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A Comparative Analysis of Social Play in Birds

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Summary
Although social play is broadly distributed among mammals, it is infrequently encountered in other vertebrate taxa. It is, however, displayed in a fully realized and complex form in several groups of birds. Unambiguous accounts of social play have been recorded from thirteen species of parrots, seven species of corvids, and several hornbills and Eurasian babblers. We conducted an analysis of the avian play literature, testing for differences between avian taxa, as well as for correlations between play complexity, brain size, and age of first reproduction. Corvids were far more likely to show social object play than parrots. Corvids, parrots, and hornbills had larger relative brain sizes than would be predicted from a class-level allometric regression, but brain size was not associated with the complexity of social play among genera within taxa. Play complexity within parrots and corvids was, however, significantly associated with the age of first reproduction. The likelihood of complex social play appears to increase when delayed reproduction is accompanied by persisting relationships between adults and post-fledging juveniles. The adaptive significance of social play in birds thus offers intriguing parallels to similar analyses in mammals.

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Introduction

Social play is pervasive among juvenile mammals, forming a central element in the social behavior of even relatively solitary species (Bekoff and Byers, 1998). Birds are also known to play socially, but very few avian taxa exhibit the full range of play behaviors, from play chases to complex reciprocal object play (Fagen, 1981; Ortega and Bekoff, 1987). Because birds and mammals share only a very remote evolutionary history, it seems likely that social play has evolved convergently in these groups, with possibly several independent origins. A close comparative analysis of social play in birds may, therefore, cast light on the selective factors that have encouraged its development, forming a parallel to similar studies of social play in mammals (Iwaniuk *et al.*, 2001).

Play behavior has been recognized in birds for over a century (Groos, 1898) and has since been described in ten orders of birds (Fagen, 1981; Ortega and Bekoff, 1987; adjusted to accord with Monroe and Sibley, 1993). Examples of avian social play, however, are generally uncommon (Skeate, 1985). Most instances of avian play behavior described in the literature are essentially solitary, either locomotory play (*e.g.* aerobatic flight of raptors, gulls and frigate birds in Stonehouse and Stonehouse, 1963; Simmons and Mendelsohn, 1993; Pandolfi, 1996; Gamble and Cristol, 2002) or object play, in the form of repeated manipulation of inappropriate items (*e.g.* "play caching" by pinyon jays, *Gymnorhinus cyanocephalus*, in Marzluff and Balda, 1992 and magpies, *Pica pica*, in Deckert, 1991; tossing stones by warblers, *Sylvia borin* in Sauer, 1956; bouncing on food by motmots, *Eumomota superciliosa*, in Smith, 1977).

Social play is prevalent in many groups of mammals (Brereton, 1971; Ewer, 1973; Ficken, 1977; Fagen, 1981; Barber, 1991; Bekoff and Allen, 1998). Some forms of play have also been described in reptiles or even fish (Fagen, 1981; Burghardt, 1998), but these species do not display the robust, reciprocal social play that is exhibited in its most elaborate forms in wolves, chimpanzees and humans (Beach, 1945; Mech, 1970; Fossey, 1978; Garvey, 1990; Parker and Milbrath, 1994; Power, 2000).

Parrots and corvids are generally considered to exhibit more extensive social play than other birds (Ficken, 1977; Fagen, 1981; Iwaniuk *et al.*, 2001). Within these groups, the most frequently cited exemplars of avian play have been keas (*Nestor notabilis*) and ravens (*Corvus corax*) (Fagen, 1981; Ortega and Bekoff, 1987; Heinrich and Smolker, 1998; Diamond and Bond, 1999). Play in these two species is certainly vigor-

ous, complex, and socially reciprocal and may well provide an equivalent to the social play of canids and higher primates (Fagen, 1981). How common social play may be among birds is difficult to assess, however. Descriptions of ostensible avian play in the literature are often too brief and anecdotal to categorize (Ficken, 1977). In fact, detailed studies of play in birds have focused mainly on keas, ravens, and a series of studies of the Australasian magpie (*Gymnorhina tibicen*; Pellis, 1981a, 1982).

