

AVIAN PLAY

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ABSTRACT.—Play is more difficult to distinguish from other activities in birds than in mammals. Some cases of play reported in the literature appear to be due to threshold lowering, a type of activity that is usually differentiated from play. The various types of avian play are reviewed. Like mammals, birds exhibit object manipulation and some types of locomotory play. Subsong shows some remarkable similarities with characteristics of nonvocal play as noted in mammals, and birds may engage in other types of acoustic activities with playlike features. The corvids, particularly the Common Raven, exhibit the most complex play known for birds, and these activities, which are part of the learning process in the young, are probably important in the species' adaptation to a wide variety of habitats. Of all animals, only birds and mammals play, and play evolved independently in the two groups probably because of similar selection pressures acting on the developmental process to produce flexibility of behavior and the perfection of certain motor skills.—*Department of Zoology, University of Wisconsin—Milwaukee, Milwaukee, Wisconsin 53201. Accepted 12 January 1976.*

PLAY is one of the most mysterious activities of animals. Why do animals, especially young ones, engage in play? Even in the more intensively studied species of mammals little is known about the neurophysiological basis or motivation of play, and its ultimate selective advantage is still only poorly understood. Recently there has been a surge of interest in mammalian play, resulting in a better understanding of how play activities differ from other activities of young animals (e.g. Loizos 1966), descriptions of play patterns in a variety of mammals (e.g. Wilson and Kleiman 1974), and some insight into the role of play in the developmental process (Welker 1971, Bekoff, 1972).

Play is much better understood in mammals than in birds and lower vertebrates, where such activities, if they occur at all, are more difficult to recognize and interpret. The purpose of this paper is to review suggested examples of avian play found in the literature and to examine these critically in the light of the conceptual framework for evaluating and interpreting mammalian play. Finally some comparisons are made between mammalian and avian play.

CHARACTERISTICS OF PLAY

What is play and how does it differ from other activities of animals? This question is sometimes difficult to answer for mammals, and even more so for birds. In most cases no specific motor patterns are used exclusively in play; rather, play often utilizes actions occurring in other contexts. In mammals, play types may be classified as object, activity, and social (Meier and Devanney 1974). Prey-catching movements and manipulation of objects are found in a variety of species; other play activities include various nonsocial locomotory activities, and finally, social play in which two or more individuals interact is common, especially in the more social mammals. If we examine all the different types of play in mammals, it is apparent that play has certain characteristics that usually distinguish it from other, nonplay activities (Loizos 1966, Marler and Hamilton 1967, Ewer 1968, Hinde 1970). Some of the more important differences are: (1) incomplete sequences, reordered sequences, and incomplete movements. While the motor patterns of play are often similar to those used in other contexts, play sequences often lack elements found in similar nonplay ac-

tivities. Also, the movements themselves may be incomplete. The play sequence may have a different ordering of motor patterns than is found in comparable nonplay activities. (2) Exaggeration and repetition. Individual play movements may be exaggerated in form and certain movements within the sequence may be repeated more often than they usually would be in a nonplay activity. (3) Elicitation. Play behavior is often elicited by a wider range of stimuli than other activities.

Although a given play activity may show only some of these characteristics, and not one of these characteristics is general to all behavior termed play, these characteristics may be useful in attempting to distinguish between play and other activities (Hinde 1970).

MOTIVATION OF PLAY

Although the motor patterns of play may be similar to those of other activities, the motivational basis is different (Lorenz 1956, Ewer 1968, Eibl-Eibesfeldt 1970, Hinde 1970). According to this viewpoint play fighting, for example, would have a different motivational basis than true fighting. The exact nature of the motivational difference between play and other activities is often unclear, but several types of differences have been noted. For example, Thorpe (1956) suggests that play differs from other activities in not being directed to a specific consummatory situation, but rather the play activity itself seems to be its own consummatory act. In this sense play could be considered self-rewarding. Lorenz (1956) distinguishes play from vacuum activities (see below).

Play is low on the priority of behavior types, the animal playing when there is nothing else to do (Marler and Hamilton 1967). It often occurs when the animal is free from conflicting environmental pressures and is therefore more common in young animals whose parents provide for them (Loizos 1966).

