifestation of attack-escape motivation (see Moynihan, 1965*a*: 242).

*Redirection* occurs in contexts similar to those of displacement, but is fundamentally different in causation according to Moynihan (1955*a*: 242) who has defined redirection as "autochthonous activities of a drive directed toward an object or animal other than the one releasing and usually directing them (although the releasing object or animal remains available, or partly available, as a potential goal at the time)." Both redirected attack (Moynihan, 1955*a*) and redirected sexual behavior (Ficken and Dilger, 1960) have been noted in birds. Young (1949) described a male Robin (*Turdus migratorius*) which tried to copulate with a female but she threatened him each time; the male then "copulated" with a mound of earth and a crumpled newspaper before the female responded sexually.

Animals sometimes start to perform a movement but do not complete it. Heinroth termed these *intention movements* because they indicate to the observer what the animal is going to do (Marler, 1956*a*: 4). Such acts often occur when an animal is in a situation in which two tendencies are in conflict, and they are considered to indicate ambivalence.

#### MAINTENANCE ACTIVITIES

*Maintenance activities* are those "concerned with locomotion and the general health and efficiency of the body, mostly occurring throughout the year" (Marler, 1956*a*: 8). Of these, motor patterns involved in the care of the body surface have been called *comfort movements* or *toilet behavior*.

Maintenance activities are often easily observed, yet they remain virtually unrecorded for some families. These activities are described for various species, particularly by Nice (1943), Andrew (1956), Heinroth and Heinroth (1958), Wickler (1961*b*), Ficken (1962*b*), Meyerriecks (1960), Coutlee (1963), and McKinney (1965).

The study of maintenance activities is important, aside from the fact that they are necessary for the survival of the animal. Since such movements often evolve into components of display (see p. 647), knowledge about them is essential to an understanding of the evolution of bird displays. Further, they are usually stereotyped and of potential value in taxonomy, particularly at the ordinal and familial levels (see Table 1, below). We shall describe briefly some of the more significant movements with the hope of encouraging further observations.

*Stretching* movements of two types occur in all carinate birds (Nice, 1943). One involves the stretching down of one wing and the corresponding leg, typically also with a spreading of the tail. However, Kilham (1959) notes that woodpeckers do not stretch the corresponding leg. The other is a stretching of the wings (closed or perhaps somewhat extended) over the back. During this latter, some species spread their tails symmetrically at the same time (Heinroth and Heinroth, 1958: 112). Some, such as herons, stretch their neck forward during both types of stretching (Meyerriecks, 1960: 11). The stretching downward of both wings which occurs in some young passerines, has also been reported in some adult parrots (Nice, 1943) and in adult emberizines (Andrew, 1956). The straightening of both legs while the bird is standing (usually without involvement of the wings) occurs in young birds but less frequently in adults (Nice, 1943; Ficken, 1962*b*: 159). Comparative studies of these movements, giving the finer details of form, sequence (see Ficken, 1962*b*), and ontogeny, may be of taxonomic value.

*Preening* involves manipulating feathers with the bill. Preening of the tarsi (Whitaker, 1957*a*) has also been noted in several species of passerines. Preening movements and sequences are unknown in most birds, but they may be of taxonomic value. For instance, oscines and anatids distribute oil over the plumage in different ways. Oscines take oil from the uropygial gland with the tip of the bill, then scratch, first touching the tip of the bill with the claw of the second toe and subsequently rubbing the claw all over the top of the head. Anatids bite their oil gland and press oil into the feathers growing on or about the gland; they then rotate the head against these feathers (Lorenz, 1956).

*Anting* was described by Whitaker (1957*b*: 195) as "the application of foreign substances to the plumage and possibly to the skin." Ants are typically used, but a variety of other objects may stimulate the behavior.

Simmons (1959) distinguished two types: direct (the bird anointing itself) which occurs in over 100 species from many passerine families, and indirect or passive anting (the ants swarm over the bird) which occurs in certain larger birds such as corvids, turdids, grallinids, and cracticids. Recent reviews include those by Whitaker (1957*b*), Simmons (1957*a*, 1959), and Poulsen (1956). Recently Kelso and Nice (1963) reviewed the experimental evidence of Dubinin (1951–1956) that anting functions to destroy external parasites.

*Bathing* movements are described by Nice (1943). Morris (1955) described the variations in the form and sequence of bathing and drying movements in several birds. Records of species which bathe in water, dew, snow, and dust are scanty.

