

CHAPTER 9

DESCRIPTION OF BIRD BEHAVIOR FOR COMPARATIVE PURPOSES

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1. INTRODUCTION

Ethology arose as a discipline within zoology, with distinctly different aims and methods from psychology (Tinbergen, 1963). From its inception, ethology embraced phylogenesis, inheritance, "survival value," and adaptation—research areas that relied on comparative observations and inductive reasoning (Darwin, 1859, 1872). Our understanding of animal behavior has increased through many fine descriptive studies and because ethology has become more rigorous, quantitative, experimental, and interdisciplinary. Ethology needs a richness of research philosophies and approaches because animal behavior, however it is viewed or defined, is complex, dynamic, and influenced by many internal and external factors with enormously diverse time courses. A comprehensive understanding of behavioral attributes of bird feeding, for example, demands knowledge of motor patterns, feeding mechanisms, diet, development, sensory biology, behavioral ecology, food choice, functional morphology, and other subjects. At the other extreme, progress toward understanding broad transspecific behavioral trends, or toward better standardized descriptive methods in ethology,

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depends on a knowledge of diverse taxa (Schleidt *et al.*, 1984; Leonard and Lukowiak, 1984).

Interdisciplinary approaches across a wide range of taxa are important for the development of general ethological principles (e.g., Hailman, 1977a; Brent, 1984), but most workaday progress depends on conceptually focused research on specific taxa (Van der Steen and Ter Maat, 1979). Because of this, and because "almost anything written in ethology has some relation to evolution or to comparison among species" (Hailman, 1976:993), it is necessary to restrict any discussion of comparative behavioral studies. In this chapter I emphasize areas I think are neglected, particularly important, or timely. These areas include behavioral "structure," description, quantification, and analysis. Good, repeatable descriptions are essential for the comparative study of behavior, particularly for research on adaptation, phylogeny, and behavioral ecology. Descriptions are acutely needed for many avian taxa, because opportunities for studying their behavior in a natural context are dwindling, and many species face extinction. This situation, coupled with the difficulty in publishing extensive descriptive material, also makes it important to standardize protocols for behavioral description and to establish repositories for ethological data.

2. DESCRIPTION OF BEHAVIOR

Our view of behavior depends on how we describe it, which depends in turn on the purposes of our description and on our theoretical or conceptual assumptions (Tinbergen, 1963; Golani, 1976; Drummond, 1981). A study's purposes and assumptions are themselves closely related. It is therefore difficult to treat behavioral structure and description separately, particularly at higher levels of integration (e.g., social system). In this section I emphasize the description of motor patterns, since they are the major focus in studies on the causation and control of behavior, they provide clear examples of homoplasy, they can be readily described quantitatively, and they are the starting point for descriptions in most observational and comparative studies. The relevance of behavioral structure to an understanding of behavior is highly variable; at one extreme, behavioral structure can be irrelevant, and only consequences of behavior are of interest (McKearney, 1977; Van der Steen and Ter Maat, 1979). However, all kinds of behavior involve postures or movements, and problems with describing motor patterns characterize many general problems with behavioral description and so serve as a useful vehicle for discussion.

2.1. Descriptive Frames of Reference

The frame of reference is a vital component of almost any description, regardless of its purpose. Golani (1976) suggested that there are three basic frames of reference, that postures and movements can be described with reference to an animal's own body, to the environment, or to a social partner. In a different formulation, Drummond (1981:6) distinguished five "domains" for behavioral description: "location of the animal in relation to its environment, orientation of the animal to the environment, physical topography of the animal, intrinsic properties of the animal, and physical effects induced in the environment." These two outlines overlap and suggest several general frames of reference for describing motor patterns:

2.1.1. Absolute and Bodywise Frames of Reference (Fig. 1)

Description of the body, limbs, plumage, air sacs, etc. is done with reference to the general environment (usually taken as a level surface) to other body parts, or to both. Few descriptions refer only to an absolute or bodywise frame of reference. Wilson (1974) estimated neck, trunk, and tail angles of the Red Jungle Fowl (*Gallus gallus*) relative to the horizontal in studying agonistic behavior, and Oehme (1985) estimated wing angles and distances relative to body parts in a study of bird flight. However, records of the three angles of individual Red Jungle Fowl could be transformed so that relations among body parts were described, and Oehme's descriptions are of level flight, thus implying reference to gravity. Most descriptions in this category refer jointly to relationships among body parts and to the horizontal, though the latter is often just implied.

2.1.2. Reference to Specific Stationary or Fixed Features of the Environment (Fig. 2A)

Many descriptions refer to or imply behavior with respect to stationary, unresponsive, or fixed features of the environment, usually physical features. When displaying to perched females, male Anna's Hummingbirds (*Calypte anna*) orient to the sun so that they reflect sunlight from their iridescent throats toward the female (Hamilton, 1965), and male weavers (*Ploceus vitellinus*) adopt specific postures relative to the nest during nuptial displays (Crook, 1964). Most descriptions of this sort refer to easily identified single features close to a bird such as eggs, sessile food items, or shelter.

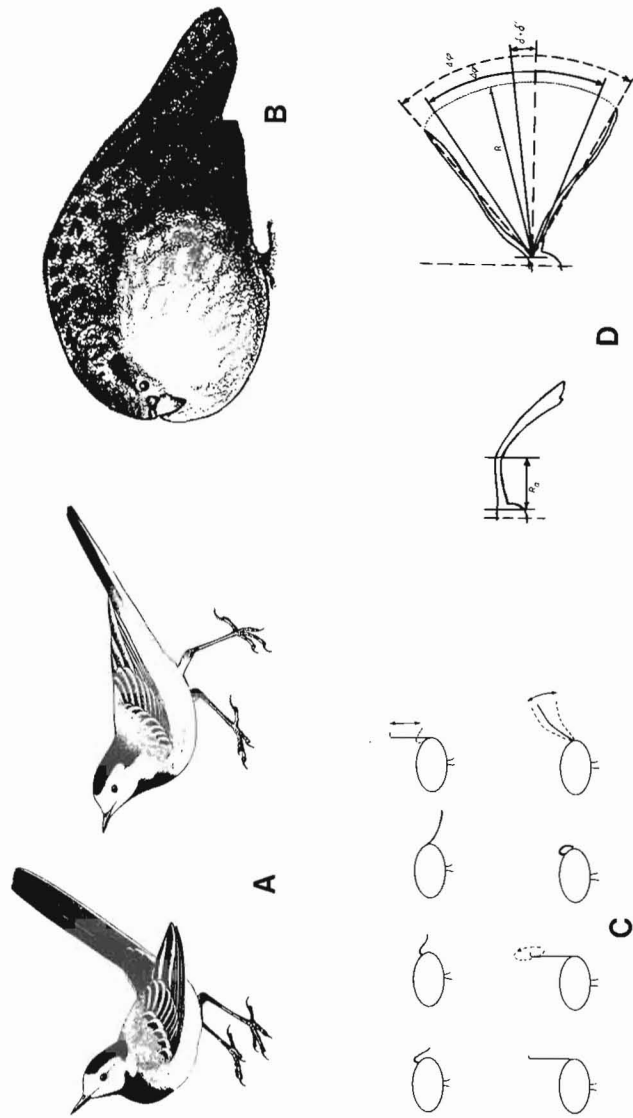


FIGURE 1. The concept of frame of reference in behavioral description (part I). Behavior with reference to the actor's own body or body parts in (A) White Wagtail (*Motacilla alba*), (B) Kakapo (*Strigops habroptilus*), (C) Canada Goose (*Branta canadensis*), and (D) Black-headed Gull (*Larus ridibundus*). From Fig. 1 of Zahavi (1971), Fig. 4 of Merton et al. (1984), Fig. 1 of Radesater (1974), and Fig. 7 of Oehme (1985).

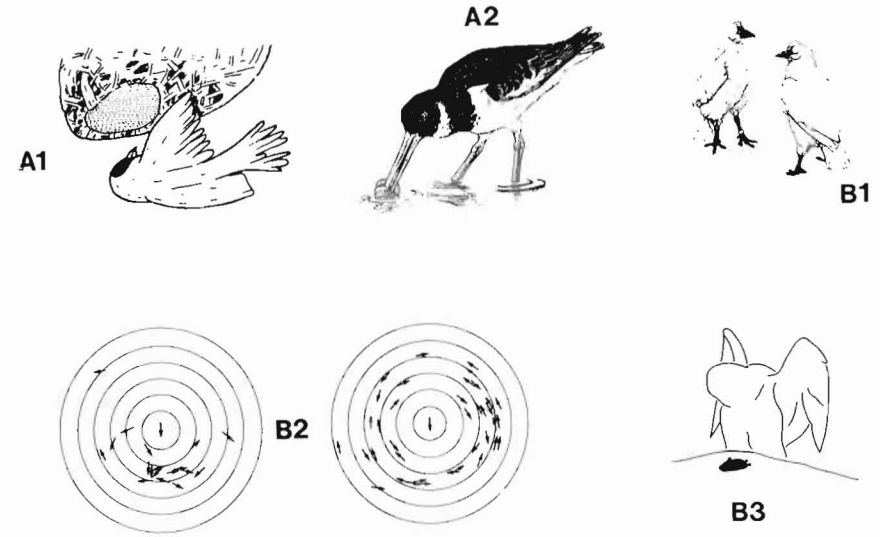


FIGURE 2. The concept of frame of reference in behavioral description (part II). (A) Behavior with reference to stationary environmental features in the weaver *Ploceus vittellinus* (A1) and European Oystercatcher (*Haematopus ostralegus*) (A2). (From Fig. 11 of Crook (1964) and Fig. 7 of Glutz et al. (1977).) (B) Behavior with reference to nonstationary environmental features in the Lesser Sheathbill (*Chionis minor*) (B1), Green-winged Teal (*Anas crecca*) (B2), and Snowy Owl (*Nyctea scandiaca*) (B3). The male sheathbills are displaying at one another during a pause in their fight, and are exposing their carpal spurs. The diagrams for the teal depict the orientation of males during two kinds of displays; the male's positions are shown in concentric rings (at 1-ft intervals) around a female (represented by a central arrow). The male owl is looking back at a female while hiding a lemming from her view (visible in front of the male) (see text). From Fig. 4 of Miller (1984, after Burger, 1980), Fig. 16.1 of McKinney (1975), and Fig. 11 of Taylor (1973).

2.1.3. Reference to Nonstationary Features (especially biotic features) (Fig. 2B)

Nonstationary features include minor ones, such as a moving branch on which a bird tries to land, plus major ones, like interacting social partners, predators, or mobile prey. Because of the importance of social interactions in this general category, Golani (1976) referred specifically to a "partnerwise" frame of reference in description. The main distinction of this class from that described in Section 2.1.2 above is the movement and responsiveness of the environmental feature referred to.

For example, birds adjust and respond to one another dynamically during social interactions, and the interaction itself has emergent characteristics beyond the interactants' behavior. A courting male may continually adjust his orientation and distance to a moving female, who may be seeking a different orientation to the male or a greater distance from him (Fig. 2B). In interactions such as fighting, or responding to a predator or dangerous prey individual, a bird's specific motor patterns and orientation to other aspects of the environment may be subsidiary to the most important feature: maintaining a particular distance and orientation to the interactant. Fighting birds may assume a great variety of postures, use wings or feet to balance, lie on their sides or stand upright, etc. to maintain a particular defensive orientation. In such cases it is important to include description of the interaction itself and the orientation of the interactants, not just isolated behavior of individuals (Golani, 1976). Hailman (1977a,b) provides many relevant examples of orientation and design features of optical signals in birds.

Many or most behavioral situations demand more than one frame of reference in a description. Examples are male Anna's Hummingbirds orienting to both sun and female, parent birds attempting to divert predators from the vicinity of a nest or brood, and male Snowy Owls (*Nyctea scandiaca*) looking back at the female during ground courtship while concealing a food item such as a lemming (used in the display) from her view (Fig. 2B) (Taylor, 1973). Frames of reference that are appropriate for a behavioral description may also span different levels of integration. For example, large flocks of Sandhill Cranes (*Grus canadensis*) seem to comprise smaller, well-coordinated groups structured on individual distances (Miller and Stephen, 1964), so descriptions of spacing should include distance and orientation among these subgroups as well as among individuals.

The choice of descriptive frames of reference must be made with the study's purposes in mind. General comprehensive descriptions ("ethograms"), however, must anticipate a variety of uses by other workers; they should include extensive, detailed, and quantitative information about orientation, distances, and dynamics of behavior for all frames of reference an observer judges to be relevant. To decide on them demands judgment about the relative importance of environmental features, and this is both impossible to avoid and desirable, in any case, since the observer is in the best position to judge the possible significance of what he or she is observing. Observers should bear in mind that the effects or importance of behavior may be short- or long-term, or both, and that the patterning of behavior may be very subtle, so the choice of frames of reference should be liberal.