Interpretation of play of human children often colors interpretations of animal play as well. For example older studies of animal play suggested that it occurred because of "surplus vitality" (Armstrong 1942) or because it was "fun" (e.g. Groos 1898), but as Beach (1945) points out, such interpretations of play do little to advance our understanding of its causation and function. As is the case for other behavior, an attempt should be made to analyze play in objective terms.

FUNCTIONS OF PLAY

In human terms we often contrast "play" with work and think of play as having no function and not being "serious." Play activities of animals often show no obviously immediate biological function. In other words, they do not immediately enhance the animal's chances of survival and reproduction as do many other activities. Current workers on play emphasize that play has several important functions in preparing the young animal for adult life: (1) Play enhances muscular development in young animals, keeping them in good physical condition, which is important in their later lives (Beach 1945, Ewer 1968). (2) Play results in discoveries and experimenting with the relationship between the animal's own actions and the external world (Beach 1945, Ewer 1968). Play can contribute to very important learning processes, although in some animals the motor patterns of play themselves may be largely instinctive (Eibl-Eibesfeldt 1970). (3) In social animals play is an important way of adjusting social relationships that are important in later life (Beach 1945). These views stress that play by young animals is an important sort of learning for adult life. Undoubtedly no single function occurs for all species or even for a given type of play (Beach 1945).

PLAY IN BIRDS

Assessing reports of avian play from the literature presents numerous problems. Often the accounts, especially in the older ornithological literature, are too brief and anecdotal and lack pertinent details. The term "play" has also been used for activities that may have a different motivational and functional basis than those activities we usually consider to be play. Groos (1898) in his book devoted to play in animals gives many examples of avian play. Many of these activities would not meet current criteria of play. For example he uses the term for almost any low intensity activity of young birds. Not all activities of young birds should be considered play. For example, some young birds spend considerable time manipulating nest material (Thorpe 1956). This and other low intensity activities of young birds are presumably due to incomplete maturation and such behavior is distinguished from play by Thorpe (1956). In mammals incomplete movements are often characteristic of play, although usually with other features that distinguish play and nonplay activities.

Further difficulties with assessing avian play come from behavior that may be vacuum activities, redirection, or responses to suboptimal stimuli possibly affected by deprivation, particularly in captive birds. These activities are generally not considered to be play. Lorenz (1956) pointed out that vacuum activities result from threshold lowering while play does not. Vacuum activities arise from a high intensity of a drive as if internal factors force its expression, while play is more affected by stimuli from the immediate environment such as the animal's own body, an object, or companion (Thorpe 1966). Lorenz (1956) suggests the term "play" be applied to movements that are performed "independently of the proper releasing object and also without any threshold lowering." Despite these theoretical differences between vacuum activities and play, in birds it is often difficult to distinguish between the two. Young captive birds often engage in what appears to be frenzied escape movements. Such behavior might occur in captivity where the normal stimuli eliciting escape are often absent and the threshold for performing the act is lowered so much that the act occurs spontaneously. Animals sometimes direct activities toward an object or animal other than the one that normally releases a particular behavior. This is termed redirection and was defined by Moynihan (1955) 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." I watched a young male American Redstart (*Setophaga ruticilla*) direct courtship behavior toward a young conspecific female that consistently rebuffed or was indifferent to his advances. Finally the male made copulatory movements on a pile of droppings in the cage (Ficken and Dilger 1960). There are similar reports of sexual behavior in other species, both in the field and in captivity, being directed toward inappropriate objects (Ficken and Dilger 1960). The only apparent distinction between redirection and reactions to subnormal stimuli is the fact that in redirection the usual stimulus situation initiates the behavior. Such activities should probably be distinguished from play, but these situations may arise commonly in captive birds, particularly young ones. Kilham (1974) noted that captive Red-bellied Woodpeckers (*Centurus carolinus*) frequently store useless objects such as nails or wood chips. Eibl-Eibesfeldt (1970) reports that captive Woodpecker Finches (*Camarhynchus pallidus*) after feeding regularly took left-over mealworms and put them in holes and crevices and then poked them out again with twigs. He considered this a type of play. It is possible that these captive birds, deprived of conducting their normal food seeking by probing with twigs, exhibited threshold lowering for performing these activities.