In *body shaking*, the contour feathers are first evenly and slowly ruffled. The shaking begins with the torso, and then usually involves the neck and head. In owls, this progression is reversed (Heinroth and Heinroth, 1958).

*Sunbathing* involves a ruffling of the body feathers, spreading the wings and tail, and often leaning to one side, as described for many species by Hauser (1957) and Gibb (1947). The stimulus for this behavior is not known, although Hauser suggests that humidity is more important than high air temperature and Lanyon (1958) thinks that a sudden warming of the bird's immediate environment may initiate it. Its function is uncertain.

In *head-scratching*, birds scratch in one of two distinctive ways. Some lower one wing and bring the corresponding leg over the shoulder (indirectly or "over the wing"). Others bring the foot directly to the head, with no wing lowering (directly or "under the wing") (Heinroth and Heinroth, 1958; Simmons, 1957*b*, 1961). Head-scratching probably functions in arranging and oiling the feathers of the head, and possibly in relieving irritating stimuli (Simmons, 1961).

Observations on the method of head-scratching of many common species remain unpublished. Since the type of head-scratching is almost always consistent within a species, it is useful as a taxonomic character (Table 1). Some nonpasserine families scratch indirectly, others directly; most passerines scratch indirectly. In a few cases there is variation within a family, e.g., Psittacidae (Simmons, 1957*b*; Breton and Immelmann, 1962). There is also occasional variation within a genus, as in *Seiurus* (Ficken and Ficken, 1958).

In a few known cases there is a change with age. For example, some waterthrushes (*Seiurus*) scratch directly for a few days when the behavior first appears and then switch to the indirect method (Ficken and Ficken, 1958). The reverse of this process is unknown (Wickler, 1961*b*).

In *sleeping* some birds (e.g., passerines) place the bill under the scapulars while many others (e.g., pigeons) draw their heads between their shoulders. Diverse sleeping postures are found in other groups, some of them apparent adaptations to peculiar anatomical features. For example, herons place the bill between the bend of the wing and the body (Heinroth and Heinroth, 1958). The hanging parakeets (*Loriculus*) sleep hanging upside down, and the related *Agapornis pullaria* also sometimes sleep in this position (Dilger, 1960).

*Locomotion* obviously includes several types of movement. Since flight is so often modified in displays, a knowledge of the normal form of flight in a species is particularly important. Flight patterns are often diagnostic of groups and may separate superficially similar groups such as swifts and swallows.

The legs are used for locomotion in walking, running, hopping, sidling, and swimming. Although there are many exceptions, walking and running are characteristic of ground foraging birds. Some species, such as the Song Sparrow (*Melospiza melodia*), employ both, depending on the environmental conditions. Many species which walk as adults, hop when they first leave the nest (Nice, 1943). The only bird known to do the opposite is the Wheatear (*Oenanthe oenanthe*) (Neal Smith, pers. comm.). There is variation even within a genus; all species of *Carduelis* hop, except *C. flavirostris*, a tundra dweller which walks. Walking and hopping are thus rather plastic behaviors and vary according to habitat (see Wickler, 1961*b*).

The motor patterns of *feeding* for even a single species, are poorly known although they are obviously of great importance. A few feeding patterns which show interesting taxonomic distributions are discussed here. A prying movement (sometimes called gaping or "Zirkeln") occurs in at least eight passerine families. The birds stick their bills into the ground, a soft substance, or a crack, and then open them with considerable force.

Some ground foraging birds scratch the vegetational substrate, but others apparently never do (e.g., the Ovenbird, *Seiurus aurocapillus*, uses its bill in moving leaves aside). Two different scratching procedures have evolved. Gallinaceous birds scratch backward first with one foot and then the other, while other groups (e.g., some emberizines, thrushes, timaliids) use both feet at once (Wickler, 1961*b*: 323). There is no apparent relationship between type of locomotion on the ground and type of scratching, although Wickler (1961*b*) suggested that scratching arose from an existing locomotory type.

The practice of holding food with one or both feet shows a spotty distribution in both nonpasserines and passerines. For example, among nine-primaried oscines it occurs in at least some icterids and carduelines but is absent in emberizines and parulids (except for the Yellow-breasted Chat,

*Icteria virens* [Neal Smith, pers. comm.]). Wickler (1961*b*) discusses the peculiar distribution of this motor pattern and suggests it is at least partly related to tarsal structure.

#### COMMUNICATION

Communication, which occurs "whenever the activities of one animal influence the activities of another animal" (Alexander, 1960: 38), is a major field of research. Birds are an especially favorable group for study because of the similarity of their sensory systems to our own and the consequent predominance of signals involving color vision and hearing.