2.2. Behavioral Units and Categories

2.2.1. General Comments

The concept of a "unit character" has been useful in taxonomy, morphology, phenetics, and other fields, but the concept remains pragmatic and operational, without a "natural" basis (Sneath and Sokal, 1973). The notion of a species-specific unit of behavior was proposed by C. O. Whitman and was developed and propounded by Konrad Lorenz (Schleidt, 1974). The concept has changed since Lorenz's formulation but retains both a key characteristic (stereotypy) and the assumption of being genetically determined (Schleidt, 1974; Dawkins, 1983, 1986). Stereotypy characterizes both the form of each element in a "fixed action pattern" (FAP) and their sequence (Barlow, 1968). The concept of the FAP has furthered our understanding of behavioral causation, behavioral evolution, the use of behavioral attributes in phylogenetic inference, and behavior genetics (Moltz, 1965). However, it has focused attention on discrete motor acts or groups of acts and has thereby diverted attention from the description and recognition of elementary motor patterns. In this section I discuss some basic approaches to the quantitative description of motor patterns, point out the dependence of descriptions on reasons for making them, and conclude that "natural" units are as elusive in ethology as in taxonomy.

An early step in describing motor patterns is breaking down an animal's stream of behavior into parts that can be described, counted, and measured. In practice, gross muscular contractions set the limit of resolution (for ethologists, "the muscle is a convenient statistical averaging device": Dawkins and Dawkins, 1974:120). Behavioral categories that are established on structural criteria should often be validated by finer analysis (Barlow, 1968; see Bond *et al.*, 1985). One way to do this is to describe components quantitatively and search for modes that may suggest that finer subdivision is necessary. As an example consider the Wing-lifting display of male Eastern Bluebirds (*Sialia sialis*) toward females (Fig. 3A):

The wing is lifted away and up from the body in a vertical plane. Depending on the intensity, the wing can remain folded or be unfolded as it is rapidly lifted above the back then back to the side. When highly motivated the display appears almost as a "blur"; low intensity Wing-lifting may be just a quiver with the wing hardly leaving the supporting feathers or a frequent jerk of the wing up to the level of the back (Krieg, 1971:81).

If we accept that Wing-lifting is a behavioral category in its own right, then we can count its occurrences, estimate its duration, and so on. We can test whether it is a single category by considering its char-

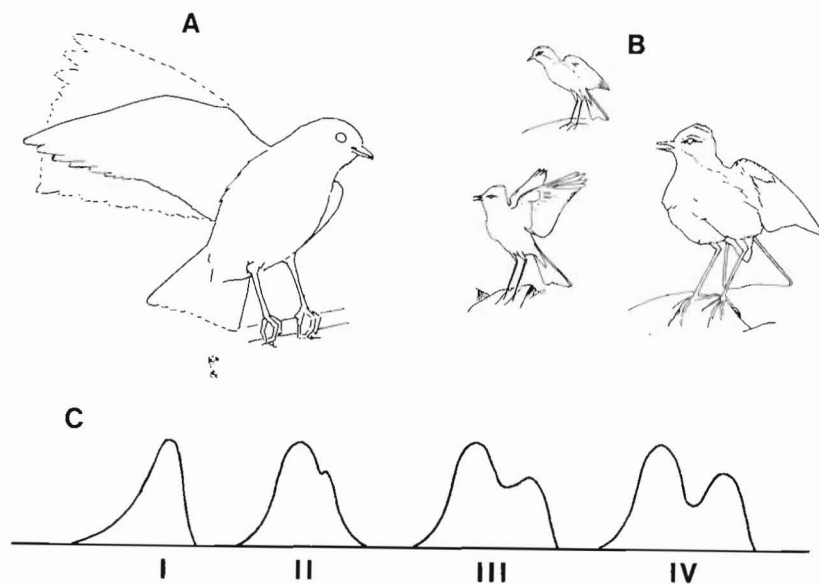


FIGURE 3. (A) Wing-lifting display of male Eastern Bluebird (*Sialia sialis*). From Fig. 28 of Krieg (1971). (B) Variants of wing raising in the ground tyrant *Muscisaxicola albilora*. From Fig. 3 of Smith (1971). (C) Frequency distributions of height of wingtip in wing-lifting display of the Eastern Bluebird, illustrating hypothetical situations ranging from clear unimodality (I) to clear bimodality (IV) (see text for discussion).

acteristics in greater detail. A frequency distribution of durations may reveal modes, for example, as also might one of height of wingtip as estimated from random samples on movie film (Fig. 3C). If the wingtip is raised smoothly to a certain point, where it remains until lowered, then a negatively skewed unimodal curve will result, suggesting one display mode (Fig. 3C-I; note the importance here of how the behavior is sampled: if wingtip height is estimated only for stationary phases, instead of for random spot samples, the frequency distribution might just be a normal curve without skew). But if many displays occur with intermediate values, then the frequency distribution can assume various forms (Fig. 3C II, III). Whether we then establish subdivisions of a single category or several different categories depends on the study's purposes and other kinds of information. In a purely descriptive quantitative analysis, there is no basis for judging whether or not modes are "real," because there is no theoretical or functional significance to the modes. At best, for the example given, we might recognize two modes on structural grounds if they seem distinct enough (e.g., Fig. 3C IV);

Todt and Fiebelkorn (1980) did this (see their Fig. 6). Even here, we must be cautious, however, because sampling biases and different frequencies of occurrence of behavioral acts affect the results. Say that one of two modes is oversampled, perhaps because we can film male bluebirds in one context more easily than in another; alternatively, two modes may occur naturally at very different frequencies. In either case, we may obtain frequency distributions like those in Figure 3C II or III, where the two modes are not distinct. The only way to make sense out of such frequency distributions is with other information.

Several other kinds of information intrinsic to motor patterns are generally available. In the example developed above, Wing-lifting was considered to have several characters, such as temporal duration and height of wingtip, each with a continuous range of states. What is considered to be a character or a state depends on our level of description; at a coarser level of description, Wing-lifting could be a state of the character "wing position," for example. Similarly, Wing-lifting could be broken down into smaller characters and character states, such as angle of the manus relative to the forearm, or angle of the wing plane relative to the body's sagittal plane. These could then be subjected to analyses one by one or together, to provide a more detailed picture of what constitutes a mode at the level of Wing-lifting (see Section 2.2.4).

Another source of information intrinsic to motor patterns lies in other variables. Van Rhijn (1981) analyzed postures of the Black-headed Gull (*Larus ridibundus*) in detail, because his group found that existing behavioral categories were inadequate. He recognized four characters and a variable number of states for each: angle of the body's long axis (3 states); wing position (4 states); neck position (5 states); and angle of the bill long axis (4 states). Together these allowed for a maximum of 240 different postures; 114 were observed. Van Rhijn took the 49 most frequent of these postures and described other properties of them, including frequency of occurrence, mean duration, and coefficient of variation. These properties plus the original postural characteristics were then used as variables in a cluster analysis that provided the basis for classification.

Different behavioral components occurring simultaneously with Wing-lifting can also be included in the analysis. For the Wing-raising display of the ground tyrant *Muscisaxicola albilora*, for example, other components could include head position, wing fluttering, ruffling of plumage, and tail spreading (Smith, 1971) (Fig. 3B). They could also include many attributes that are difficult to describe quantitatively, such as change in color of soft parts or in pupil size. Extreme situations are those in which components or subcomponents vary closely in par-

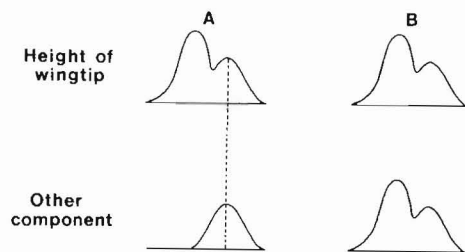


FIGURE 4. Hypothetical frequency distributions of height of wingtip in wing raising of the ground tyrant *Muscisaxicola albilora*, where another behavioral component occurs simultaneously only with the minor mode (A) or varies in parallel (B) (see Fig. 3B). The situation depicted in A suggests that two modes should be distinguished; that in B does not.

allel, or where (sub)components are independent of one another; most situations will fall in between. If combinations differ qualitatively among the putative modes, then it seems warranted to recognize them as distinct (Fig. 4A). An example is Facing-away in Laughing Gulls (*Larus atricilla*), which is superimposed on a variety of postures. This display (or display component) exhibits two distinct modes with few intermediates: White Facing-away, in which the lateral margins of the hood are nearly vertical, and Black Facing-away, in which they are nearly horizontal (Fig. 5) (Beer, 1980). In general, if (sub)components are uncorrelated or only weakly correlated with one another, this is good evidence for recognizing modes (Barlow, 1968; Wiley, 1975). If (sub)components are closely correlated, then we have no more evidence

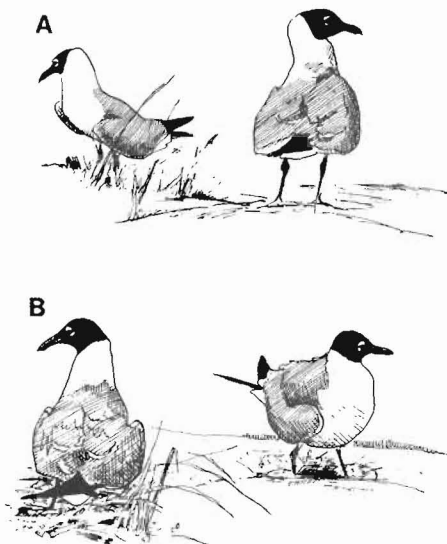


FIGURE 5. Facing-away in the Laughing Gull (*Larus atricilla*). (A) White facing-away. (B) Black facing-away. From Fig. 3 of Beer (1980).

for erecting new categories or subcategories than was present from the univariate frequency distribution (Fig. 4B).

Information extrinsic to motor patterns of interest is also used commonly. In Van Rhijn's (1981) study, for example, information about the seasonal occurrence of postural classes provided one of the variables used in cluster analysis. Clumping and allopreening behavior of the Red Avadavat (*Amandava amandava*) are influenced by nonbehavioral factors including individual preference, gender, reproductive state, and plumage (eclipse or nuptial) (Sparks, 1964). Wiley (1975) validated the communicative significance of structural modes in the Song-spread of male Carib Grackles (*Quiscalus lugubris*) by considering context: beak and wing elevation varied independently of one another according to whether a display's recipient was a male or a female and whether the display was "spontaneous" (no obvious recipient within 1 m).

In studies of communication, relevant extrinsic information generally includes social characteristics of senders and receivers, distance and orientation to receivers, receiver behavior, and functional significance of the context (e.g., threat, courtship). An example of the importance of context comes from Lind's (1961) analysis of agonistic ground encounters in the Black-tailed Godwit (*Limosa limosa*). Several postures (Upright-I, Forward, Crouch, and Tail-up) occurred in contexts of both attack and retreat, but their components such as plumage ruffling and tail lowering/spreading differed among contexts. For example, the dorsal plumage was ruffled in Upright-I postures in 14% of an Attack context but 5% of Retreat. In contrast, ruffling occurred in Crouch postures in 52% of Attack and 100% of Retreat contexts (Table 3 of Lind, 1961; see Table II of Miller, 1984). Few studies are as detailed as Lind's, but contextual variables should clearly be considered whenever possible in erecting behavioral categories.

In the preceding discussion I have discussed mainly structural features of single postural components to point out the need for microbehavioral analysis in many studies and to make some suggestions about how to do it. Questions about how many categories to recognize and whether to recognize particular structural variants as behavioral categories depend completely on a study's purposes. Thus, a study on the causation or taxonomic significance of preening behavior will recognize many categories (e.g., Van Iersel and Bol, 1958; McKinney, 1965; McFarland and Baher, 1968; Potts, 1976), whereas studies on time, activity, or energy budgets are likely to recognize few or even none (e.g., Wolf and Hainsworth, 1971; Walsberg, 1978; Afton, 1979; Pinkowski, 1979). Furthermore, studies that recognize the same behavioral categories will often attribute different meanings to them: resting in a

conspicuous location may be considered as static-optical advertising in a study on communication, as resting in a study on behavioral energetics, or as behavior with a high risk factor in a study on vigilance in parental behavior (see Miller, 1984). In erecting categories, behavior should be described and characterized rigorously, but this does not lead automatically to natural categories. There are many kinds of "natural" categories that depend on questions of interest and that reflect the fact that, functionally, birds rarely do just one thing at a time.

2.2.2. Description of Movements

In the preceding section I stressed the need to quantitatively assess the boundaries of behavioral categories using both intrinsic and extrinsic information. In this section I focus specifically on describing movements.