A third type of difficulty in deciding which activities of birds should be termed play is that some avian activities were considered play because at the time they were described, their functions were unknown or poorly understood. For example, Groos (1898) included as play certain behavior of adult birds the motivation and function of which were poorly understood at the time he was writing. We would now consider many of these activities as courtship or threat displays.

In the discussion of avian play that follows, I have selected examples of various kinds of activities that have been termed "play," but have ignored many examples that merely seem to be low intensity behavior patterns of young birds. Thorpe (1956) and Thompson (1964) present brief reviews of avian play. In addition, two more recent papers deal with play in particular groups of birds, Gwinner (1966) with Common Ravens (*Corvus corax*) and Kilham (1974) with woodpeckers. It is probably premature to attempt to classify avian play, but here the types that seem similar are treated together.

Aggressive and sexual play.—Young birds often exhibit low intensity or incomplete sequences of aggressive or sexual acts, and such activities are sometimes classified as play. Nice (1943) noted that young Song Sparrows (*Melospiza melodia*) often hop on top of each other and peck. She had the impression that these activities were play as they seemed "not in earnest." Young birds go through a period of aggressiveness early in their lives that may be a part of the normal maturation process, and such activities are usually distinguished from play (e.g. Hinde 1970). Kruijt (1964) in a comprehensive study of the development of aggressive and sexual behavior in young Red Junglefowl (*Gallus gallus*) noted that often in the early stages of development, sexual and aggressive behavior are incomplete and directed at inappropriate objects, such as a feather in the case of sexual behavior and the bird's own tail in the case of aggression. He points out that some of the differences between the behavior of young and adult junglefowl parallel what has been called the differences between play and other behavior. Thus fighting in young birds is often incomplete, not elicited in the same way as in adults, and the activities are not grouped into the adult sequence. Kruijt suggested that using the term "play" for these activities does not help in understanding their organization and is superfluous. This points to some of the difficulties encountered in determining just what avian activities should be termed play at our present state of knowledge of ontogenetic, causal, and functional organization of these activities. Certainly, unlike many species of mammals, birds do not seem to have any special motor patterns typical of aggressive or sexual play.

Play with objects.—Play with objects, more common in young than in adults, is evidently widespread both in captivity and under natural conditions in hawks and eagles (Sumner 1931, Herrick 1934, Bond 1942, Battersby 1944, Cade 1953, Chisholm 1958, Thompson 1964) and involves manipulating either dead prey or objects such as twigs, pieces of wood, stones, etc. The object is often carried into the air, dropped, and then caught with the feet, with the acts repeated many times, in some cases for as long as an hour (Chisholm 1958). Other predaceous birds engage in similar behavior. Cormorants and pelicans play with fish and stones (Groos 1898, Meyer-Holzappel 1956), and young Great Frigatebirds (*Fregata minor*) swoop, pick up, and then drop leaves or other floating objects (Thompson 1964). Swallows sometimes play with feathers (Hailman pers. comm.).

It is difficult to see any substantial differences between a hawk repeatedly releasing and catching an object in midair and a kitten pouncing on a ball of yarn. Such activities in mammals are usually considered play and no valid reasons exist for not

applying the same term to similar activities of birds. The widespread distribution of playing with objects by predatory birds and mammals indicates that it may be an important way in which the young acquire skills in catching and manipulating prey.

The decorating of the bower by male bowerbirds has sometimes been called play (Söderberg 1929, Armstrong 1942, Thompson 1964), but as the bower seems to have an immediate sexual function (Marshall 1954, Gilliard 1963) considering it a type of play seems far-fetched.

Corvids certainly have the most complex play known in birds. Much of their play combines locomotory activities and manipulating objects. Play with objects often involves complex series of acts. Ravens carry pieces of twigs and heather that they drop and catch in the air (Thompson 1964). A captive raven repeatedly threw a rubber ball vertically in the air and caught it, often lying on its back and shifting objects from beak to claws and back again (Thorpe 1966).