Communication is characteristic of all birds and is mostly by *display*, that is, "those peculiarly standardized and often exaggerated performances, including all vocalizations and many movements and postures, which have become specialized and modified as social signals or releasers" (Moynihan, 1955*a*: 240). Displays usually are fixed action patterns (see p. 638).

The process of ritualization results in inter- and intra-specific signals or displays. The evolution of display systems involves simultaneous modification of the motor patterns and releasers of the actors and the patterns of response and readiness to respond of the reactors. However, certain movements of birds may communicate information without being peculiarly standardized or exaggerated to serve a communicatory function—for instance, the coordinated flight of birds in a flock. In some cases it is difficult to differentiate between ritualized and non-ritualized movements, e.g., some pre-flight movements. The analysis of displays has been of primary concern to ethologists, perhaps even to the neglect of other areas.

*Causation.*—Recent studies have indicated that displays are produced by dual or multiple motivational factors (see Tinbergen, 1959). Agonistic displays (the term "hostile" was formerly used) are those where presumably both attack and escape tendencies are primarily involved. Courtship displays usually involve sexual, attack, and escape tendencies (Morris, 1956), thus analysis of motivation in these cases is especially difficult. There are as yet no ideal studies which can be used as models for the analysis of causation and it is obvious that many attempts at causal analysis are needed before the best methodology can be established.

Three closely related approaches to the analysis of causation have often been used (see Tinbergen, 1959).

First, the specific social and environmental situations evoking certain behaviors are often determined. For example, in territorial species, the bird usually exhibits "pure" attack to an intruder within his territory, while the intruder exhibits "pure" escape. Most displays occur at or near



territorial boundaries, where it might be expected that escape and attack tendencies are in conflict.

Second, study of the separate elements of a complex display may suggest what tendencies are involved. Tinbergen (1959: 11) has shown that in the "Upright" display of gulls, which occurs in agonistic situations, the attack tendency is indicated by the raising of the carpal joints and stretching of the neck with the bill pointed downward. These movements are characteristically found in intention movements of two types of attack, i.e., delivering wing beats with the folded wing and pecking at an opponent from above. However, other components of the Upright display are indicative of the escape tendency. The related Great Skua (*Stercorarius skua*) does not raise the carpals in a similar display, a fact correlated with the absence of wing beating in fights.

Stokes' study (1962) of the agonistic behavior of the Blue Tit (*Parus caeruleus*), however, somewhat contradicts the idea that different elements of a display indicate different tendencies. He found that a given element rarely led to a highly predictable subsequent behavior, since individual elements often simultaneously represented tendencies to attack, stay, and escape. Also the relationship between elements of the display and subsequent behavior changed seasonally.

Finally, the use of "time scores" involves analyzing the sequential patterning of behavior acts over time. This yields quantitative information on the relative strengths of the tendencies involved since they represent "the relative proportion of observed attacks and withdrawals linked with each display" (Tinbergen, 1959: 33). This method is properly used when behavioral patterns alternate in quick succession. An animal in an unchanging environment usually does not have rapid motivational shifts. Thus if a display alternates rapidly and consistently with other movements, it may be concluded that the display and these movements have roughly the same motivational state. This method is difficult to employ in field studies because of the interaction between the displaying bird and the reactor(s). This difficulty can be overcome by analyzing only those cases where the recipient's behavior is relatively constant. Models or mounted specimens are sometimes useful as "constant stimuli" (Tinbergen, 1959: 32-33).

Although the preceding examples of causal analysis have dealt with visual displays, the motivation underlying vocalizations can be determined in much the same manner. Examples of such studies are those by Andrew (1961*b*) on the Blackbird (*Turdus merula*) and Ficken (1962*a*) on the American Redstart (*Setophaga ruticilla*).

*Function.*—Displays are releasers and their functions or "signal values" are determined by observing the reaction of the recipient of the display.

The reactions may be covert, overt, or both. Covert reactions are usually more gradual physiological changes, e.g., stimulation of ovulation in budgerigars by the calls of males (Vaugien, 1951; Ficken *et al.*, 1960; Brockway, 1966). Overt responses usually occur immediately after the communicated signal is received. For example, observations by Tinbergen (1959: 23) and his co-workers showed that a female Black-headed Gull approached a hidden male immediately after an "Oblique-cum-Long-Call" in 13 out of 16 cases; when she failed to do so she was engaged in squabbles with another bird. The female did not approach the male when he was not calling. Thus one can conclude that the function of the call is to induce the female to approach. Assessing function is often difficult and large numbers of examples are needed (e.g., Stokes, 1962), and some displays, such as "song," may have more than one function. Marler (1956*b*) discusses in detail the functions of the vocalization of the Chaffinch.