Definitions of play behavior have been discussed extensively in the literature (*e.g.* Bekoff, 1976; Fagen, 1981; Bekoff and Byers, 1981; Bekoff, 1984; Barber, 1991; Bekoff and Allen, 1998; Power, 2000; Spinka *et al.*, 2001; Burghardt, 2001). This study focuses on social play, that is, play behavior that involves at least two individuals who interact with and respond to each other and are thus capable of exchanging information (Bekoff, 1974; Ficken, 1977; Fagen, 1981). Social play in birds shares many characteristics with social play in mammals. For example, it generally incorporates actions from a variety of contexts into labile temporal sequences and the actions are often repeated by mutual initiative. Social play most commonly involves juveniles (Power, 2000), but different kinds of social play may have different players and developmental time courses (Bekoff, 1974; Fagen, 1981; Simmons and Mendelsohn, 1993). Social play lacks consummatory behaviors (Lorenz, 1956), so that interactions are not resolved, but rather are repeated with the partners alternating roles, until they are distracted by other stimuli.

Behavioral evolution is most readily addressed through comparative studies, which aid in establishing functional associations between behavior and morphology or ecology (Lorenz, 1956; Bekoff *et al.*, 1981; Felsenstein, 1985; Harvey & Pagel, 1991; Bond and Kamil, 2002; Bond *et al.*, 2003). Studies of play in mammals have commonly used a comparative approach, but systematic comparative studies of play in birds are rare (Ortega and Bekoff, 1987; Fagen, 1981; Burghardt, 1998). Surveys of avian play have suggested that it is associated with altricial development (Ortega and Bekoff, 1987; Power, 2000), with larger relative brain size (Ortega and Bekoff, 1987; Heinrich and Smolker, 1998), and with higher degrees of sociality (Skutch, 1987; Collar, 1997). In this article, we describe the form and incidence of social play in the most unambiguous accounts in the avian literature and relate the similarities and differences to aspects of the species' taxonomy, morphology, and life history.

A survey of avian social play

To place avian play in a broader systematic context, we categorized instances of social play recorded in the literature. Our criteria were derived from classification systems proposed over the last forty years (Ficken, 1977; Fagen, 1981; Bekoff, 1984, 1995; Ortega and Bekoff, 1987; Pellis and Pellis, 1996; reviewed in Power, 2000). Conspecifics, in our view, engage in social play when they respond to one another, not just when they act in each other's presence. Social play may include various components that are facilitated (*e.g.* Ashmole and Tovar, 1968; Negro *et al*., 1996; Gamble and Cristol, 2002), but facilitation alone does not constitute sufficient evidence for social play. Our approach thus contrasts with that of Harvey *et al.* (2002), who divided play in captive Hawaiian crows (*Corvus hawaiiensis*) into solo and social play based on the proximity of the mate regardless of whether or not the birds were responding to each other.

We distinguished among four empirically separable categories of social play: play chasing, play fighting, play invitations, and social object play. Play chasing occurs when one bird follows another in flight or on the ground. It can be distinguished from flocking or other facilitative movements by the absence of consummatory behavior at the end of the chase and by the repeated exchange of roles of pursuer and pursued. Play fighting involves action patterns derived from agonistic behavior, but which are performed in ways that minimize injurious consequences. Play fighting also includes only a limited portion of the aggressive repertoire of the species. Play invitations are action patterns that occur predominately in the context of social play. They occur at the onset of a play interaction or after a brief interruption, and they are followed by play fighting or social object play. Social object play occurs when two or more individuals engage in repeated interaction with one or more inanimate objects in the environment without subsequent consummatory behavior. The best evidence of social object play is provided by contests over items that cannot be otherwise turned to useful purposes. Role reversals are common in social object play, and the interaction often ends with the contested item simply being discarded.