Some corvids participate in social games. Two young African White-necked Ravens (*Corvus albicollis*) engaged in a kind of "king of the castle" game. While standing on a mound one bird picked up and brandished a lump of dung or a small stick. The other then charged and attempted to seize the object. On one occasion the bird with the twig actually threw it to the other (Moreau and Moreau 1944). In some cases games may be played with another animal or a human. For example, a Common Raven (*Corvus corax*) developed a play activity with a dog that suggests the gestures and intention movements of the two species must have been mutually understood, as they took turns chasing each other around a tree (Thorpe 1966). One of the few reports of a complex social play involving a species other than a corvid is one of the Australian mudnest builders (*Grallinidae*). White-winged Choughs (*Corcorax melanorhamphos*) frequently play "follow the leader." Also one will sometimes seize a small stone and resist the efforts of others to take it from him (Chisholm 1958).

Gwinner (1966) presents the most detailed descriptions of corvid play. Common Ravens, Carrion Crows (*Corvus corone*), and Rooks (*C. frugilegus*) frequently hang upside down on twigs or electric wires. They typically fall forward or backward from their normal perching position, hanging upside down by their feet with wings outspread, then often letting go with first one foot and then the other. In ravens, such activities also often involved the manipulation of objects. While carrying a piece of food and hanging upside down, a bird switched the object from the beak to a foot and back again repetitively. Balancing games were often conducted in connection with the upside down behavior and its many variations, the birds picking long thin branches, often balancing their way from a basal part to the end and then starting all over again. Often they made this game more challenging by manipulating objects while balancing. For example one bird balanced on a thick round piece of wood while standing on it on a branch. In some cases the upside down posture was actually used in hiding food in otherwise inaccessible locations.

Gwinner's captive ravens showed a great deal of individual variation. When one bird developed a particular balancing and manipulation sequence the other cage-mates imitated the actions and were still doing them 3 years later. Play behavior seemed to be contagious; other birds in the cage performed similar behavior at the same time. For example one game involved repeatedly sliding down a smooth piece of wood and for the most part all the birds played the same thing at the same time.

As Gwinner (1966) pointed out, ravens demonstrated a great deal of invention in developing complex behavioral sequences from relatively simple building blocks. Corvids, particularly the species of *Corvus*, are unusual among birds in being "spe-

cialized nonspecialists" (Lorenz 1959) and in occupying a wide variety of habitats from the tundra to the tropics. Corvids, particularly the Common Raven, are noted for their learning abilities. Many behavior patterns are quite variable individually, and learning at least partially through play while young is of great importance in adjusting behavior patterns to an individual's special surroundings (Gwinner 1966). Similarly complex games involving such extensively learned motor patterns are not otherwise known among birds (Gwinner 1966). Lorenz (1959) has characterized the Common Raven as a species with instinctive movements that are initially associated with no specific situation. Through play it has to learn which of these motor patterns are best suited for which situation (Gwinner 1966). As the raven develops adjustments and flexibility of behavior through play, it has the potential for inhabiting a much greater range of environments than birds whose behavior is less flexible (Gwinner 1966).

The marked propensity for imitation, particularly by the young enables the learning of acts that others have perfected. Common Ravens are quite sociable in youth and have a remarkably long developmental period, spending 5 months with their parents. At the end of this period they join other groups of young, but then become solitary at the end of the third year (Gwinner 1964). With such a social species it is not surprising that ample opportunity occurs for imitative learning of skills acquired through play. Unlike many species of social mammals, ravens do not seem to engage in much active social play with each other. Rather, play performed by one individual seems to stimulate solitary play, which is frequently imitative, in another. In mammals social play seems to facilitate social skills in later life. Play in ravens, on the other hand, seems principally to function in enhancing nonsocial skills, such as food acquisition and manipulation.