Tinbergen (1959: 24) has, from the functional standpoint, classified displays involved in agonistic interactions and pair formation into two groups: spacing out, or distance-increasing, and distance-reducing displays. The first group includes threat displays which tend to make the opponent retreat or cease advancing (Tinbergen, 1959; Moynihan, 1955*c*). In most species several threat displays have evolved with slightly different functions—some are more offensive, some defensive, some for long-range signalling (e.g., song), and others for short-range signalling (Tinbergen, 1959: 25).

Distance-reducing displays are also widespread in birds. Appeasement or submissive displays inhibit aggression by the opponent. Many of these displays are composed of "reversed movements" of attack, i.e., opposite movements from those indicating a strong attack tendency (see Marler, 1956*a*). For example, many passerines adopt a fluffed submissive posture which is very unlike the posture of an attacking bird, which sleeks its feathers and directs its head toward the opponent. Distance-reducing displays are particularly important in promoting social bonds between members of a pair, young and parent, etc.

*Origin of displays.*—Display components seem to be "derived" activities, having ultimately evolved from precursors which did not have signal value (Tinbergen, 1952). The origin of vocalizations is very poorly understood, but Spurway and Haldane (1953) suggest that they are derived from breathing movements. Moynihan (1955*a*) has given four sources of visual displays. First, displacement activities are often incorporated into displays. An example is the mock preening of the Mallard (*Anas platyrhynchos*)—a similar display also occurs in many other ducks—in which the male, while courting the female, reaches his bill behind his

slightly lifted wing, moving the bill over the underside producing a "Rrr" sound. In some species specially modified feathers are exhibited during this display (Lorenz, 1951-53). Mock preening seems clearly derived from real preening, which, in a courtship situation, is "out of context."

Displays may also be derived from redirected activities, but examples are rarer. Moynihan (1955a: 243) and Tinbergen (1959) suggest that the pecking into the ground and pulling of vegetation in some gull displays during territorial clashes probably had their origin in redirected aggression.

Third, intention movements are commonly ritualized into display components; Daanje (1950) gives many examples. Both sexual and agonistic displays may have components derived from the lowering of the breast and the wing and tail movements which precede jumping up or flying.

Finally, higher intensity movements characteristic of the tendencies producing the display may become ritualized. Moynihan (1955a: 241) cites examples of the "Swoop" and "Soar" displays of the Black-headed Gull which include attack and escape elements of greater "vigor and elaboration" than intention movements which are low intensity movements.

Since many displays are composed of more than one posture or movement, often with different evolutionary histories, it is necessary to consider each component separately. In many cases the same component occurs in more than one display and this often facilitates analysis. Determining the derivation of components may be relatively simple when they are similar to an unritualized behavior pattern (see Daanje, 1950; Marler, 1956a; Tinbergen, 1959). However, in other cases, e.g., the complex courtship displays of manakins (Pipridae) (Sick, 1959) and birds of paradise (Paradisidae) (Armstrong, 1942), the movements have undergone so much elaboration that their precursors are unrecognizable. In these cases comparative studies of a group of related species, some of which possess the movement in question in a less ritualized form, provide many useful clues to derivation. The study of the ontogeny of displays is an important but seldom used method of obtaining evidence about derivation and the developmental integration of form and function (Moynihan, 1959).

The types of changes involved in the ritualization of a movement have been discussed by Daanje (1950), Morris (1957), Blest (1961), and Hinde and Tinbergen (1958). We mention here a few of the more obvious changes which occur. Conspicuous structures which are correlated with a movement often are developed. As Hinde and Tinbergen (1958: 258) point out, "there has probably always been a parallel elaboration of structure and movement." For example, warblers which habitually spread their

tails have striking tail markings while those that wag or flick their tails do not (Ficken and Ficken, 1962*a*).

Changes in the nature of the movement, such as exaggeration (Lorenz, 1952: 7; Daanje, 1950), and changes in speed of performance as compared with the precursor (Blest, 1961) also occur. Rhythmic repetition may develop, as in the "dancing" movements of estrildine finches (Morris, 1957). There are also often changes in coordination (Daanje, 1950) as, for example, the simultaneous occurrence of a component of the first phase of take-off (crouching) and one from the second (tail lowering).