Our initial literature review provided examples of social play in eight families of birds (Table 1). Accounts of play chasing, particularly if they were contextually ambiguous and unaccompanied by other forms of social play, were subsequently excluded from our analysis (*e.g. Pygoscelis adeliae,* Muller-Schwarze, 1978; *Tauraco fischeri,* Moreau, 1938;

Table 1. Avian social play

Species	Play chase	Play fighting	Play invitation	Social object play	References (c = captive; w = wild)
Psittaciformes					
PSITTACIDAE					
Chalcopsitta sintillata	X				Collar, 1997 (w)
Pseudeos fuscata	X				Collar, 1997 (w)
Eolophus roseicapillus	X				Rowley, 1990, 1997 (w)
Nestor notabilis	X	X	X	X	Diamond and Bond, 1999 (w); Keller, 1975 (c); Potts, 1969 (c)
Nestor meridionalis	X	X	X		Diamond and Bond, 2002 (w); Jackson, 1963b (w)
Psephotus chrysopterygius	X				Collar, 1997 (w)
Melopsittacus undulatus	X	X			Engesser, 1977 (c)
Strigops habroptilus		X	X		Elliott, 2002 pers. com. (w)
Anodorhynchus hyacinthinus		X	X		Hick, 1962 (c)
Ara chloropterus	X	X	X		Deckert, 1991 (c); Hick, 1962 (c)
Myiopsitta monachus	X				Shepherd, 1968 (c)
Forpus conspicillatus	X				Garnetzke-Stollmann & Franck, 1991 (c)
Amazona albifrons	X	X	X		Levinson, 1980 (w,c); Skeate, 1985 (c)
Bucerotiformes					
BUCEROTIDAE					
Ceratogymna brevis		X			Moreau and Moreau, 1944 (w)
BUCORVIDAE					
Bucorvus leadbeateri	X	X		X	Kemp, 2001 (w); Kemp and Kemp, 1980 (w)
Passeriformes					
CORVIDAE					
Corcorax malanorhamphos	X	X		X	Chisholm, 1958 (w); Heinsohn, 2003 pers. com. (w)
Struthidea cinerea	X	X	X	X	Baldwin, 1974 (w); Chisholm, 1958 (w)
Pica pica	X				Deckert, 1991 (c)

Table 1. Avian social play (continued)

Species	Play chase	Play fighting	Play invitation	Social object play	References (c = captive; w = wild)
Corvus brachyrhyncos				X	Kilham, 1989, 1984 (w)
Corvus corax	X	X		X	Eklow, 1988 (w); Gwinner, 1966 (c); Heinrich and Smolker, 1998 (w)
Corvus albicollis				X	Moreau and Moreau, 1944 (w)
Gymnorhina tibicen	X	X	X	X	Pellis, 1981a, b (w)
SYLVIIDAE					
Turdoides malcolmi		X			Gaston, 1977(w); Hutson, 1954 (w)
Turdoides squamiceps	X	X		X	Posis, 1984 (w); Zahavi, 1990 (w)
Turdoides striatus	X	X			Gaston, 1977 (w)

Circus pygargus, Pandolfi, 1996; *Gypaetus barbatus*, Blumstein, 1990; *Dendrocopos villosus* and *D. pubescens*, Kilham, 1974). This was a particular problem with accounts of play chasing in raptors, because we could not distinguish observations of social play from facilitated flight movements (Simmons and Mendelsohn, 1993). The final data set thus consisted of 25 species in five families of parrots, hornbills, Eurasian babblers, and corvids (Table 1).

Social play in the Psittacidae

Most of the accounts of social play in our survey were recorded from parrots —thirteen species from this family alone (Table 1). In seven of these, social play consists solely of play chases and/or play fighting. For example, Collar (1997) describes small nursery flocks of newly fledged golden-shouldered parrots *Psephotus chrysopterygius* engaging "in wild careering flights" in and out of the trees. Similar behaviors have been seen in galahs (*Eolophus roseicapillus*), monk parakeets (*Myiopsitta monachus*), yellow-streaked lories (*Chalcopsitta sintillata*), dusky lories (*Pseudeos fuscata*), spectacled parrotlets (*Forpus conspicillatus*), and budgerigars (*Melopsittacus undulatus*) (Shepherd, 1968; Engesser, 1977; Garnetzke-Stollmann and Franck, 1991; Rowley, 1997; Collar, 1997).