Profiles of simple movements over time are a good starting point for discussing how units of behavior can be distinguished temporally. Zweers's (1974, 1982) detailed studies on feeding in the Mallard (*Anas platyrhynchos*) and Rock Dove (*Columba livia*) are a good example of this kind of approach. He restricted his observations to a clearly defined functional context, and attached or implanted markers on the head and recorded their locations using high-speed cinematography and radiography (Fig. 6). Zweers used the time profiles as a major source of information about the structure and integration of behavioral components involved in feeding. For the Rock Dove, he recognized four temporal components between visual fixation on a food item, grasping, catching at the rictal level, positioning along the caudal palate, and arrival of food at the esophagus (Zweers, 1982). Each of the components was fairly inflexible once begun, and variation in pecking therefore arose mainly from variation between the components.

A study along similar lines is the analysis of drinking in chicks of *Gallus domesticus* by Dawkins and Dawkins (1973). Using film analysis, they plotted the vertical position of the chick's head (estimated by height of eye above the cage floor) against time, in studying the organization of the drinking act. The height-time profiles showed that the predictability of head movement depended on position in a drinking sequence: after drinking and beginning to raise the head, for example, it was extremely likely that a chick would continue to raise its head; behavior was much less predictable when the head was fully erect (Fig. 7). Experimental manipulations of water depth, temperature, and palatability revealed that some parts of the drinking sequence were modifiable and some were much less so (Dawkins and Dawkins, 1974). The

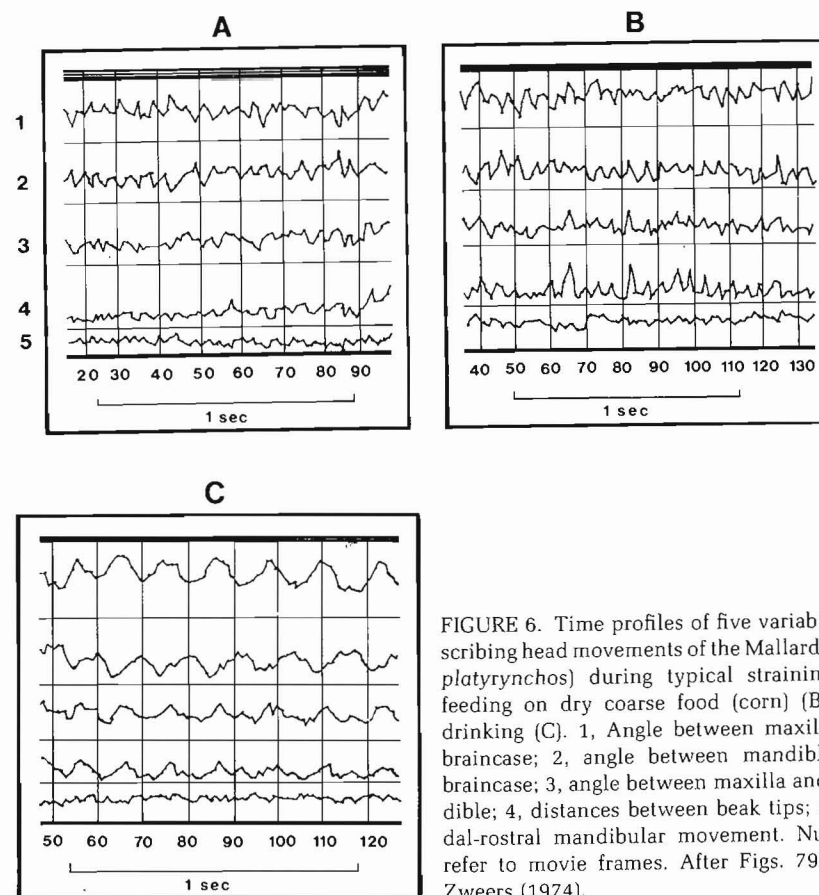


FIGURE 6. Time profiles of five variables describing head movements of the Mallard (*Anas platyrhynchos*) during typical straining (A), feeding on dry coarse food (corn) (B), and drinking (C). 1, Angle between maxilla and braincase; 2, angle between mandible and braincase; 3, angle between maxilla and mandible; 4, distances between beak tips; 5, caudal-rostral mandibular movement. Numbers refer to movie frames. After Figs. 79–81 of Zweers (1974).

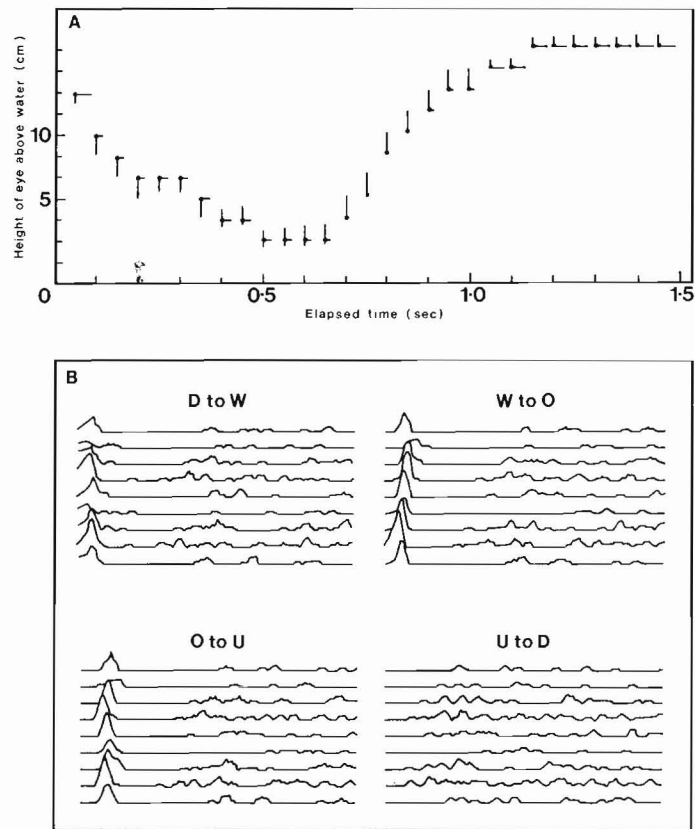


FIGURE 7. (A) Diagrammatic representation of the predictability of chick (*Gallus domesticus*) behavior in a drinking sequence. The direction in which the lines point represents the direction in which movement is likely; the length of the lines is proportional to the probability of movement in the directions shown. For example, following a drink (beginning at 0.5 sec), it is extremely likely that the chick will raise its head continuously for about 0.3 sec. From Fig. 3.2 of Dawkins and Dawkins (1974), after Fig. 5 of Dawkins and Dawkins (1973). (B) Predictability of behavioral transitions in drinking behavior of nine chicks (abscissa, time). D, Start of downstroke; W, bill strikes water; O, bill comes out of water; U, end of upstroke. Knowing when D, W, or O occurs permits accurate prediction of other behavior, but this is not true of U. From Fig. 3.5 of Dawkins and Dawkins (1974).

modifiable parts were those with lowest predictability (times of "decision"; Fig. 7A). Thus, overall changes in a chick's rate of drinking resulted from alterations in the interdrink phase, which was the most unpredictable (Dawkins and Dawkins, 1974). This finding is similar to some of Zweers's (1982) and suggests that both studies identified meaningful behavioral units within the distinct functional contexts examined.

Higher-order temporal organization of behavior can be explored through techniques such as spectral analysis or time-series analysis, which can reveal information about periodicity of behavior, for example (Fagen and Young, 1978; see also Binkley *et al.* 1973; Dörrscheidt and Beck, 1975; Sokolove and Bushell, 1978). Such techniques can be applied to temporal profiles such as those of Zweers (see Fig. 6), but most ethological applications concern temporal sequences of recognized behavioral categories, a topic I will discuss further below (Section 2.2.3).

Fairly simple behavioral "trajectories" can be summarized in temporal profiles like those in Figures 6 and 7, but most behavior is too complex for that (e.g., Fig. 8). To summarize the temporal flow of complex behavior in the absence of recognized categories, it is necessary to identify behavioral variables and describe their changes over time, within an explicit frame of reference. Many behavioral attributes of birds can be described meaningfully in terms of their three-dimensional movements, but many cannot (e.g., changes in soft-part coloration, pupil size, plumage fluffing, erection of ear tufts). Such changes can be described and coded, however; thus Morris (1956) distinguished Sleeked, Relaxed, Fluffed, and Ruffled states of plumage. Movements of body parts can be described within chosen frames of reference. In communication, at least two frames of reference are generally needed (body-wise and partnerwise).

A comprehensive system proposed for describing mammalian motor patterns is the Eshkol-Wachman (EW) movement notation (Golani, 1976), and this could be modified for use with birds. The technique relies on cinematographic (or videotape) analysis and begins with the recognition of serially connected "limb" segments. In a bodywise frame of reference, the movement of the distal end of a limb segment is described with reference to its proximal end. Thus, the movement of a bird's wrist joint would be described relative to the elbow, movements of which would be described relative to the shoulder. If one envisages the proximal joint at the center of a sphere, then movement of the limb segment's distal end describes a trajectory on the surface of a sphere (Fig. 9A). The time course of this trajectory provides a remarkably complete description of movement. In practice, the imaginary sphere

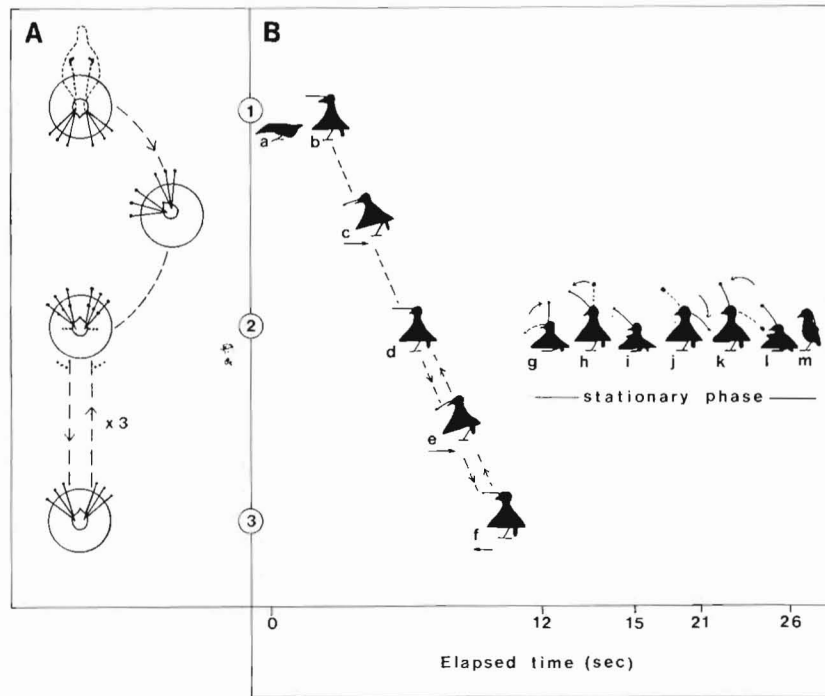


FIGURE 8. High-intensity courtship display of Lawes's Parotia (*Parotia lawesii*) to illustrate the richness and complexity of behavior before it is broken up into categories for purposes of analysis. (A) Positions of displaying male from the initial display-bob (dotted figure) at point 1, through the semicircular dance at point 2, and the back-forward dance between points 2 and 3, to remain at point 2 for the stationary phase. Various positions of the occipital plumes are indicated for point 2. (B) Silhouettes of displaying male corresponding to positions in the left panel. Arrows below silhouettes indicate male's direction of movement. Movements of occipital plumes are from dotted line to solid line. After Fig. 1 of Frith and Frith (1981).

must have a coordinate system superimposed upon it, so that estimates of position can be made (Fig. 9B). The actual recording of data using the EW system is a linear record of locations of ends of limb segments at fixed time intervals; many other kinds of information, such as form of movement between positions, may be included (Golani, 1976). One important kind of information for bird behavior concerns rotatory movements; a bird may rotate a "limb" segment (e.g., head) without altering any spatial relationships. This would be important to code.