In ritualization a variable behavior often becomes more constant in form. Wide ranges in the strengths of the eliciting factors are accompanied by slight changes in form of the display, giving it a *typical intensity* (Morris, 1957; Hinde and Tinbergen, 1958). The courtship display of the male Cutthroat Finch (*Amadina fasciata*) remains similar in form despite motivational shifts (Morris, 1957). In contrast, *graded displays* are ones where slight motivational shifts are reflected in display movements (Marler, 1961*a*: 107).

Emancipation occurs when ritualized responses become freed from the causal factors of their precursors. There are few examples of this phenomenon and it may not be as widespread as once thought (Hinde and Tinbergen, 1958: 259). Blest (1961) discusses the topic at length.

*Naming displays and the problem of homology.*—Displays should be given descriptive names, not ones that suggest their causation or function, particularly because concepts about these may change (Tinbergen, 1959; Dilger, 1962: 85). Displays are usually named for their most obvious component or combination of components (Tinbergen, 1959). Names of displays are usually capitalized to distinguish them from names of other behaviors.

Behavioral homology, as with morphological homology, implies common phylogenetic descent. However, homologies are rarely known with certainty. Tinbergen (1959: 7) suggests that similarity in form, wide and continuous distribution through the group, and similar motivations, functions, and derivations, are indicative of homology. Difficulties arise when the same name is applied to similar displays in two species since this implies homology. The number of descriptive terms to use for a given type of display is limited, however. It may be best at this time to use the most useful descriptive words and to state that no homologies are implied with behavior patterns, of other species, that might bear the same name.

## BEHAVIOR AND EVOLUTION

*Intraspecific and interspecific variation in behavior.*—The evolution of behavior at the intraspecific level has attracted attention only relatively recently. In a few cases the selective pressures responsible for geographic variation are known. Curio (1961: 47) demonstrated numerous differences between two subspecies of Pied Flycatchers; these were manifested mainly in changes of threshold and motivation. One difference which has obvious survival value is that the northern subspecies mobbed a predator, the Red-backed Shrike (*Lanius collurio*), strongly, while the southern subspecies, which is outside the range of shrikes, did so much more weakly. Adaptive geographic variation is also shown in the begging notes of nestling Snow Buntings (*Plectrophenax nivalis*). On Bylot Island nests are accessible to weasels and the nestlings are usually silent (Drury, 1961). However, in Greenland there are no weasels and the young have loud and frequent begging calls (Tinbergen, 1939).

In addition to extensive individual differences in song (Weeden and Falls, 1959; Marler, 1961*b*), there is also geographic variation in some cases (e.g., Mayr, 1942; Benson, 1948; Lanyon and Fish, 1958; Thorpe, 1961; Borror, 1961). In many cases song "dialects" (interpopulational differences) are phenotypic rather than genotypic differences. Local dialects may be signs of incipient speciation (Marler and Tamura, 1962).

Behavior may also be remarkably similar between isolated populations of the same species. Dilger (1960) found that the four subspecies of *Agapornis personata* are very much alike in such features as courtship feeding, precopulatory displays, the manner of carrying nest material, and nest building, although they differ distinctly in color. In some birds the songs of two isolated subspecies are remarkably similar, e.g., the songs of the British and Tenerife Island forms of both the Corn Bunting (*Emberiza calandra*) and Blackbird (Marler, 1960).

Polymorphism in behavior has been infrequently described. A well studied case is that of the White-throated Sparrow (*Zonotrichia albicollis*). Some individuals have a white median stripe on the crown and others a tan stripe; matings are usually of birds of opposite morphs (Lowther, 1961). White-striped females sing a nearly normal song and react to song playback, but tan-striped females do neither. White-striped males react to playback longer and stronger than do tan-striped males. The assortative mating is probably a result of these behavioral differences (Lowther, 1962). Huxley (1955) cites examples of behavioral polymorphism in birds in host preference, vocalizations, nest-construction, and breeding season.

Sexual dimorphism in behavior is common and is often associated with dimorphism in color pattern. In the Common Grackle (*Quiscalus quis-*

*cula*) both sexes give all but one of the displays of the other, but differences occur in the relative frequency with which they give these (R. Ficken, 1963: 70). Such differences between the sexes are probably due to differences in threshold, as are some differences in the frequency of homologous displays among related species (Hinde, 1959a: 94) and among populations of the same species (Curio, 1961: 47). Threshold differences also may be responsible for individual variation and the rare occurrence of a behavior. For example, a display common in one species of *Agapornis* was seen only twice in another species despite years of observation (Dilger, 1960: 682). Threshold changes are a convenient way of retaining the potential for possible rapid shifts of behavior in response to changing selective pressures (R. Ficken, 1963: 70).