Parrots that play fight usually "fence" or feint with the bill, push with the feet, or bite the feet or feathers of the play partner. Budgerigars, for example, try to bite their play partner somewhere on the body, usually in the feathers or the feet. The play partner parries with its beak, sometimes while producing soft croaking sounds, and the behavior often develops into a repeated beak duel, initiated by first one partner and then the other (Engesser, 1977). That such actions are play, rather than serious aggression, is suggested by the fact that they are performed slowly, that the interactions are reciprocally initiated, and that there is no apparent resolution, no winners or losers in the contests. Play fighting in white-fronted parrots (*Amazona albifrons*) is also readily distinguishable from actual aggressive interactions (Skeate, 1985). During aggressive interactions, these birds direct bill-gapes and bill-lunges at the opposing bird's head, but during play bouts, play-biting is directed mainly at the feet and toes of the other bird.

Play fights in keas and kakas (*Nestor meridionalis*) show many similar action patterns, but the event sequences appear to be generally more complex in keas (Diamond and Bond, 1999). Kakas engage in long, repetitive bouts in which one individual rolls over on its back while the partner jumps on its stomach, with mutual bite attempts and foot pushes (Diamond and Bond, 2002). They often sequentially reverse positions. Although keas roll over and jump on each other's stomachs, their play sequences commonly include actions taken while standing, including bite attempts, foot pushes, and bouts of mutual jump and flap. Fighting play also seems more aggressive in keas than in kakas, particularly with respect to their use of biting and wrestling with the bill. While kakas often gape at each other during play, we rarely observed them to bite their partners even during vigorous interactions. Kea play, in contrast, includes long bouts of bill locking, twisting and wrestling with each other using the bill, bouts that may persist even while one bird is standing on the stomach of the other. We repeatedly observed keas to bite each other during play, grabbing their partner by the tail, feet, or legs with their bills and even occasionally dragging the partner across the ground (Diamond and Bond, 1999).

Play fighting among wild parrots is most commonly observed among juveniles. In captivity, however, adult or subadult parrots often exhibit play fighting either between members of a mated pair or in interactions with human caretakers. A pair of captive red and green macaws (*Ara chloropterus*), for example, showed intense play fighting for

up to 30 min at a time on the roof of the nest box, standing between branches or hanging head down (Deckert and Deckert, 1982). Captive kakapos (*Strigops habroptilus*) play fight by raising their wings at each other, waving their feet, and lunging at each other, in a manner similar to what we have observed in keas (Elliott, 2003, personal communication), and a captive hyacinth macaw (*Anodorhynchus hyacinthinus*) commonly sought out opportunities to wrestle playfully with zookeepers (Hick, 1962).

Compared to play fighting, play invitations occur among relatively few species. Both species of *Nestor* parrots show play invitations of a generally similar form. For example, both species display a head cock at the onset of a play interaction, both perform a distinctive, hopping approach to a prospective play partner, and both species roll over on their backs as a means of soliciting initiation or resumption of social play. Keas in captivity have been recorded as showing additional forms of play invitation behavior. Keller (1975) reported four different play invitations in captive keas: 1) a stiff legged walk with the head directed toward the partner; 2) non-directed throwing of objects; 3) lying on the back, frequently with the head between the legs; and 4) parrying or lifting a foot while ducking and touching. In our observations of wild kea, most play sessions were initiated with head-cocks, hopping approaches, or rolling over. Tossing in keas was only associated with play among mature birds of opposite sexes, inferred to be a form of courtship play (Diamond and Bond, 1999).

Aside from our observations of wild kea and kaka, play invitations have been noted only in captive or semi-captive parrots: kakapos, white-fronted parrots, red-and-green macaws, and hyacinth macaws. For example, Elliott and his associates observed hand-reared kakapos to roll on their backs, waving their feet in the air as a play invitation to human handlers (Elliott, 2003, personal communication), similar to play invitations in *Nestor*. Like kakas, captive hyacinth and red and green macaws solicit human play interaction by a hopping approach with the head obliquely inclined, followed by rolling over on their backs (Hick, 1962; Deckert and Deckert, 1982). White-fronted parrots solicit play by sidling up to the other bird with head and body lowered (Skeate, 1985).