The EW system holds promise for summarizing some of the richness of avian motor patterns and may be particularly useful if applied

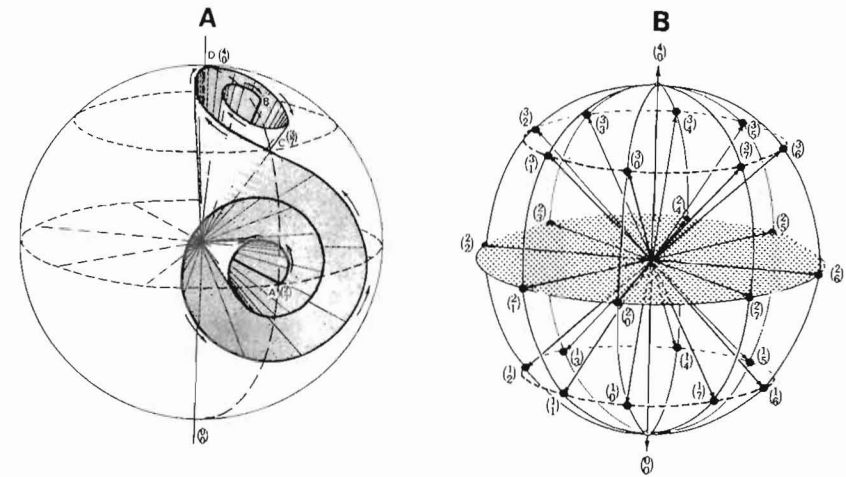


FIGURE 9. (A) Movement of the distal end of a limb segment relative to its proximal end. The latter is at the center of an imaginary sphere; the limb segment's distal end moves, describing a complex pattern on the sphere's surface, from A through C and D, ending at B (numbers are coordinates). (B) The Eshkol-Wachmann coordinate system, shown for basic units of movement of 45°. "Movement" is thus operationally defined as none (within 22.5°), 1 unit (within the range 22.5-67.5°), and so on, with this system. From Figs. 2 and 3 of Golani (1976).

to wing, tail, and head movements. In more traditional kinds of description, movements are typically described in terms of gross directional changes or transitions two-dimensionally and with only a coarse time frame at best (Fig. 10). Such descriptions are invaluable summaries and facilitate comparative studies, but they fail to portray the spatiotemporal richness of avian motor acts and cannot reveal spatiotemporal patterning or regularities.

2.2.3. Description of Sequences

Most descriptions and analyses of behavioral sequences are restricted to the temporal dimension and rely on discrete, nonoverlapping behavioral categories (for general discussions, see Hinde and Stevenson, 1969; Slater, 1973; Lehner, 1979; and Fagen and Young, 1978). Analysis of sequences is strongly affected by characteristics of a behavioral category and how it is recorded. A very simple situation is one in which a behavioral category is distinctive, the behavior varies little in form within or between repetitions, other kinds of behavior can be ignored, and the behavior is brief relative to intervals between

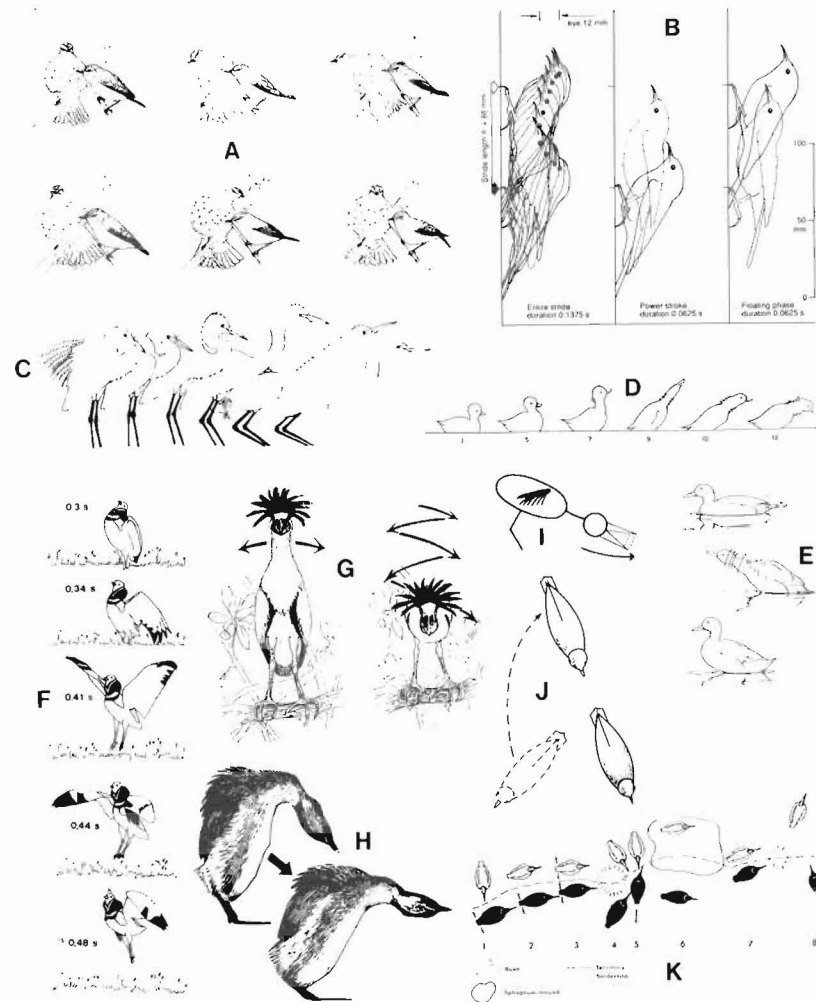


FIGURE 10. Examples of graphic portrayal of movements. (A) Sequential postures using sketches, with no time base (swaying display of male to female Red-eyed Vireo, *Vireo olivaceus*). From Fig. 4 of Barlow and Rice (1977). (B) Sequential postures and positions using superimposed outlines, at 1/80-sec intervals (left); the central and right sketches show beginning and end of particular phases (climbing by Brown Creeper, *Certhia familiaris*). From Fig. 2 of Norberg (1986). (C) Sequential postures using partly overlapping sketches, at 1/6-sec intervals (stab-crouch by Great Egret, *Casmerodius albus*). From Fig. 11 of Mock (1978). (D) Sequential postures using nonoverlapping outlines, with movie frame numbers indicated (film speed, 16 frames per second) (Shake by Chilean Teal, *Anas flavirostris*). From Fig. 1 of Standen (1980). (E) Sequential postures using sketches, with no time base; rotatory movement of the head and neck is indicated in the middle sketch (swimming-shake by Mallard). From Fig. 3 of McKinney (1965). (F) Sequential postures using sketches, with time base (leaping display by Little Bustard, *Tetrax tetrax*). From Fig. 25 of Schulz (1986). (G) Head-and-neck movements (both sketches) and body

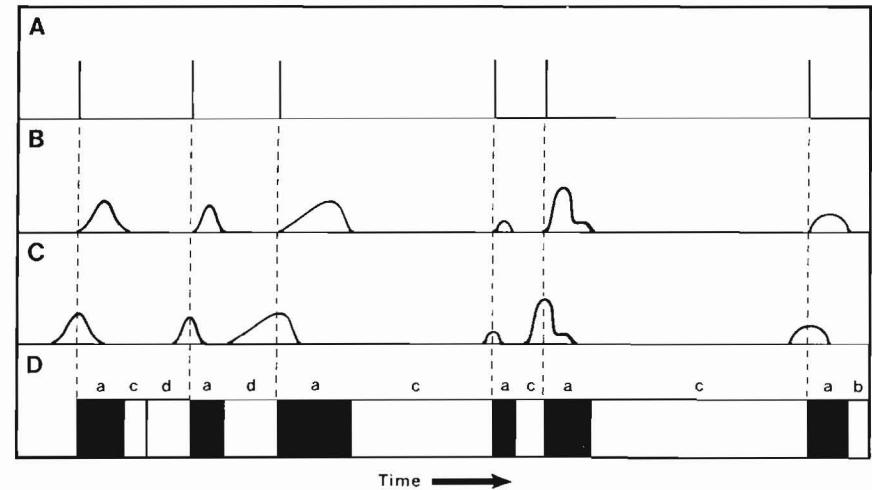


FIGURE 11. Simple sequence of point events with no intervening behavior (A). Data can be put in a similar form in various ways, for example, by noting the onset (B) or peak intensity (C) of each behavioral event or by noting onset of each occurrence of a while ignoring intervening events b, c, d (D).

its recurrence (in many applications the behavior is considered to be a point event, but Heiligenberg (1974) points out that behavioral categories that vary little in duration are also useful). A sequence of pecks by a bird doing nothing else of consequence is an example (Caraco, 1982). One can force any behavioral sequence to assume that form, of course—for example, by noting only a behavior's onset, termination, or peak intensity, and by ignoring all intervening behavior (Fig. 11). However one arrives at that form, the data can be analyzed to assess

FIGURE 10 (continued). movements (right) using sketches plus arrows (erect and bowing forms of tail rocking by Boat-billed Heron, *Cochlearius cochlearius*). From Fig. 9 of Mock (1975). (H) Sequential postures using sketches, with no time base (rearing display during platform courtship by Hoary-headed Grebe, *Poliiocephalus poliocephalus*). From Fig. 7 of Fjeldsa (1983). (I) Head, neck, and bill movements using diagram, arrow, and dashed lines (indicating rapidly repeated bill clattering) (balancing posture by Lesser Adjutant Stork, *Leptoptilos javanicus*). From p. 104 of Kahl (1972). (J) Sequential positions, distances, and orientation of birds to one another using diagram and arrow (male spin during precopulatory display of the Sociable Plover, *Pluvianellus socialis*). From Fig. 10 of Jehl (1975). (K) Sequential positions, distances, and orientation of birds to one another and to territorial boundary plus natural features, using diagram; wing-and-tail plus repeated whole-body movements are indicated by arrows (parallel running in Great Snipe, *Galvanago media*). From Fig. 9 of Lemnell (1978).

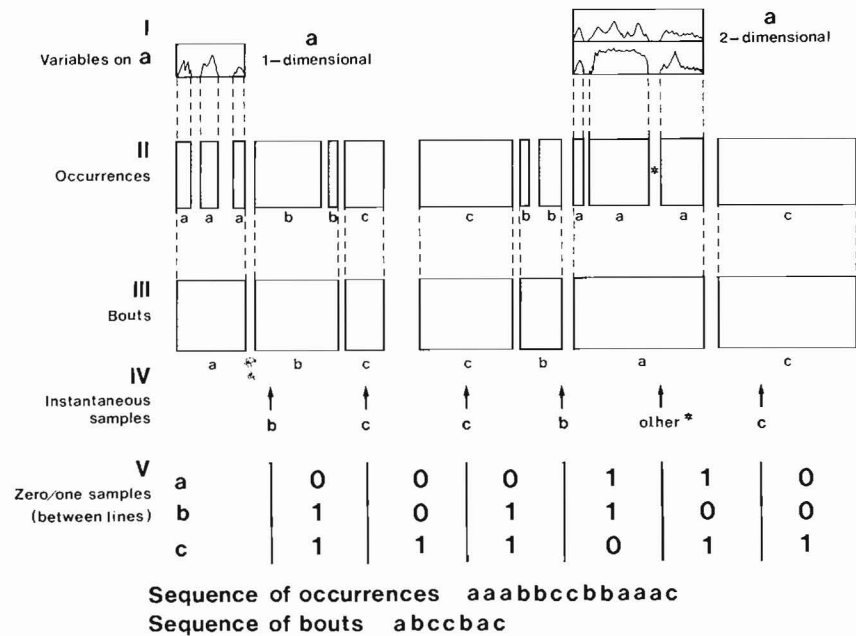


FIGURE 12. Some ways to record or describe behavioral data. Three behavioral categories are distinguished (a, b, c). At the top (I) are shown hypothetical time plots of variables where a is one- or two-dimensional. Below are shown the observed sequence broken into occurrences (II) and with occurrences lumped into bouts (III). The consecutive occurrences of c were judged to be too far apart to be within a single bout. The upward-pointing arrows indicate equally spaced times of instantaneous samples (IV); note that the spot sample between the last two occurrences of a (marked by an asterisk) could be recorded as "other," even though it is within the bout of a. The 1/0 sample scores for a, b, and c are noted between those times (V). After Fig. 1 of Slater (1978).

whether behavior has temporal structure—e.g., if there is some periodicity in behavior, or whether behavior occurs in bouts or at random.