Do ravens exhibit complex play because they are intelligent or are they intelligent because they play? The answer is probably both. Because they are intelligent they are capable of diverse and complex play activities, and it is also probable that through play they learn relationships with the environment that contribute to their plasticity of behavior and great ecological success in many different habitats.

Locomotory play.—Some activities of birds involve repetitions of a locomotory act with no apparent immediate purpose. An Anna's Hummingbird (*Calypte anna*) floated down a stream of water from a hose, repeating it over and over again (Stoner 1947). A group of Common Eiders (*Somateria mollissima*) rode down a rapids, continually dashing back to the same spot to repeat the activity (Roberts 1934). Adélie Penguins (*Pygoscelis adeliae*) ride on small ice floes on a tide run, only to return to the starting point to repeat the activity (Thompson 1964). Such activities are reminiscent of the sliding games of otters.

It is difficult to decide if some other locomotory activities of birds should be considered play. Lorenz (*in* Nice 1943) coined the term "emotion dissociated fleeing movements" for the behavior, particularly prevalent in young birds, that involves what in other contexts would be considered escape behavior, except that in some cases no stimulus eliciting escape is apparent. Goodwin (1953) noted young captive Red-legged Partridges (*Alectoris rufa*) running at full speed within a restricted space, making short flights and sudden turns. These movements are those used in escape when surprised in the open by a bird of prey. Lorenz (*in* Nice 1943) reported that geese and ducks performed all the motor patterns used when a bird of prey is behind them in the absence of any appropriate stimulation. Nice (1943) reported "frolicking" in young Song Sparrows in which they made dashing flights and many sharp turns,

and Sutton (1943) noted that several times a day young sparrows had periods of extreme restlessness and acted as if terrified, but no cause could be found for the panic. Young woodpeckers frequently dodged around trees when there appeared to be no stimuli eliciting escape (Kilham 1974).

Difficulties exist in interpreting the motivation of such behavior. As mentioned earlier it is difficult to determine whether threshold lowering is occurring. Kruijt (1964) suggests that these escape movements may be triggered by movements of the bird's own body, especially the tail. This suggests that they are not truly vacuum activities (which occurs in the absence of external stimuli) but that threshold lowering is involved. Most of these reports are from young captive birds that are presumably rarely in a natural stimulus situation for eliciting escape. It is thus doubtful whether such activities should continue to be considered as examples of play.

Acoustic play.—While recent workers have stressed the communicatory function of avian vocalizations, Armstrong (1963) and Hartshorne (1973) suggested that, in addition, vocalizations may be considered as a form of self-expression that gives pleasure to the singer. Such an interpretation poses difficulties for objective analysis, as it is not subject to the usual methods of verification, while the communicatory function of vocalizations has been well documented. Hartshorne (1973) and Thorpe (1956) suggested that, in particular, the acoustic behavior of young birds can be considered a kind of play as it apparently lacks any immediate function but is enjoyed for its own sake. It is of course impossible to determine if young birds enjoy vocalizing; but it is possible to analyze the vocalizations of young birds. Examining the characteristics of play as ascertained for visual behavior determines if similarities occur between the vocalizations of young birds and play activities described for other contexts.

Of all vocalizations subsong has the greatest resemblance to play. It has certain characteristics that distinguish it from song: it is given by young birds; it consists of random, muted warblings of greater duration than ordinary song; it usually contains recognizable call notes, but does not have the overall patterning typical of primary song; most notes are different in structure than notes in song; it is often composed of a greater frequency range than song; and it has no communicatory value in young birds but evidently provides the basis from which primary song is crystallized (Thorpe and Pilcher 1958, Lanyon 1960). Comparing these characteristics with those of play we see that subsong does share some features of play in the reordering of sequences, incomplete sequences, repetition of patterns, elaboration of new motor patterns, being more common in young birds, and having little or no immediate function. It also clearly fulfills one of the functions attributed to play, namely practice for adult activity. In addition the motivational factors underlying subsong may differ from those for song. For example, subsong is evidently produced at much lower levels of testosterone than primary song (Thorpe 1956).