One of the most striking differences between keas and other parrots that are known to play, including kakas, is in their use of objects. Among keas, object play is a common component of both individual and group activities (Diamond and Bond, 1991, 1999). Whereas kakas

share many features of kea play, we never observed them to use objects in their social play (Diamond and Bond, 2002). A pair of fledgling keas, however, will often contest for a single object, such as a stick, a bone, or a piece of cloth, pulling at it from both ends or repeatedly stealing it away from one another. That such interactions are actually play, rather than simple competitive aggression, is suggested by the fact that object-oriented games often give way to active play fighting, leaving the contested object behind. A frequent type of object play in keas involves repeatedly tossing a small item in the air (Potts, 1969).We recorded keas tossing rocks, bottle caps, seed pods, walnuts and other small objects, especially during play interactions between individuals of opposite sexes, during which the tossing bird would also vocalize, jump and flap, and roll over (Diamond & Bond, 1999). Solitary object play is pervasive, but it is also highly facilitative. One kea playing with an object will often attract several more, leading eventually to a group of young birds all excitedly tugging on the same item. We once observed a group of fledglings spend almost an hour pulling on a long piece of surgical gauze, walking around with it and periodically hopping, jumping, and foot pushing (Diamond & Bond, 1999). With the exception of keas, social object play has not been unambiguously recorded in parrots. Although all parrots manipulate and demolish inedible items, they apparently do not commonly incorporate these objects into their social play interactions.

Social play in other birds

Other than parrots, social play has been recorded in only four families of birds: two families of hornbills, Eurasian babblers, and corvids. Among those species that engage in social play, there are more similarities than differences. Two species of hornbills have been recorded as showing play chases and/or play fighting (Table 1). Juvenile southern ground hornbills (*Bucorvus leadbeateri*) engage in fast aerial chases, bill wrestling, jumping on or over each other (Kemp, 2001). Young silvery-cheeked hornbills (*Ceratogymna brevis*) "barge" each other and wrestle with their bills (Moreau and Moreau, 1944). Kemp (2001) has also recorded social object play in ground hornbills, noting that juveniles "play tug-of-war with twigs."

Social play has also been observed in several species of Eurasian babblers. Jungle babblers (*Turdoides striatus*) perform mock fights in which some individuals lie on the ground, while others roll on top of

them or gently peck them. This species also engages in play chases in which several juveniles fly rapidly and apparently aimlessly among the branches of a tree, twisting and turning in aerobatic maneuvers (Gaston, 1977). Similar play chases and mock fights were observed in large grey babblers (*Turdoides malcolmi* Hutson, 1954; Gaston, 1977). According to Zahavi (1990), play in Arabian babblers (*Turdoides squamiceps*) is similar to that of young mammals, including mock fighting and rolling on the ground. They play chase, trying to replace one another from particular locations, and "playtug" twigs with one another (Posis, 1984, cited in Zahavi, 1990).

The corvids are the only group of birds other than parrots in which social play appears to be broadly distributed (Fagen, 1981; Ortega and Bekoff, 1987). Ravens, in particular, have frequently been cited as exhibiting social play that is on a par with that of keas (Gwinner, 1966; Ficken, 1977; Fagen, 1981; Van Vuren, 1984; Ortega and Bekoff, 1987; Heinrich and Smolker, 1998). Raven social play primarily involves play chases and social object manipulation. Ravens play chase in flight, slide down inclines, and hang upside down, sometimes with one foot dangling, and play tug of war with sticks (Gwinner, 1966; Heinrich and Smolker, 1998). Ravens have been observed play fighting with mutual bill biting while grasping each other's claws (Eklow, 1988), but this may not occur in all raven populations. Heinrich and Smolker (1998) noted that "young ravens do not engage in the kind of obvious play fights that are so pervasive in young felids or canids" (p. 42). These authors similarly state that they did not observe play invitations in ravens. American crows (*Corvus brachyrhyncos*) and white-necked ravens (*Corvus albicollis*) engage in social object play, but have not been recorded as showing other forms of social play. Kilham (1989) recorded yearling crows as playing tug-of-war with Spanish moss. White-necked ravens have been observed playing "king of the castle," where a bird standing on a grass clump would pick up a piece of dry cow dung or a small stick. His opponent would then charge up to him and wrestle for the object. Once the challenger leapt at the other bird and struck with its feet. Another time, the bird with the twig appeared to throw it at his opponent (Moreau and Moreau, 1944).