Various techniques exist for quantifying or detecting periodicity of behavioral events (e.g., Binkley *et al.*, 1973; Dörrscheidt and Beck, 1975; Sokolove and Bushell, 1978). Van der Kloot and Morse (1975) analyzed display sequences of the Red-breasted Merganser (*Mergus serrator*) and found strong periodicity in the occurrence of one display (Salute-curtseys) but not another (Head-flicks) within individual sequences (see also Fagen and Young, 1978). Such analyses can test the extent to which a behavioral occurrence is correlated with subsequent occurrences after chosen time intervals, or lags. The measure of "occurrence" can be a behavior's presence or count within a sample period or can be the level of a chosen variable; alternatively, the intervals

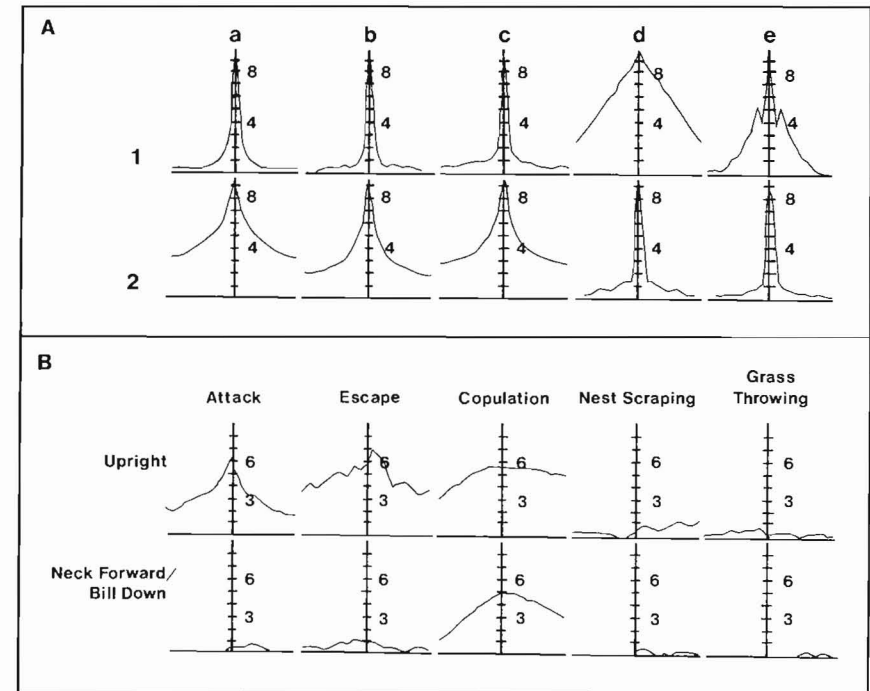


FIGURE 13. Association functions for behaviors of the Great Skua (*Catharacta skua*) over ± 10 consecutive 10-sec sample periods. A: Autoassociation functions for 1a, Attack; 1b, Escape; 1c, Nest Scraping; 1d, Copulation; 1e, Genital Contact; 2a, Upright; 2b, Neck Forward/Bill Down; 2c, Neck Straight/Bill Strait; 2d, Neck Backward/Bill Up; 2e, Oblique/Long Call/Wing-raising. B: Cross-association functions for some of the same behaviors. After Tables 3 and 1, respectively, of Andersson (1976).

between consecutive occurrences can be used (see Delius, 1969). By calculating the correlation coefficients (r) between samples at different lags, it is possible to plot r vs. lag as an autocorrelation function (for a single behavioral category) or as cross-correlation functions (for 2 different behavioral categories); r may be replaced by some other measure of association, and Andersson (1974, 1976) suggests that using presence/absence of behaviors in sample intervals alleviates the problem of r varying with the sample interval chosen (Figs. 12–14).

Analyses of time intervals between occurrences of a single kind of behavior have emphasized the temporal structure of behavior in terms of bouts (Slater, 1974a, 1975; Machlis, 1977; Fagen and Young, 1978; Slater and Lester, 1982). According to Fagen and Young (1978:91):

Intervals between behavior bouts may exhibit very different types of probability distributions, each type corresponding to a particular type of behav-

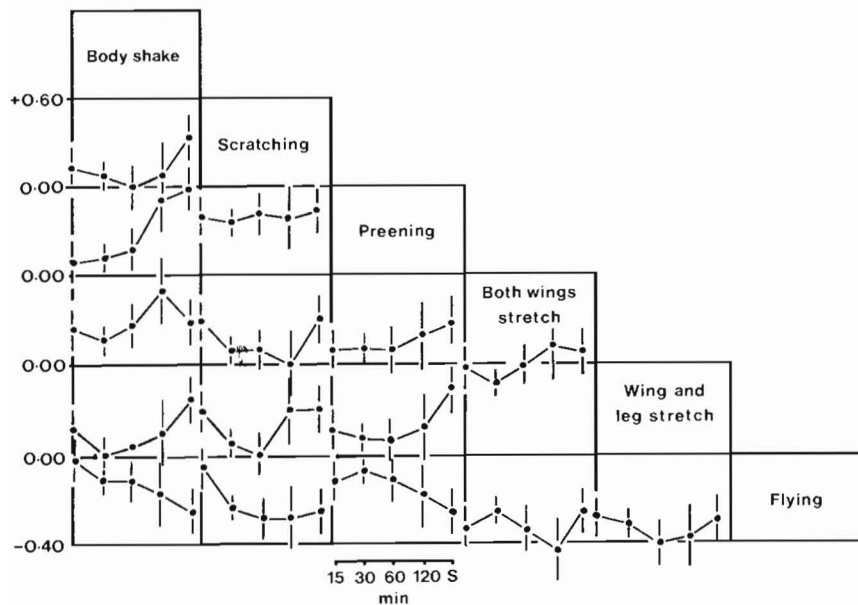


FIGURE 14. The relationship of cross-correlation estimates to duration of sample intervals during which behavioral counts were made. Spearman's r_s is the vertical scale for each cell; the five estimates of r_s for each cell were based on sample intervals of 15, 30, 60, and 120 min; "S" is for a large sample of observations on a single male, using a 90-min sample. After Fig. 16 of Delius (1969).

ioral control. . . . In some cases, the probability of a new bout starting remains constant between bouts, and the intervals are purely random; their lengths have a negative exponential distribution. In other cases, bouts of behavior are overdispersed in time. They are separated by intervals having a characteristic length.

One can treat behavioral durations in the same way, to test hypotheses about the timing of a behavior's termination with respect to its onset (Fagen and Young, 1978). A widely used technique is survivorship analysis, in which the log (number of intervals greater than t) is plotted against t , the interval duration. If a behavior's recurrence is independent of its previous occurrence, then a straight line descending from the plot's upper left to bottom right will result; this is analogous to a plot of survivorship where the probability of mortality is independent of age. Behavior that occurs in bouts shows an excess of brief intervals (Fig. 15A), whereas "overdispersed" occurrences show an excess of long intervals (Fig. 15B). The inflection points for curves like that in Figure 15A can be used to demarcate intervals between occurrences within bouts and those between bouts (see references above). The most detailed analysis along these lines to date is by Machlis (1977) on

pecking by chicks of *Gallus domesticus*. She applied several models to her observations to decompose the observed frequency distributions of interval lengths into parts that corresponded to different behavioral states. For example, one model assumed that intervals between pecks resulted from three different states and that the intervals were Poisson-generated (Fig. 15C).

As noted by Delius (1969) and Andersson (1974, 1976), the duration of a sample can influence measures of auto- and cross-association. Similarly, how an act is defined can influence results of bout analysis. Slater (1973:138) described this problem well:

Zebra finches . . . groom in sessions several minutes long, during which preening of the feathers with the bill is interrupted little by other acts, with the exception of scratching of the head. A preening bird lowers the head to a small area of the body, preens one or a few feathers, and raises the head again. The next series of preening movements is most likely to be directed to the same area of the body as the last. There are thus at least three ways of defining an act of preening:

1. The preening of a single feather, several such acts often taking place between each raising of the head.
2. The series of movements between each raising of the head, which may involve several feathers.
3. The series of movements directed to the same area of the body, which may be interrupted by several instances of head raising, depending on how an area of the body is defined.

For this example, the definition of "act" would obviously affect the results of interval analysis and the observed organization of bouts. For sequence analysis generally, it is therefore important to focus on particular questions of interest and to use behavioral categories that are internally homogeneous, distinctively different from one another, and at the same level of organization (Slater, 1973).

2.2.4. Multivariate Analysis and Behavioral Similarity

Behavior is multidimensional and has a complex "trajectory" over time, so univariate description can only be a starting point. Indeed, a series of univariate statistical analyses can provide misleading results overall (Hummel and Sligo, 1971; Willig et al., 1986). Most behavioral descriptions are inherently multivariate, and the mental process of recognizing behavioral categories uses both the multivariate nature of behavior and an assessment of similarities among categories. The process is often not explicit or formal, however. Many treatments of multivariate statistics in ethology are available (see Morgan et al., 1976; Short and Horn, 1984; Schnell and Woods, 1983; Schnell et al., 1985; Hazlett, 1977; Colgan, 1978). Here I concentrate discussion on estimating similarity.

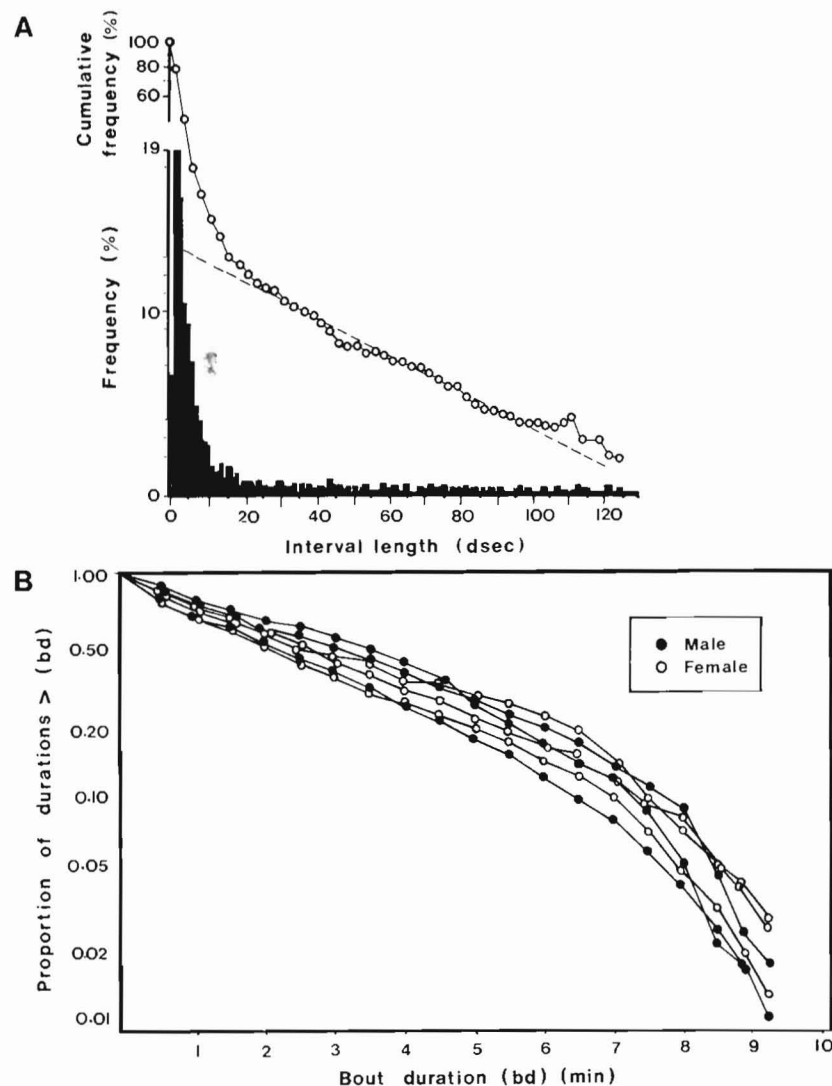


FIGURE 15. Log-survivorship plots of intervals and durations. (A) Frequency histogram and survivorship curve for intervals between pecks in a chick of *Gallus domesticus*. After Fig. 7 of Machlis (1977). (B) Survivorship curve of durations of stand-bill-over-back in six Black Oystercatchers (*Haematopus bachmani*), showing excess of long durations; the multiple lines for males and females represent different breeding stages. After Fig. 9 of Purdy (1985). (C) Illustration of a model for causation of temporal organization in pecking sequences of chick *Gallus domesticus*. Each process underlying intervals within bouts, between bouts, and between clusters has its own characteristic survivorship function. When these operate simultaneously, a composite curve resembling many empirically observed survivorship plots results. After Fig. 4 of Machlis (1977).

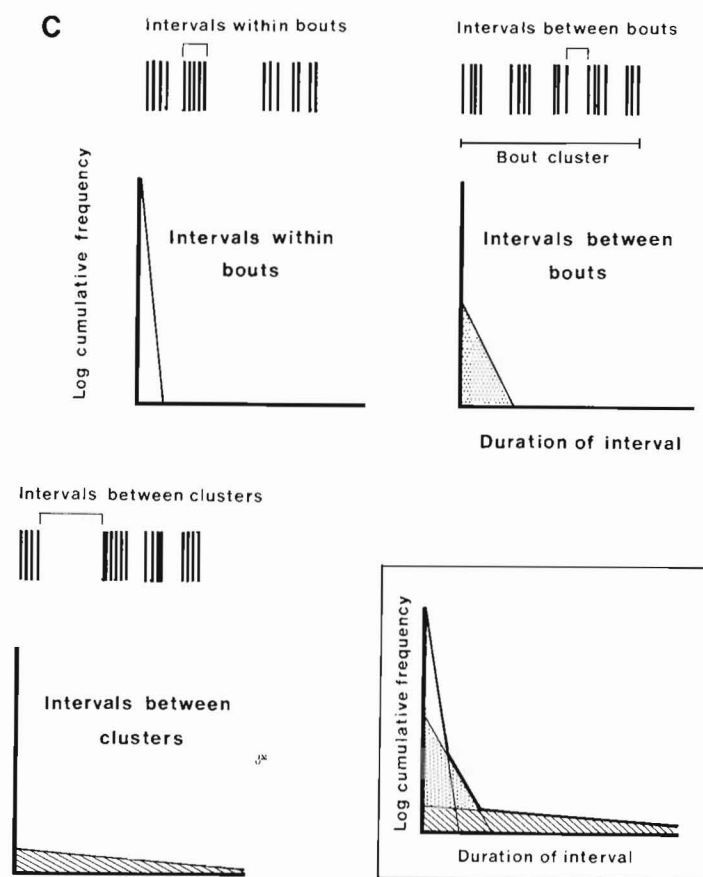


FIGURE 15. (Continued)

Information about intercorrelations of behavioral variables is needed for most multivariate analyses. It is necessary, because variables usually are intercorrelated in some way, so the erection of categories by treating variables as though they were independent is wrong or misleading. For example, if several highly correlated variables are used to distinguish categories, this is really equivalent to using just one of them (see Fig. 4). Conversely, if several uncorrelated variables are used, a lot of valuable information is lost by not considering them all. Most situations fall between these extremes and demand rigorous consideration of relationships among variables.