Displays and associated releasers, such as color patterns, are often involved in maintaining reproductive isolation among closely related sympatric species. Thus, there often is selection for differences in behavior patterns, particularly those involved in pair formation and courtship.

In birds with a long period between pair formation and copulation, displays preceding copulation need not be as specific as those in birds in which copulation occurs at the initial meeting (e.g., Marler, 1957: 28; Hinde, 1959a: 89–90). In most species males are more active in courtship than females and their displays are more species typical.

Hinde (1959a) discusses at length the nature of species differences in courtship. These include differences in the actual and relative strengths of the tendencies to attack, escape, and behave sexually toward the mate. For example, Chaffinch and Bullfinch (*Pyrrhula pyrrhula*) males are less aggressive toward their mates than are the Goldfinch (*Carduelis carduelis*) and Canary (*Serinus canarius*). The Chaffinch and Bullfinch are also strongly sexually dimorphic in color pattern, while the Goldfinch and Canary are not (Hinde, 1959a: 93–94). The females of non-dimorphic species may release more aggression because of their plumage color (see also Hamilton, 1961).

In some closely related sympatric species colors and patterns are more divergent than the display movements (Hinde, 1959a: 96; Ficken and Ficken, 1962a).

A good example of modification of courtship, as a result of selection on some other feature, occurs among the Ploceinae (Crook, 1959). The nest of primitive members is globular and males display just below the entrance, which is near the top. In other species the nest is modified and the entrance is underneath; the birds display with the same orientation to the entrance, but hang upside down.

*Behavior and speciation.*—The role of behavior patterns as isolating mechanisms between two sympatric populations has recently been re-

viewed by Hinde (1959a), Spieth (1958), and Mayr (1963). Although there are several other types of mechanisms reducing the probability of interspecific crosses (pre-mating mechanisms) or of their success (post-mating mechanisms), behavioral isolating mechanisms are probably the most important (Mayr, 1963: 95). Vocalizations and visual behavior are effective in various combinations in reducing mixed pairings (Dilger, 1956a; Stein, 1958, 1963; Lanyon, 1960a; and Hinde, 1959a, give many examples). It has been suggested that learned behavior may be important as an isolating mechanism (see Cushing, 1941), but Hinde (1959a: 100) suggests that this is improbable although he states that "learned mating preferences could tide the species over a period in which the courtship displays had altered somewhat but there had been no corresponding genetic change in responsiveness to these displays by other individuals." In some cases although the signals themselves may be innate, the response to them may be learned (Marler, 1961a: 116).

Habitat preference and feeding behavior differences may reduce competition and enable reproductively isolated populations to coexist sympatrically (Hinde, 1959a; Dixon, 1961, gives examples in *Parus*). Although there are often morphological differences which supplement these behavioral differences, MacArthur (1958) found that in five species of sympatric *Dendroica*, which did not differ appreciably in body length or bill size, behavioral differences in the method of feeding were of prime importance in allowing coexistence in the same habitat.

Brown and Wilson (1956) give examples of character displacement in bird behavior including feeding habits, habitat preference, and song.

*Actions of selective pressures on behavior.*—Single environmental factors may produce a multiplicity of effects on behavior. This has been well demonstrated by Cullen (1957) in her study of the adaptations of the Black-legged Kittiwake (*Rissa tridactyla*) to cliff nesting. Such nesting situations, when compared with the open ground nesting of most gulls, result in relaxation of predator pressure and restrictions imposed by the limited area and danger to the young of falling off the cliff. Both factors have produced numerous changes in behavior; the alarm call is rare, and the submissive display is exaggerated, thus obviating falling.

Most often many forces shape a single behavior pattern. For example, if song (and certain call notes) has the primary functions of attracting conspecific females and repelling rival males, there are many variables which would influence its evolution. Songs with properties which promote ease of location by conspecifics would be advantageous but, at the same time, would render the singing individual more vulnerable to predation.

Furthermore, individual recognition by conspecifics of the song of males on neighboring territories reduces aggression (Weeden and Falls, 1959).