The endemic Australian corvids, particularly apostlebirds (*Struthidea cinerea*, Baldwin, 1974), white-winged choughs (*Corcorax malanorhamphos*, Heinsohn, 2003, personal communication; Chisholm, 1958), and Australasian magpies (Pellis, 1981a, b, 1982), show a full range of play behaviors, including play chases, play fighting, play invitations, and social object play. Australasian magpies and apostle-

birds may be the only avian species other than keas that show all four types of social play. Some behaviors used in these corvid interactions, particularly play invitations, show similarities to those of parrots. For example, apostlebirds invite play by rolling over on their backs, much as keas and kakas do. According to Baldwin (1974), a dominant male may voluntarily turn over, relax his claws, and let other birds peck his abdomen for a while, then jump clear and lead a chase around neighboring trees. White-winged choughs and apostlebirds also engage in social object play, primarily tug-of-war with sticks and leaves, sometimes while rolling over on their backs (Chisholm, 1958; Baldwin, 1974). Australasian magpies invite play by engaging in a "bouncy walk" that typically leads to play fighting. In this display both feet leave the ground together, the head and neck are retracted, and the torso is slightly lowered at the onset of each bounce (Pellis, 1981a). Sometimes short bouts of play fighting are interspersed within longer bouts of other interactions. Social object play is apparently less common in Australasian magpies than either play fighting or play chasing and typically involves one bird attempting to take away another's play object (for example, a twig or leaf).

The most conspicuous difference between social play in corvids and that of parrots is the degree to which it revolves around objects. Black-billed magpies show only play chasing, but all other corvids known to play socially do so wholly or partly in the context of object manipulation (Moreau and Moreau, 1944; Kilham, 1989; Deckert, 1991; Heinrich and Smolker, 1998). When compared across all available species records, using one observation per genus to reduce statistical dependencies (Harvey and Pagel, 1991), social object play was significantly more frequent in corvids than in parrots (Fisher's exact test, $p = 0{:}01$), suggesting that social play has evolved a distinctly different appearance in the two families and possibly serves different functions.

Play, brain size, and development

Ortega and Bekoff (1987) remarked that parrots and passerines, two groups of birds in which play has commonly been observed, also have relatively larger brains than other avian taxa. Whether brain size is statistically predictive of the occurrence of social play in birds is not evident from the literature, however. The occurrence of play has also been associated with altriciality, behavioral flexibility, and soci-

ality (Ortega and Bekoff, 1987; Skutch, 1987), and these variables are to some degree intercorrelated with brain size (Bennett and Harvey, 1985a, b; Lefebvre *et al.*, 2002, 2001, 1998, 1997; Sol and Lefebvre, 2000; Timmermans *et al.*, 2000; Sol *et al.*, 2002). To explore the relationship between social play, brain size, and ontogeny in individual species, we categorized the species of Psittacidae and Corvidae in Table 1 (the families for which we had the most extensive data) based on whether they showed only play chases or play fighting (here considered "simple" social play) or whether they additionally showed play invitations or social object play (categorized as "complex" social play). The resulting "play index" (1 = simple; 2 = complex) is comparable to the methods used by Iwaniuk *et al.* (2001) to categorize play complexity in mammals.