Relationships among behavioral variables are at the heart of a "phenetic" approach to behavioral structure, but the relationships are harder

to assess than in morphometric studies. One reason for this is that behavioral variables generally occur over only restricted ranges of behavior; outside those ranges, they assume a zero state. Height of the wingtip during Wing-raising of male Eastern Bluebirds is a good example (Fig. 3): outside the display, the wings are generally kept folded, so height would be estimated as zero. Since the same thing happens with most other components, it becomes difficult to compare behavioral categories meaningfully. In contrast, in a standard morphometric study, one takes measurements on a set of continuous variables that are generally present on all specimens. One way to deal with this problem is to restrict an ethological study to a subset of closely related behavioral categories at a similar level of organization (Slater, 1973). This is probably the sort of situation in which detailed quantitative analysis of structure is most useful anyway. Consider Figure 6, where five plots of behavioral variables are plotted over time for three feeding situations. Here one could measure the curves' height at, say, 100-msec intervals for each 1-sec sample, thus yielding 30 figures for each of the five variables. Correlations among the variables could then be computed and used as a basis for further analysis.

Another reason for the difficulty in assessing relationships among behavioral categories lies in the great number of ways to estimate behavioral similarity, paralleling a diversity of concepts and hypotheses. An equal diversity of questions are asked of morphometric data, but the form of the data proper is much less variable. For example, to assess behavioral similarity, one could use structural or contextual features, extrinsic data, or sequential relationships. Two variants of Wing-raising (A, B) could be judged to be similar purely on phenetic grounds, because they share a context, or because they are associated temporally with one another. Even temporal association can be measured in various ways: in direct transitions from A to B and vice versa, or the occurrence together of A and B in behavioral bouts or in sample intervals.

Structural similarity of behavioral categories may be important, but many studies ignore behavioral structure and analyze temporal relationships. The assumption is that behavior with common or similar underlying causation will be clumped temporally and will often be linked. Furthermore, linkage will be expressed in a high occurrence of transitions between "related" or "similar" behavioral categories. Such reasoning is probably valid to a point, but behavioral acts occurring together also share external factors that may elicit them, and they share one another's presence; thus, their association may reflect functional effects or chaining (Hinde and Stevenson, 1969; Slater, 1973, 1974b).

The notion of "similarity" needs precise definition in any ethol-

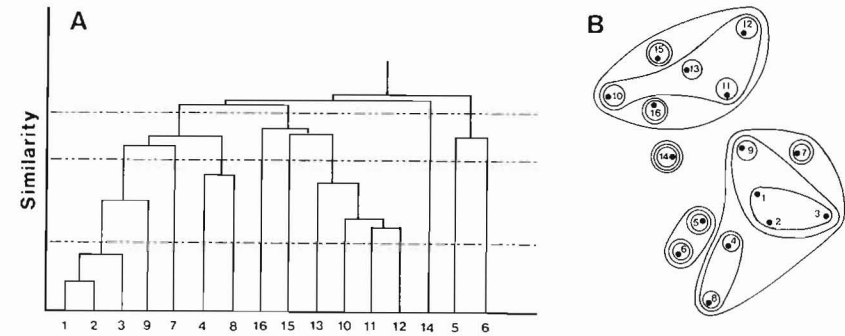


FIGURE 16. (A) Dendrogram based on a single-linkage cluster analysis of transitions among 16 behavioral categories in the Herring Gull (*Larus argentatus*). The horizontal lines mark several clusters which are distinguished in part B. (B) Two-dimensional multidimensional scaling solution for the same data. Behavioral categories are clustered according to the marks in part A. This representation is one recommended by Shepard (1974). After Figs. 16 and 17 of Morgan *et al.* (1976).

ogical study, for it closely reflects conceptual assumptions and also affects quantitative measures of similarity (Morgan *et al.*, 1976). For example, Morgan *et al.* (1976) reanalyzed data of Baerends *et al.* (1970) on incubation behavior in the Herring Gull (*Larus argentatus*). Whereas Baerends *et al.* used a complex similarity measure based on the asymmetric transition matrix of behaviors, Morgan *et al.* summed reciprocal off-diagonals, thus using all AB and BA transitions as an estimate of similarity between A and B (Fig. 16).

Some quantitative applications are particularly well suited for ethological data and concepts. Hierarchical cluster analysis is a good example. It summarizes hierarchical relationships among behavioral variables or categories, a form of relationship that seems to be relevant to behavioral control and causation (Powers, 1973; Dawkins, 1976). The technique can describe the pattern in a data set when no behavioral categories have been established (e.g., the 30 five-variable samples from Fig. 6, discussed earlier); the resulting clusters may suggest categories that can be recognized (e.g., Davies, 1978; Van Rhijn, 1981) (Fig. 16). It can also be used to summarize relationships among recognized behavioral variables or categories. Morgan *et al.* (1976) analyzed the data of Baerends *et al.* (1970) with single-linkage cluster analysis and non-metric multidimensional scaling (a robust ordination technique); their results are shown in Figure 16. Several clear clusters of behaviors are evident. Thus, "Sitting on nest" and "Looking down while sitting on nest" (1, 2) are closely linked with one another and, successively, with

“Re-settling” (3) and “Head-shaking” (9). The nest-maintenance behaviors “Picking up nest material” (5) and “Sideways nest-building” (6) are moderately linked.

In the preceding example, cluster analysis was usefully coupled with an ordination technique that highlighted the relationships among categories. The analysis was a fairly typical example of the successful use of multivariate statistics to “search for structure” in an ethological data set. It must be remembered that the techniques and options chosen must reflect the behavioral processes of interest. In hierarchical cluster analysis, for example, a data set can result in different hierarchies depending on the method of analysis chosen; yet each of the hierarchies can be biologically significant in its own right. Consider four behavioral categories that have intercorrelations of $AB = 0.3$, $AC = 0.6$, $AD = 0.6$, $BC = 0.1$, $BD = 0.7$, and $CD = 0.9$. If one chooses to form clusters beginning with the most highly correlated behaviors, then adding categories according to the mean correlation with all members of the existing cluster, the sequence of clusters formed would be CD , ACD , then $ABCD$. Alternatively, if the highest correlation with any member of the existing cluster is chosen as the criterion for inclusion, the sequence of clusters would be CD , BCD , then $ABCD$. In this latter procedure, one often generates long, straggly clusters (Sneath and Sokal, 1973), a characteristic that may be useful and realistic for finely graded behavior but not for behavior that occurs in discrete modes.

The generality and usefulness of results like those of Morgan *et al.* (1976) are crucially dependent upon how categories are defined, how similarity is measured, and which analytical techniques are used. Slater (1973) provides some hypothetical data on preening, with different criteria for distinguishing acts. Whether acts were recognized as preening single feathers, as series of movements, etc. (see his quote, above, p. 369) had a strong influence on data analysis. Should invariant transitions (e.g., A always followed by B) be considered as single categories? Should transitions between acts or bouts be used? Is temporal proximity or sequential proximity a better estimate of “similarity” between categories? These and other questions once again emphasize the practical and largely arbitrary nature of defining behavioral categories and of estimating their similarity. The best guideline is to do what is appropriate and biologically meaningful for the question at hand.

2.3. Variation

“Describe, don’t categorize” is an important rule of thumb that makes us pause and focus attention on the naturalness and boundaries of behavior (James and McCulloch, 1985). It also prevents us from

making uncritical and coarse-grained assumptions about behavioral homologies. Quantitative descriptions of behavior are necessary for analyzing behavioral variation that is significant in behavioral ecology, ontogeny, individuality, and microevolution. Major recent publications on variation are Yablokov (1974), Barlow (1977), and Wright (1978). Barlow’s (1968, 1977) important papers propose a behavioral unit (“modal action pattern” or MAP) to replace the FAP, plus quantitative applications. Many workers have started to use Barlow’s MAP designation, but often inappropriately (e.g., Miller, 1975; Machlis, 1977), and it is probably wise to drop it—like any term, it induces us to use it to categorize behavior rather than describe behavioral properties, and the latter are the starting point for analyzing variation.

Variation can be quantified most simply for continuous variables by the coefficient of variation (C.V. or V). Sokal and Rohlf (1981) suggest use of the estimate V^* to correct for bias ($V^* = (1 + (1/4n))V$), and this can appreciably increase estimates based on small sample sizes. There is a remarkable dearth of quantitative information on variation in motor patterns of birds (Barlow, 1977). The least variable motor patterns reported to date are in the strut display of male Sage Grouse (*Centrocercus urophasianus*). Wiley (1973) reported data on one temporal attribute for which V^* ranged from 1.1% to 4.9%. Intervals between successive Struts were more variable (10–34%). The greater variation of intervals may reflect communication of changes in a male’s internal state (Wiley, 1973), but they may also arise from the measurement of a behavioral category that has fewer natural boundaries than does the Strut. The behavioral categories used by Nol (1984) in her study of oystercatchers are coarser than those recognized by Wiley, and they may also be more open to environmental change, thereby inflating variation further; some of her estimates are plotted in Figure 17B: all are above 100%. Many more data are needed to adequately characterize levels of variation that typify well-defined avian motor acts and behavioral categories, but Nol’s data seem like reliable benchmarks, despite high levels of variation, for the curves shown in Figure 17B are significantly concordant (Kendall’s $W = 0.746$; $p < 0.05$).

When V (or V^*) is estimated for several variables for a behavioral category or for a single variable across categories, it is useful to summarize the trends graphically in a *variability profile* in which the variables or categories are arranged logically along the abscissa (Yablokov, 1974). Representative profiles for variation of “usual flock displays” of the Common Goldeneye (*Bucephala clangula*) and of drinking phases of chicks are summarized in Figure 17A; the Common Goldeneye data are replotted on a logarithmic scale in Figure 17B, for comparison with the variable data on oyster catchers. This sort of a representation is a

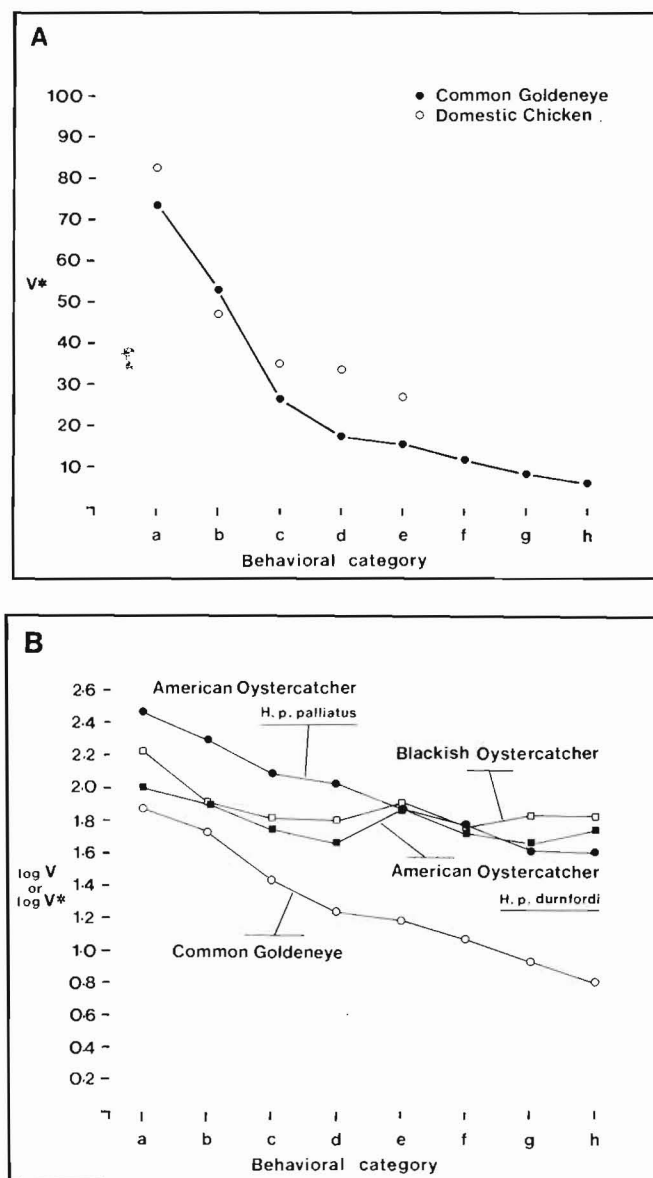


FIGURE 17. Variability profiles for behavioral categories of several species. (A) Variability profiles (arithmetic scale) of durations of "usual flock displays" in the Common Goldeneye (*Bucephala clangula*) and phases of drinking in chicks of *Gallus domesticus* (medians of 6 chicks plotted) arranged from most to least variable. For Common Goldeneye: a, nodding; b, masthead; c, tick; d, bowsprit; e, head-flickering; f, head-throw-bowsprit (fast); g, head-throw-kick (short); h, simple head-throw. For chicks: a, interdrink; b, downstroke; c, upstroke; d, in-water; e, total drink. Data from Dane *et al.* (1959) and Table 3 of Dawkins and Dawkins (1973). (B) Variability profiles (logarithmic scale) of