TABLE 1  
EXAMPLES OF THE USE OF BEHAVIORAL CHARACTERS IN TAXONOMY

<i>Activity</i>	<i>Level used</i>	<i>Taxonomic discrimination</i>
Method of head scratching	Familial	<i>Recurvirostra</i> , <i>Himantopus</i> , and <i>Haematopus</i> related to charadriids rather than scolopacids (Simmons, 1957 <i>b</i> )
	Subfamilial	Suggest Psittacinae may be polyphyletic (Breton and Immelmann, 1962)
Holding food with the foot	Familial	Separates <i>Icteria virens</i> from Parulidae (Ficken and Ficken, 1962 <i>b</i> )
Dust bathing	Subfamilial	Supports relationship of <i>Passer</i> to ploceids (Mayr, <i>et al.</i> , 1953: 120)
Water bathing method	Familial	Separates timaliids from most other passerines (Simmons, 1963)
Method of oiling feathers	Familial	Separates timaliids from most other passerines (Simmons, 1963)
Visual agonistic displays	Generic	Splits <i>Hylocichla mustelina</i> from <i>Catharus</i> spp. (Dilger, 1956 <i>b</i> )
	Generic	Often useful at this level in Anatidae (Johnsgard, 1961)
Song	Tribal	Useful at this level in estrildine finches (Delacour, 1943)
	Intergeneric	Shows relationship of <i>Setophaga ruticilla</i> and <i>Dendroica</i> (Ficken and Ficken, 1962 <i>a</i> )
	Intragenetic	Shows close affinities of <i>Vermivora pinus</i> and <i>V. chrysoptera</i> and of <i>V. peregrina</i> and <i>V. ruficapilla</i> (Saunders, 1951)
Flight call notes	Subfamilial	Suggest relationship of <i>Fringilla</i> and carduelines (Marler, 1957)
Length of pair bond	Subfamilial	Separates estrildines from ploceids (Steiner, 1955 <i>in</i> Mayr, 1958)
	Subfamilial	Separates Anatinae from some other subfamilies (Johnsgard, 1961)
Bower construction	Subfamilial and familial	Subdivides Ptilonorhynchidae into two subfamilies and places cat-birds in a separate family (Ailuroedidae) (Marshall, 1954: 183)
Form of courtship display	Subfamilial	Shows affinity between <i>Fringilla</i> and carduelines (Andrew and Hinde, 1956)
	Interfamilial	Presence of tail quivering suggests possible relationship among corvids, estrildines, and ploceids (Andrew, 1961 <i>a</i> : 561)
Nest construction	Ordinal	Evidence for relationship between hummingbirds and swifts (Pearson, 1953; Amadon, 1959)
	Intergeneric	Indicates close relationship between <i>Hirundo</i> and <i>Ptyonoprogne</i> (Mayr and Bond, 1943)
	Familial	Separates <i>Peucedramus</i> from Parulidae (George, 1962)
Time of initiation of incubation	Subfamilial	Separates estrildines from ploceids (Steiner, 1955 <i>in</i> Mayr, 1958)
Participation of sexes in parental care	Subfamilial	Separates <i>Anseranas semipalmata</i> from other Anatidae (Johnsgard, 1961)
Feeding of nestlings	Subfamilial	Separates estrildines from ploceids (Steiner, 1955 <i>in</i> Mayr, 1958)
Nest sanitation	Familial	Separates <i>Peucedramus</i> from Parulidae (George, 1962)



However, this advantage is counterbalanced by the stereotypy needed for species recognition (Marler, 1957, 1960). Local dialects may help induce the return of males and females to their birthplaces (see Marler and Tamura, 1962: 375) where they may be best able to survive. The physical characteristics of the habitat may have important effects on the form of song. Thus, limited visibility within dense habitats may result in a high degree of dependence on vocal signals (Dilger, 1956*b*: 350) and can favor the development of low frequency songs which carry farther (Ficken and Ficken, 1962*a*). Species specificity is strongly selected for in areas with rich avifaunas where each song must stand out conspicuously from the general background of sound (Marler, 1960: 350).

Other factors may influence the evolution of bird vocalization. Certain distantly related, but ecologically competing, species have developed similar threat calls (Dilger, 1956*a*: 196; Dixon, 1961: 199–200) which could result in some increase in spacing. Social structure is also influential. Dueting (antiphonal singing or calling) is associated with long-term or close contact between members of a pair and occurs in some tropical and temperate zone species which remain mated through the year and also in a few migratory but colonial species (see Armstrong, 1942: 156–159). Songs of estrildine finches are of low volume and specificity, qualities correlated with their use only as close range sexual signals; in these birds pair formation occurs in the flock so the female sees a potential mate before she hears him and males do not sing in territorial defense (Hall, 1962). The whole subject of “song” is further complicated by the wide range of differences among species in the degree to which a song is modified by learning (Lanyon, 1960*b*; Thorpe, 1961; Marler *et al.*, 1962) and also by the difficulty of defining it.