The social play index was combined with additional data from the literature on brain size, body size, and age of first reproduction (Table 2). Body masses were generally obtained from Dunning (1993), after standardizing the taxonomy to that of Sibley and Ahlquist (1990) and Monroe and Sibley (1993), though values for several species had to be obtained from other sources (Fernandez *et al.*, 1997; Woxvold, personal communication, 2003). Brain sizes were obtained from Mlikovsky (1989, 1990), integrated with more recent data (Rehkämper *et al.*, 1991; Fernandez *et al.*, 1997; Iwaniuk and Nelson, 2002). Brain masses were unavailable for several species known to play socially, but in four cases, we were able to substitute values from congeneric species of comparable body (*Amazona leucocephala* for *A. albifrons*; *Chalcopsitta atra* for *C. sintillata*; *Psephotus haematonotus* for *P. chrysopterygius*; and *Forpus passerinus* for *F. conspicillatus*). The only species for which brain sizes could not be approximated from published sources were the Australian Corcoracinae—*Struthidea* and *Corcorax*. Age of first reproduction was estimated from the literature for all but one of the species (citations in table). In general, birds showing more complex social play tend to be larger, to have absolutely larger brain sizes, and to take longer to reach sexual maturity. With only one exception, larger birds with longer development times show complex social play, while smaller, more rapidly developing birds show simple play.

To determine the influence of brain size and ontogeny on social play independent of body size, we extracted relative measures as residuals from allometric regressions (Jerison, 1973; Bennett and Harvey, 1985a; Gaillard *et al.*, 1989; Timmermans *et al.*, 2000; Iwaniuk *et al.*, 2001). For the brain size measures, we log-transformed our tabled values and calculated residuals from Nealen and Ricklefs' (2001) major axis regres-

Table 2. Play, morphometrics, and age of first reproduction in parrots and corvids

Species	Play index	Body mass (g)	Brain mass (g)	First rep (yr)	Reference to age of first reproduction
Psittacidae					
Chalcopsitta sintillata	1	195	5.90	1-2	Low, 1977; Higgins, 1999
Pseudeos fuscata	1	149	4.20	1-2	Low, 1977; Higgins, 1999
Elophus roseicapillus	1	337	6.78	2-3	Rowley, 1990
Nestor notabilis	2	868	15.50	3-4	Jackson, 1963a
Nestor meridionalis	2	455	9.50	2-3	Holland, 1999
Psephotus chrysopterygius	1	70	2.00	1	Forshaw, 1977
Melopsittacus undulatus	1	29	1.37	≤1	Forshaw, 1977
Strigops habroptilus	2	1670	14.50	9	Elliott *et al.*, 2001
Anodorhynchus hyacinthinus	2	1500	24.50	4-7	Lücker and Patzwahl, 2000
Ara chloroptera	2	1400	23.40	5-7	Munn, 1992
Myiopsitta monachus	1	92	3.83	2	Martín and Bucher, 1993
Forpus conspicillatus	1	25	1.20	1	Forshaw, 1977
Amazona albifrons	2	233	6.40	3-5	Levinson, 1980
Corvidae					
Corcorax melanorhamphos	2	364	—	4	Rowley, 1978
Struthidea cinerea	2	131	—	3-4	Chapman, 1998
Pica pica	1	183	5.76	1-2	Birkhead, 1991
Corvus brachyrhynchos	2	421	8.00	3-5	McGowen, 1996
Corvus corax	2	1144	15.26	3-4	Ratcliffe, 1997
Corvus albicollis	2	900	12.00	–	
Gymnorhina tibicen	2	330	4.98	3-4	Veltman, 1989

sion of avian brain and body masses. To correct the age of first reproduction for body size effects, we combined the values in Table 2 with the broader survey provided in Appendix 2 of Gaillard *et al.* (1989) and conducted a major axis regression on the log-transformed data (Sokal and Rohlf, 1981; Seim and Saether, 1983). Body size and age of first reproduction were significantly associated, with the allometric regression accounting for 93% of the variance (mean log body mass = 5.94; mean log age of maturity = 0.62; slope = 0.255).

Residual measures of brain size and age of first reproduction were then analyzed for effects of play complexity (Figure 1). To reduce

