

mates or to the density indices derived from counting all birds during a 10-min watch.

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Avian Play: Comparative Evolutionary and Developmental Trends

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Play is an important behavior in higher vertebrates (Byers 1981, Fagen 1981, Bekoff 1984, Bekoff and Byers 1985, Martin and Caro 1985). Most quantitative studies of animal play are limited to mammals (for reviews see Bekoff and Byers 1981, 1985; Fagen 1981; Martin and Caro 1985), whereas descriptions of play in birds are mainly anecdotal (Ficken 1977, Fagen 1981). Recent reviews of avian play (see especially Ficken 1977, Fagen 1981: 244-246) have allowed us to determine whether individuals of a particular species played and the type of play exhibited. Play was defined broadly as "all motor activity performed

postnatally that appears to be purposeless, in which motor patterns from other contexts may often be used in modified forms and temporal sequencing" (Bekoff and Byers 1981: 300; other definitions in Fagen 1981 and Martin and Caro 1985). Typically, play is most common in the young of a species. Types of play (Bekoff and Byers 1981: 300-301) also were classified as locomotor play, "frantic flight about (the) environment"; object play, "activity directed toward an inanimate object"; and social play, "activity directed toward another living object."

We classified extant avian orders as having species with either primarily altricial or precocial young (Van Tyne and Berger 1971, Reid and Williams 1975, Welty 1982). Thirteen (48.1%) of the 27 orders we consid-

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TABLE 1. The distribution of three types of play within 13 avian orders. A = altricial young, P = precocial young.

Order	Locomotor	Object	Social	References
Sphenisciformes (A)	Yes			Thompson 1964, Müller-Schwarze 1978
Pelecaniformes (A)		Yes		Gibson-Hill 1947, Stonehouse and Stonehouse 1963
Anseriformes (P)	Yes			Roberts 1934
Falconiformes (A)		Yes	Yes	Sumner 1931, Bond 1942, Battersby 1944, Cade 1953, Munro 1954, Huxley and Nicholson 1963, Mueller 1974, Johnson and Gayden 1975, Parker 1975
Psittaciformes (A)	Yes	Yes	Yes	Porter 1947; Jackson 1963; Brereton 1971; Keller 1975, 1976 (<i>in Fagen 1981</i>)
Cuculiformes (A)			Yes	Gurney 1909, Young 1929, Moreau 1938
Galliformes (P)	Yes			McCabe and Hawkins 1946, Goodwin 1953, Guhl 1958, McBride et al. 1969
Strigiformes (A)		Yes	Yes	Trollope 1971, Meyer-Holzappel and Räber 1976
Charadriiformes (A, P)	Yes	Yes		Knappen 1930, Ashmole and Tover S. 1968
Coraciiformes (A)			Yes	Moreau and Moreau 1941, 1944
Apodiformes (A)		Yes		Ball 1943, Stoner 1947
Piciformes (A)	Yes	Yes	Yes	Kilham 1974
Passeriformes (A)	Yes	Yes	Yes	Sprunt 1944; Goodwin 1951; Skutch 1951; Sauer 1956 (<i>in Müller-Schwarze 1978</i>); Gwinner 1966 (<i>in Fagen 1981</i>); Gaston 1977; Pellis 1981, 1983

ered include species in which play has been observed. Only the Charadriiformes, which have both altricial and precocial species, were excluded from our analysis.

Of the 26 orders comprised of either precocial or altricial species, 10 (38.5%) contained precocial species and 16 (61.5%) contained altricial species. Play has been described in species of 12 (46.2%) of these 26 orders. A *G*-test of independence (with Williams' correction; Sokal and Rohlf 1981) indicated an interaction between the degree of physical development at hatching and whether an order contained species in which play has been reported ($G_{adj.} = 4.434$, $df = 1$, $P < 0.05$). Specifically, 10 (83.3%) of 12 orders in which play occurred were comprised of altricial species, and in 10 (62.5%) of 16 orders comprised of altricial species play has been observed. Only 2 (20.0%) of 10 orders with precocial species contained species in which play has been described. Object play was the most common type of play displayed and occurred in 8 (61.5%) of 13 avian orders that play (Table 1).

In mammals, play may be related to the size and development of the cerebral cortex (Fagen 1981). Mammals have larger cerebral cortices relative to the mass of the entire brain, higher encephalization quotients (EQ's; Jerison 1973, Eisenberg 1981), and show a greater incidence of play than do other vertebrates (Fagen 1981). In addition, the amount of postnatal neuronal arborization and the development of intricate synaptic networks in the brain may be extremely important in the elaboration of play and the ability to make use of information gained through play (Byers pers. comm.). In mammals, play presumably

is important in learning and in the development of behavioral plasticity (Bekoff and Byers 1981, 1985; Fagen 1981; Martin and Caro 1985).

Among birds there is evidence that higher species have more developed forebrains, a brain area important in learning (reviewed in Stettner 1974). Two of the 3 orders with species that displayed all three types of play (Psittaciformes and Passeriformes) also contain species with generally more developed forebrains when compared with species in which only locomotory types of play have been reported (e.g. Galliformes). Thus, play and its diversity in birds appears to be correlated with increased forebrain development, as is the case in mammals. However, an association between highly developed forebrains and play does not necessarily mean that the existence of play is a criterion by which "intelligence" or cognitive abilities can be predicted. Conversely, the presence of sophisticated learning skills does not necessarily imply the existence of play. The similarity between mammals and birds suggests that avian play is also important in learning and in the development of behavioral flexibility.

Altricial young probably spend considerable time socializing with adults and nest mates. This is a consequence of the prolonged post-hatching period spent in and around the nest. Further, altricial young may have more time to play and socialize because they do not forage for themselves, as do precocial young. From these assumptions we predict that social play should be more prevalent in orders that contain primarily altricial species. Indeed, the species in all seven avian orders that displayed social play were classified as primarily altricial (Table 1). The length of time that

young birds remain with siblings and adults, however, may not be as important in predicting the occurrence of social play as is the necessity for precocial young to spend large amounts of time feeding themselves. For example, ducks and geese are raised in large groups, but only locomotory types of play have been described in this order (Roberts 1934).

The diversity of behaviors classified as object play is not surprising, because birds are visually oriented (Ficken 1977). Organisms that rely heavily on vision are not committed to exhibit object play, but the types of intense object play displayed by birds seem to be associated with their well-developed visual skills. For example, many raptors play with various objects, including live prey (Fagen 1981), in a manner similar to play shown by mammalian carnivores that pounce on and toss objects in a modified form of predatory behavior called "predatory play." Parrots also play with objects, which may help them learn to manipulate food [Porter 1947; Jackson 1963; Keller 1975, 1976 (in Fagen 1981)].

Descriptions of play in birds are often anecdotal. Also, some behaviors such as vacuum activities (behaviors performed in the absence of an obvious stimulus; Lorenz 1950), displacement activities, and various patterns of threat or courtship may incorrectly be called play (Ficken 1977). Nonetheless, we found patterns in the types of avian play consistent with mammalian trends. First, the orders with mostly altricial species tend to exhibit more play, especially social play, than do orders with precocial species. Second, object play is most common, especially in raptors. The importance of other life-history characteristics (e.g. body size, specialists vs. generalists, migratory vs. nonmigratory species, species typically characterized as having helpers vs. species in which helping is rare or nonexistent, and species-typical social organizational patterns) also may influence the elaboration of different types of play. Derived generalizations on the role of avian play await quantitative comparative analyses.

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