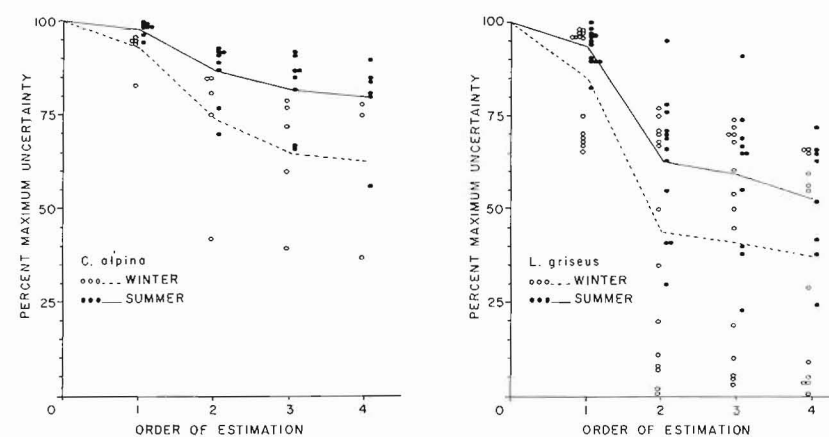


FIGURE 18. Seasonal and interspecific differences in variation of feeding sequences in Dunlin (*Calidris alpina*) and Short-billed Dowitcher (*Limnodromus griseus*). High values of "uncertainty" denote high variation (= low predictability about which behavioral component will occur next in sequence). The graphs show that winter feeding sequences are less variable (less predictable) in summer than in winter and that feeding sequences just a few components long are more variable in Dunlin than in dowitchers. From Fig. 5 of Baker (1973).

useful summary and starting point for analysis. The plot suffers from the usual drawbacks of any plot of single measures, where intercorrelations are not accounted for. Thus, though the oystercatcher profiles are significantly concordant, this may be because variation in several variables covaries. Such certainly seems to be the case for the chick data of Dawkins and Dawkins (1973, their Table 3), where one chick had highest V^* estimates for all six variables and one had lowest estimates for four of them. Techniques for analyzing trends in variability profiles and testing significance of V (or V^*) are summarized in Bird *et al.* (1981) and Sokal and Braumann (1980).

Variation can be quantified in many other ways. A character can be described by the number of discrete states it can have or in the relative numbers of observations for each state (analogous to "richness" and "evenness" in some ecological measures; Pielou, 1977). Baker (1973)

FIGURE 17 (continued). categories of feeding behavior in the American Oystercatcher (*Haematopus palliatus palliatus* and *H. p. durnfordi*) and Blackish Oystercatcher (*H. ater*), plus display behavior of the Common Goldeneye (data from part A). The categories for oystercatchers are arranged from most to least variable for *H. p. palliatus*, which has the greatest range. For oystercatchers: a, walk duration; b, number of pauses per walk; c, pecking-bout duration; d, number of pecks per pecking bout; e, search-bout duration; f, number of pecks per search bout; g, number of captures per peck; h, number of captures per search bout. Data from p. 137 of Nol (1984).

used three discrete behavioral categories (Halt, Walk, Feed) in a study of summer versus winter feeding in six shorebird species. He used an information measure to estimate stereotypy of feeding sequences and documented more stereotyped (more predictable) winter behavior for all species, plus substantial interspecific differences in stereotypy (predictability; variation) (Fig. 18). Mock (1980) broke down several displays of the Great Blue Heron (*Ardea herodias*) and the Great Egret (*Casmerodius albus*) into categories that could be classified visually (e.g., neck angle in the display Snap was split into low (more than 20° below horizontal), medium (horizontal \pm 20°), and high (more than 20° above horizontal)). He then computed the Shannon-Weiner information statistic (H') and found that the Great Blue Heron was more variable than the Great Egret in all five displays. Mock used the same number of categories for both species, thus controlling the "richness" component of H' , so differences in the H' estimates represented differences in equitability (evenness).

A crucial area for full understanding of the ecological and evolutionary significance of behavioral variation is variation within and among individuals: How variable is behavior of individuals at different developmental stages and at each stage, and how does this compare with variation among other classes, and among individuals? An overall population estimate of variance, even when based on equal samples from individual birds, tells us nothing about either the statistical location or dispersion of individuals relative to the population (see Machlis et al., 1985). In most naturalistic studies, individuals contribute unequally to a population estimate, and this makes matters even worse. Where individual birds are known and sampled, an appropriate technique for continuous variables is analysis of variance, which provides estimates of variance components at several levels. It is important to establish hypotheses before taking samples, because there are many relevant questions to ask about variance components. For example, a study on mate attraction and sexual selection might focus on variation in courtship displays within and among individual breeding males; a study on ecogeographic variation in sexually dimorphic behavior might sample foraging behavior of individuals of known sex within several populations. In the former case the variance components would be "among males" and "within males"; in the latter they would be "among populations," "between sexes," and "among individuals," with appropriate interaction terms.

Few studies have been undertaken in which comparisons of behavioral variation have been made. Wiley (1973) noted that the Strut display of young male Sage Grouse was not less variable than that of adults, and Bruggers and Jackson (1981) remarked on the greater vari-

ation of displays by yearling males of the Mandarin Duck (*Aix galericulata*) than by adults (see also Bekoff, 1977). However, methods of study have varied a lot, and many relevant observations have been made only incidentally.

The little published information on behavioral variation and the lack of standardization in its analysis are notable, considering the importance of behavioral variation to ecology, evolution, and many other disciplines (Bookstaber and Langsam, 1985). This is an exciting and rich area and one that merits much new description and analysis by avian ethologists.

2.4. Construction of Ethograms

2.4.1. General Comments

The term "ethogram" is widely used but poorly defined. Schleidt et al. (1984:194) attribute the term's origin to G. F. Makkink and state that it "has become the preferred term for the description of species-specific or taxon-specific behavior." Lehner (1979:46) follows J. L. Brown and describes it as "a set of comprehensive descriptions of the characteristic behavior patterns of a species." Martin and Bateson (1986:41) state that the ethogram "is a catalogue of descriptions of the discrete, species-typical behavior patterns that form the basic behavioral repertoire of the species." Interestingly, McFarland (1981) does not define the term at all. If the term is to serve an important function, then it should be characterized clearly. I view "ethogram" as roughly synonymous with "comprehensive behavioral description for a natural class":

1. The term is applicable to any natural class of individuals. It is legitimate to prepare an ethogram for 1-day-old nestlings of the American Robin (*Turdus migratorius*) on Vancouver Island, for castrated males of a breed of chicken, or for the genus *Charadrius*. It is too restrictive to apply the notion only to the species level; in any case, to do so implies that that level is evolutionarily most "natural" or intrinsically most important to ethology. Neither is true.
2. Ethograms should not be restricted to "discrete" behavior patterns but should cover all behavior irrespective of whether it can be easily segmented, quantified, and described.
3. Ethograms should not be restricted to behavior that is "typical," "characteristic," or "diagnostic" of the class in question. They should include descriptions of all behavior, many types of which will be uncommon or will only differ quantitatively from other classes of individuals.

Systematically constructed ethograms are important, because they promote standardization and improve communication, enabling objective and detailed comparisons. Where workers approach a similar problem in different ways, it is difficult or impossible to make such comparisons. A typical example comes from several studies on parental behavior of oystercatchers. In their studies, Helbing (1977), Nol (1985), and Purdy (1985) recognized 12, 18, and 20 categories of behavior, respectively. If we define "exact" correspondences to be those permitting a direct comparison of rates of occurrence and durations, then there were two exact correspondences between Helbing and Nol, three between Helbing and Purdy, and two between Nol and Purdy; only one category was common to all studies (Table I). By summing a few categories, other correspondences appear (footnote, Table I). Correspondences were clear for some extremely simple behavior (e.g., resting postures) but not for others. Helbing's "Bathing" excluded preening movements while in the water, whereas Nol's "Bathing" included them; Purdy lumped all bathing and comfort movements under "Preen." Some very important behaviors for documenting sexual differences in parental roles are difficult to compare from the studies. Thus, Nol lumped all nest building, nest maintenance, incubation, and brooding under "Brood," whereas Purdy split them up; Helbing's "Brooding" and "Incubation" correspond to Purdy's categories, but he did not include nest building or maintenance among his categories.

The authors often described the same functional class of behavior but used different or vague defining criteria. Helbing (1977:12) carefully defined Chick Feeding: "Timing began with an adult's arrival at the nest site or with terrestrial movement from a nearby forage site with a food item for the chick. Timing was terminated by the chick's intake of the food item, the adult's turning away from the chick, or the adult's initiation of another defined activity." Purdy (1985:41) excluded locomotion from her category: "holding food item in the bill which is motionless and close to the ground until the chick takes it." Finally, Nol (1985:235) described Feeding Chicks as "presenting, and breaking up food for the chick." The discordance of these descriptions prevents any comparison of durations, rates of occurrence, percentage of time spent in the activity, and other simple quantitative measures.

The two main problems in seeking comparable data from these studies are that behavioral categories were not fine enough and that behavioral measures were not operationally clear enough. Comparability is not the only reason for recommending fine-grained, operationally clear descriptions; any more specific study will want to focus on only a part of the repertoire. If one is interested in the structure and

TABLE I
Behavioral Categories Recognized by Helbing (1977) and Purdy (1985) in Their Studies on the Black Oystercatcher (*Haematopus bachmani*) and by Nol (1985) in Her Study on the American Oystercatcher (*H. palliatus*)^a

Helbing	Nol	Purdy
1. Agonistic behavior ¹		1. Agonistic ¹
2. Bathing	1. Bathing	11. Pipe
3. Brooding ²	2. Being chased by oystercatchers	111. Aerial pipe
4. Chick feeding	3. Bobbing	112. Ground-pipe
5. Copulation	4. Brooding	113. Pipe-attack
6. Feeding	5. Chasing other oystercatchers	12. Hunch
7. Flying	6. Chasing other species	121. Hunch-attack
8. Incubation ³	7. Crouching	122. Hunch-glare
9. Preening	8. Drinking	2. Copulation
10. Resting ⁴	9. Feeding chicks	3. Fly
11. Sleeping	10. Flying	4. Forage
12. Standing/misc.	11. Piping	5. Parental care
	12. Preening	51. Brood ²
	13. Resting ⁵	52. Feed chick
	14. Searching for food and foraging	53. Foraging for chick
	15. Shaking	54. Incubate ³
	16. Sitting ⁴	55. Nest-build
	17. Standing ⁶	551. Backward-throw
	18. Walking ⁷	552. Nest-press
		6. Preen
		7. Sit
		71. Sit-bill on back
		72. Sit-bill up ⁴
		8. Stand
		81. Stand-bill on back
		82. Stand-bill up ⁶
		9. Walk ⁷

^aExact correspondences are indicated by superscripts. Other correspondences are: H1 = P1 = N2 + N5 + N6 + N11; H2 + H9 = N1 + N12 + N15 = P6; N4 = P51 + P54 + P55; N8 + N14 = P4 + P53.

variation of foraging, for example, then Nol's category "searching for food and foraging: walking while pecking and feeding" is far too coarse; a suitable starting point would be her more detailed breakdown provided elsewhere (Nol, 1984).

Truly comprehensive behavioral descriptions are elusive, and the level of detail or completeness we accomplish depends on many factors, such as the investigator's time, the study's aims, the observability of study animals, and the ways in which behavior is described. However, it is important for ornithologists to prepare ethograms systematically and consistently. In the following section I outline some suggestions for preparing a general-purpose ethogram based on direct observation.