*Convergence.*—Behavioral convergence is widespread, probably as a result of various factors. One is the limited number of possibilities available, a fact seeming to account for the similarity of appeasement postures of distantly related species (Tinbergen, 1959: 61). Functional necessity may also lead to similarity, as with the female soliciting display, most of the components of which are functional in facilitating copulation (Marler, 1956*a*: 116–117). Similarity in habitats is often associated with convergence. Thus, scratching the ground by hopping backwards has appeared in eight passerine families (Wickler, 1961*b*: 323) and flycatching in at least five (Hinde and Tinbergen, 1958: 262). Hole-nesting birds of different families may exhibit similarities which are adaptive to this mode of life, e.g., gaping of the young at the darkening of the nest hole as occurs when the parents arrive (Haartman, 1957: 341), loud begging calls (Heinroth *in* Tinbergen, 1939: 35–36), and notes resembling the hissing of a snake (Sibley, 1955). Similar precursors of two behaviors may lead

to convergence, as in courtship feeding displays of different species which are derived from similar juvenile begging displays (Andrew, 1961a: 562).

*Behavior and taxonomy.*—A taxonomic character is “any attribute of an organism or of a group of organisms by which it differs from an organism belonging to a different taxonomic category or resembles an organism belonging to the same category” (Mayr *et al.*, 1953: 105). Tinbergen (1959), Hinde and Tinbergen (1958), Mayr (1958), Amadon (1959), and Wickler (1961a, b) review the subject of the use of ethological characters in taxonomy.

Examples of the use of behavioral characters in taxonomy are listed in Table 1. This table is by no means comprehensive but is designed to give an idea of the variety of types of behavior which have been used and the taxonomic levels at which they have proven to be useful. In many of these cases morphological characters substantiate conclusions drawn from behavior.

The use of behavior patterns as taxonomic characters presents many of the same problems (such as convergence) encountered in using morphological ones as well as some additional difficulties (e.g., modification through experience). Some patterns, such as call notes, visual displays, and maintenance activities, develop nearly identically under a wide range of conditions. Others, such as song and reactions to environmental stimuli (Mayr, 1958), are often easily modified (see Tinbergen, 1959: 4).

The functional significance of behaviors must be known if they are to be useful taxonomically. For example, displays and morphological features serving as releasers, which have been selected for specific distinctiveness, will be of little use above the species level (Marler, 1957). In cases in which there is interspecific communication, as often occurs with certain mobbing calls, there is often little specific distinctiveness and the calls may even be convergent (Marler, 1957: 25), thus of little taxonomic use.

Behavior characters are sometimes more useful than others since they may be more conservative (Mayr *et al.*, 1953: 119) or permit finer discriminations (Mayr, 1958). In morphologically similar groups they are particularly important since even the slightest clues must be used (Mayr, 1958: 348). Behavior has been of great value in detecting sibling species. Thus, *Empidonax brewsteri* was first detected as being different from a sibling (*E. trallii*) by its song (Stein, 1963).

Behavior patterns are generally useful as taxonomic characters in direct proportion to their improbability. Improbability increases with complexity. However, behavior patterns which are performed in one of two ways, neither seeming to be more advantageous, are often useful taxonomic characters. This is true of the form of the vertical component in tail movements and type of head scratching movement.

Comparison of "likes" between species must be done when individuals are similarly motivated. Thus, only the highest intensities of particular behavior patterns should be compared and the behaviors should be studied in similar contexts. Comparisons should, of course, be made during the same stages of the life cycle.

*The use of behavioral clues in reconstructing evolution.*—The retention of characteristics which seem to be primitive may give clues to the origin of a group. For example, some wood warblers nest low (but feed higher), sing flight songs in the forest, and have distraction displays. These behavioral patterns are characteristic of ground-adapted species and suggest that parulids may have originated from such a group (Ficken and Ficken, 1962a). Retention of apparently "useless" characters may indicate the recency of an adaptation; for example, the eggs of the hole-nesting Prothonotary Warbler (*Protonotaria citrea*) are heavily spotted.

Within a species there are two types of rare behavior. Some are found in all or almost all individuals but occur only with unusual or supernormal stimulus situations. Others are found in only a small part of the population but are not dependent on unusual stimuli. If they are common in closely related species it is highly probable that they were also at one time of more frequent occurrence in the species in question. Likewise, if a particular rare display is complex, it is also very likely that it was once more common. It is usually impossible to know whether such behaviors are being selected for or against, but they conceivably could be important to the future evolution of the group.

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