Hartshorne (1973) mentioned several other examples of acoustic play in birds, involving four species that repeatedly dropped objects and evidently listened for the sounds produced. Sauer (1956) found that young Garden Warblers (*Sylvia borin*) picked up and then dropped small stones. The behavior was evidently contagious. One bird dropped a stone accidentally in a glass making a ringing sound; all the other birds showed great interest and many began dropping stones in a dish.

Thorpe (1956) suggested that vocal mimicry can be considered a type of play as he thought it to be motivationally different from other vocalizations. Certainly no evidence indicates that mimicry has a different motivational basis than other vocaliza-

tions (e.g. song of Mockingbird, *Mimus polyglottos*, vs. other species) and mimicry appears to show few characteristics in common with play. Its function is often obscure but Thorpe and North (1966) have demonstrated that one type of mimicry, imitating the mate, functions in maintaining contact between members of a pair.

The concept of play in mammals has been used exclusively for nonvocal behavior. The parallels between subsong and play are striking, and at this point in our knowledge no valid reason exists for not considering subsong as at least sharing some important characteristics with play, as Thorpe (1956) suggested.

DISCUSSION

Not all vertebrates play. Although Marler and Hamilton (1967) reported that play occurs in all vertebrate classes except fish, the one report for reptiles is questionable. A captive Komodo dragon (*Varanus komodoensis*) noisily pushed a shovel around its cage (Hill 1946), but Wilson (1975) suggested that this could be redirection of foraging movements rather than play. While Thorpe (1966) doubted that a single species of bird or mammal lacks play, Ewer (1968) reported that play seems to be absent in some mammals and reports exist for only a few avian groups.

Just what activities of birds should be considered play are still uncertain as avian play is often more difficult to distinguish from other activities than is mammalian play. In the past activities that have been termed play include some that may be vacuum activities, or at least involve threshold lowering and reactions to suboptimal stimuli or redirection. Other activities that are usually distinguished from play are those that are incomplete because of incompleteness of maturational factors. Kruijt (1964) apparently eliminated play as a separate category of behavior for birds, but some avian activities show such striking similarities to what has been considered play in mammals, that it would seem premature to abandon the concept in birds.

Play evidently evolved independently in mammals and birds and shows some remarkable parallels in the two groups, probably because similar selection pressures acted on the developmental process. Both groups exhibit play with objects and certain types of locomotory play, but there are also some marked differences. Although we have no quantitative data for comparison, young mammals seem to spend a great deal more time at play than do young birds. Also the diversity of motor patterns involved in play seems to be much greater in mammals than in birds, except perhaps ravens. Many mammals frequently indulge in social play, and this type of play is rare in birds except for some corvids and their relatives. If subsong can aptly be termed play, this is a category of play that does not occur in mammals, which may be a reflection of the lesser importance of vocal learning in that group.

Play contributes to the learning process and is more highly developed in species that have a primacy of selection for extensive learning (Marler and Hamilton 1967). Complex play is probably also more characteristic of social mammals than of more solitary species (Bekoff 1974). These trends also occur in birds where the corvids, many of which are social for at least part of their lives and also have a great reliance on learning, show what is probably the most complex play in birds if we consider amount, complexity, and variety.

At present, we can draw only the barest outline of the picture of play in birds, having available only a few data on a limited number of species. A great need exists for detailed descriptions, controlled observations and attention to the stimuli that

elicit play (Beach 1945). Play must be defined in objective terms rather than in the anthropomorphic viewpoint that typifies some of the literature on play. More studies like those of Gwinner (1966) and Kruijt (1964) are needed. In very few cases for birds, as well as mammals, has play behavior been carefully described and analyzed and its characteristics compared with other behavior of the same species, which is a necessary first step if we are to understand play (Hinde 1970). As Hinde (1970) indicated, whether birds and lower vertebrates play cannot be answered simply by a yes or no, but rather with a delineation of the ways in which the behavior differs from the behavior of the same species in other contexts and resembles the play of other forms such as mammals. Comparative studies, so emphasized by ethologists for aid in understanding the evolution of behavior patterns, are largely lacking for avian play. In many cases we still do not really know just what species play, how they play, or why they play.

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