2.4.2. An Approach to Ethogram Construction

The suggestions that follow presume that observations are made directly, with the aid of binoculars or spotting scope and stopwatch. Cameras are essential when they can be used, but it is impossible to use them effectively in certain kinds of studies (e.g., foraging behavior of mobile flocks in the forest canopy). Movie, videotape, or audio tape equipment should also be used when possible (see remarks below).

The basic goal of an ethogram is to provide a descriptive inventory of behavior for a class of interest; this implies that behavior will be broken down into categories. Categories should be established on both structural and functional grounds and should be organized hierarchically, with an emphasis on functional characteristics at higher levels and structural features at lower levels. For example:

1. Parental behavior
 11. Nest- or egg-directed behavior
 111. Nest building or maintenance
 1111. Scraping
 1112. Sideways throwing
 1113. Adjustment of nest material
 112. Incubation behavior
 1121. Looking at eggs
 1122. Adjustment of eggs
 1123. Shading of eggs

12. Chick-directed behavior

2. Resting and maintenance behavior

Some workers suggest that behavioral categories should be at a similar organizational level and should be mutually exclusive (e.g., McFarland, 1981). The former is a useful attribute for particular studies but not for preparing an ethogram; the latter is not necessary for ethogram construction and does not reflect how behavior is organized (see remarks below).

Our perceptions of function and purpose affect how we recognize and label higher-level behavioral categories (Lewontin *et al.*, 1984). We work with current concepts about behavioral organization, so, as those concepts change or are replaced, our higher-level categories may become invalid. The best way to minimize this is to use unambiguous, uninterpretable, descriptive terms as much as possible and to provide operational criteria for distinguishing categories at all levels of the hierarchy. It is reasonable to recognize general functional groupings, such as "parental behavior," which can be operationally defined and has fairly natural functional boundaries; categories (and terms) such as "aggression" should be avoided, because they are ambiguous, do not describe unitary phenomena, and have everyday connotations that are misleading biologically.

In preparing ethograms one must take two principles into account: goals of behavior can be achieved in different ways, and particular motor acts can serve many different functions. The first of these is accounted for by organizing a hierarchy from function at the top to structure at the bottom. Such an arrangement ensures that categories marked by diverse motor patterns, but serving the same end, are placed together (e.g., various motor acts for procuring and handling food items). A useful rule for dealing with multifunctional motor patterns is to categorize them by their dominant, usual, or most proximate function, then to refer to them in other appropriate categories. For example, Purdy (1985) distinguished "forage" from "foraging for chick" and placed the latter under "parental care" (Table I). I would have placed them in the single category, "forage," broken down more finely by different motor patterns. To test the hypothesis that "forage for self" differs from "forage for chick," it would then be straightforward to document differential

use of the motor patterns or quantitative differences in particular patterns, depending on end use of the food items obtained. Similarly, the different end uses could be distinguished to estimate the percentage of time spent by parents in foraging for chicks. But in either case, "forage" should be the basic category because of the proximate behavioral consequences and common motor patterns.

General-purpose categories like "locomotion" can be treated similarly. The category can be broken down into aerial versus terrestrial locomotion, with further subdivision within each. Special kinds of locomotion, such as in the leaping display of the Little Bustard, *Tetrax tetrax* (Fig. 10F), should be a category under "locomotion" and should also be recognized within "leaping display"—but only as a component of the latter. I would decide where to put detailed description (including quantification) based on whether the locomotory pattern was unique to the display, whether it was an important display component, etc. For example, if the pattern is also used in other contexts (e.g., flutter-fighting), then I would describe it under locomotion, but I would mention the different contexts in which it appears, and possibly (as with "foraging for chick") distinguish them qualitatively and quantitatively. Here and elsewhere, the basic qualitative and quantitative characteristics of the whole category should be provided. To summarize, decisions about where to recognize or place categories for multifunctional behavior at lower hierarchical levels should be based on structural features and proximate consequences.

After a hierarchy is set up, it can be "fine-tuned" through describing behavior for each category. The process familiarizes the observer with fine points of behavior and provides data and impressions that contribute to revision. With the preliminary hierarchy in place, some suggested guidelines for describing each category are the following:

1. First describe characteristics of postures, such as tail position, head carriage, state of the plumage, and so on. Then describe movements using the same characteristics as a starting point. Describe paths of movement and how movements are executed, not just start and end points. Overdescribe: irrelevant or meaningless details can be removed later, but unrecorded important details cannot be recovered. Draw sketches or diagrams; take photographs.

2. Make a checklist of components within each category, and list their states. Some states are discrete and differ qualitatively; others grade but can be estimated quantitatively "by eye" (e.g., state of plumage erection, approximate angle of tail). Draw sketches or diagrams; list criteria that distinguish the states. Provide quantitative estimates

of act or bout durations, or both, and of features of notable components. Estimate rates of occurrence of discrete act types (or bouts of them) and their relative frequencies of occurrence.

3. Photographs, movie films, and videotapes provide invaluable detailed information about postures, movements, and behavioral components. Audio tapes should also be obtained when possible. This sort of material, plus sketches, drawings, etc., should be obtained for as much behavior as possible and is essential for recording components or behavioral states used as landmarks or criteria.

4. Make explicit use of frames of reference. All postures and movements occur within spatiotemporal frames of reference, including abiotic, biotic, stationary, dynamic, static, passive, and reactive components of the environment as well as the animal's own body. It is often valuable to note general features and locations; for example, some kinds of behavior are nonrandomly distributed within a territory (Post, 1974). Most behaviors have several relevant frames of reference. Note and comment on these. If feasible, describe an animal's behavior quantitatively (even coarsely) with respect to frames of reference judged to be relevant (e.g., in body lengths or approximate orientation in degrees). Draw sketches or diagrams.

5. Note intrinsic and extrinsic (contextual) information relevant to each category. Many behavioral characteristics are influenced by time of day, weather, date, location, etc. Many features also differ across classes of individuals according to gender, age, breeding status, and so on. Qualify descriptions accordingly and, if appropriate and feasible, provide subdescriptions (see remarks above about "forage" and "locomotion"). Keep in mind that preceding and following behaviors of a focal bird, consequences of behavior, and behavior of nonfocal interacting birds (or other reactive environmental components) are important parts of context.

6. Define categories clearly and describe them fully. Comment on practical, perceptual, or conceptual difficulties in recognizing or describing each category. Provide clear operational criteria for distinguishing each category and quantifying variables in it. At the least, ensure that the onset and termination of each act or bout are defined operationally and that acts and bouts are distinguished. This will permit comparisons of temporal measurements (durations, intervals) and rates of occurrence. Describe behavior fully and use sketches, photographs, and other kinds of illustrations.

Ethogram construction must be practical, operational, and rigorous, but no single scheme can be rigidly applied. However, we can attempt

a "best fit" approach and be rigorous within that framework. Behavior that cannot be adequately treated in that way can still be discussed and described. Thus Helbing (1977:12) described a general behavioral category ("Standing/Miscellaneous") for the Black Oystercatcher (*Haematopus bachmani*): "No consideration was given to the exact posture. . . . Movements included . . . were slow walking movements . . . momentary comfort movements, or other apparently irrelevant and infrequent movement not associated with other specific activities." An investigator can build on this category in a more detailed study, because it is clear that it is heterogeneous and comprises behavior not included within other categories recognized by Helbing (see above). In his study of preening in a Herring Gull, Van Rhijn (1977:74) explicitly erected categories at different organizational levels for practical reasons:

One complete movement of drinking, snapping-water, head-dipping or plunging was taken as one event of the element involved. The other elements [bill-washing, stamping feet, etc.] . . . mostly occur as very rapid repetitions of the same movement. Here it was impossible to count the number of separate movements. For this reason an event of . . . these elements was defined as a sequence of repetitions of one and the same movement with intervals of less than half a second.

Here, because Van Rhijn provided a clear explanation of his decisions and an operational criterion, direct comparison with his study is possible.

Ethograms can provide an enormous amount of information to comparative ethology. The purposes of ethograms are to provide information that permits comparison among classes at the same level and to provide a basis for more detailed explorations of specific kinds of behavior. Behavioral categories in ethograms are simply packages of information: they often sit on behavioral modes defined on structural (or functional/contextual) grounds, but they neither define nor characterize behavioral structure. To do this adequately demands techniques that describe the flow of behavior as just that (e.g., Golani, 1976; Golani et al., 1979).

2.4.3. Are Standard Ethograms Possible?

Schleidt et al. (1984) proposed a scheme for describing bird behavior that would promote standardization and enable descriptions to be published economically. Gordon (1985) disagreed with their emphasis on motor patterns and pointed out that context-dependent units of behavior need much more attention; Schleidt (1985) replied by saying that notes on behavioral context would naturally be included in descriptions of motor patterns. The emphases of these authors are too

divergent to be compatible. Gordon is correct in arguing that we need much more attention to context. Indeed, details of context underlie Smith's (1977, 1985) model of communication, in which each type of behavioral act encodes particular information and the information is invariant across contexts; the receiver integrates its perception of that information with contextual information in arriving at a behavioral response. A contrary view was espoused by Beer (1980), who noted that particular motor patterns commonly recur in different contexts but suggested that the patterns may contain different information in each. To resolve these important issues, it is important to couple detailed descriptions of context and motor patterns, but a generalized, standard ethogram is not the place to do it. Schleidt (1985) is correct to the extent that he states contextual information will be included in an ethogram; however, the information cannot be detailed enough to blunt Gordon's criticism. Thus, we need both approaches.

Drummond (1985) and Leonard and Lukowiak (1985) provided other criticisms of the descriptive methods proposed by Schleidt et al. (1984) and suggested that the methods are too complicated to receive general acceptance. This may be so, but I feel that the crucial test of the proposal is its applicability to classes of interest. Highly generalized and widely applicable schemes yield little profit for detailed comparative studies, of course; conversely, highly specific schemes are of insufficient general interest or significance. I think that the method of Schleidt et al. (1984) is far too specific and demands too much of both the observer and the situation in which observations are being made. The scheme will not work for naturalistic studies and thus cannot be applied to most kinds of birds.

Protocols for concisely describing avian motor patterns should be established to improve uniformity in description, to facilitate communication among workers, and to enable more ethograms to be published. The protocols should incorporate a way to summarize contextual information. Protocols would be best developed through procedures based on a generalized group description (e.g., Ardeidae); then details for members of the group could be published in concise form subsequently. Procedures and emphases for different groups are likely to vary in keeping with anatomical, behavioral, and ecological differences.

3. CONCLUDING COMMENTS

Concise descriptions have two important aspects: they encourage more uniform descriptions, and they make information more accessible through formal publication. However, extensive pictures, written de-

scriptions, and quantitative information are crucial for the comparative study of bird behavior. These conflicting requirements can be met by establishing ways to publish descriptive data economically, as proposed by Schleidt *et al.* (1984), and by archives for avian ethology (Tinbergen, 1963; Schleidt *et al.*, 1984). The latter exist in part, but are splintered taxonomically and by recording medium. The major cinematographic collection is the *Encyclopedia Cinematographica*, a scientific encyclopedia of 16-mm film with specific guidelines for content: behavioral phenomena either cannot be adequately observed by the unaided human eye, need to be compared with other phenomena but verbal descriptions are inadequate, are uncommon, are not readily available for observation, or are disappearing from the culture (see Miller, 1985). This unique film collection should be contributed to by all able researchers, but it cannot serve as a repository for the miles of unedited moving images that avian ethologists hold. A more general-purpose repository with less curatorial "overhead" is needed.

A collection of still photographs of birds was established at the Academy of Natural Sciences (Philadelphia) in 1979 (Myers *et al.*, 1984, 1986). The Visual Resources for Ornithology (VIREO) contain nearly 100,000 images of living birds for nearly a third of the world's avifauna: color transparencies, black-and-white prints, stereo images, and other types. In addition, VIREO serves as a repository for voucher photographs (e.g., of habitat) from ornithological studies (e.g., Nichols *et al.*, 1986; Anon, 1986). The critical factors behind VIREO's establishment were, C. H. Greenewalt and F. B. Gill's belief that such a collection would have immense value to scholars and educators, and the Academy's practical support. The collection is of living birds and so has potentially great value to avian ethology.

Two other kinds of collections that should be mentioned are of audio recordings and behavioral artifacts (e.g., nests). I have discussed these elsewhere (Miller, 1985). I know of no archives holding behavioral descriptions, general illustrations, field notes, data, and related material.

A major immediate and urgent task for ornithology is to identify needs and to recommend and implement action for documenting the biology of endangered and declining species. This is particularly urgent for the world's tropical avifaunas (Short, 1984; Janzen, 1986). Ethology has important contributions to make to this effort and should do so in a rigorous and standardized way, with extensive documentation that should be archived.

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