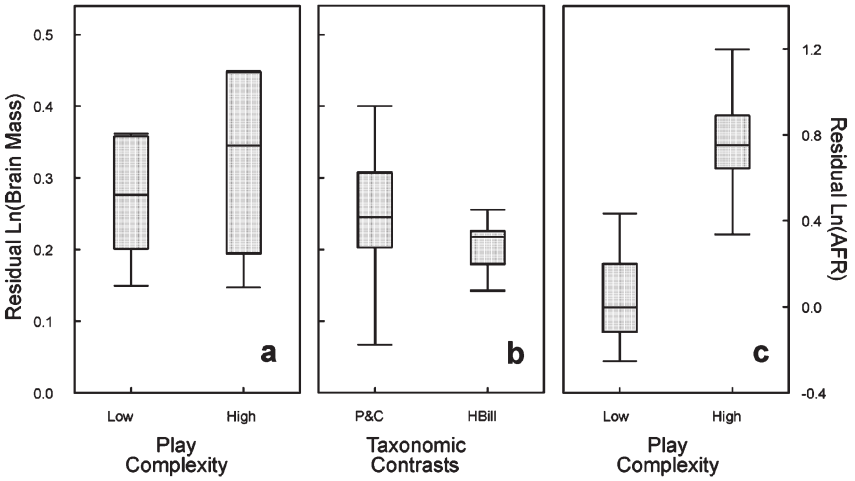

Figure 1. Contrasts in brain size and age of first reproduction (AFR). Data from individual species were log-transformed and corrected for body size effects by converting to residuals of major axis allometric regressions. Box plots display medians, hinges, and adjacent values from the distribution of residuals averaged within genera. **a**: Average residual log brain sizes for Low (N = 8 genera) and High (N = 7 genera) play complexity groups of parrots and corvids. **b**: Comparison taxa — P&C (N = 32 genera) are genera of parrots and corvids not described as showing social play; HBill (N = 6 genera) are genera of hornbills, two of which were described as showing social play. **c**: Residual log age of first reproduction for Low (N = 8) and High (N = 7) play complexity groups of parrots and corvids.

statistical dependency, average residuals were calculated for *Corvus* and *Nestor*, both of which were represented by two or more species, and analyses were conducted at the generic level (Harvey and Pagel, 1991). More precise methods for controlling for phylogenetic relationships are available (Iwaniuk *et al.*, 2001), but they could not feasibly be employed in this case, given the small sample size and the uncertain state of knowledge of parrot systematics (Sibley and Ahlquist, 1990). Residual brain sizes (Figure 1a) were significantly greater than zero for species with both simple and complex social play (simple: $t(7) = 9.26$, $p < 0.001$; complex: $t(6) = 7.23$, $p < 0{:}001$), but the two groups did not differ significantly from each other (Wilcoxon rank sums, $W^{+}(8, 7) = 64$, $p > 0.4$). Parrots and corvids are generally considered to have relatively larger brains than other, unrelated birds with similar body sizes (Ortega and Bekoff, 1987), which could account for the significantly positive residuals. The alternative hypothesis, however, is that

parrots and corvids that show any level of social play have relatively larger brains, that social play per se is associated with larger brain size (as is true, at least at the ordinal level, in mammals: Iwaniuk *et al.*, 2001).

To test this hypothesis, we constructed a comparison group, consisting of all parrots and corvids in Mlikovsky's (1989, 1990) data base that were not included in our survey of social play. Brain size and body size for this set of 66 species were log-transformed, and residual brain sizes were calculated from Nealen and Ricklefs' (2001) allometric regression (Figure 1b). For analysis, the species residuals were averaged within genera, as discussed above, and genera that were included in the social play data were removed. As expected, residual brain sizes in this comparison group were also significantly greater than zero ($t(31) = 16.2$, $p < 0{:}001$). Brain sizes for species with both simple and complex social play did not differ significantly from those in the comparison group, however (simple: $W^{+}(8, 32) = 186$, $p > 0.4$; complex: $W^{+}(7, 32) = 180$, $p > 0{:}15$). Parrots and corvids that play socially at any level of complexity do not appear to have larger relative brain sizes than are characteristic of the families as a whole. It should be noted that there are undoubtedly a number of species in our comparison group that do play socially, but that have not been observed to do so. As a result, this analysis may be unduly conservative.

Relative brain size is, however, greater in these two playful avian families than would be expected from the allometric regression of brain and body size for birds as a whole, much as Ortega and Bekoff (1987) assumed. To test whether this relationship might hold for other avian taxa from which extensive social play had been recorded, we conducted the same analysis of residual brain size averaged within genera for the Bucerotiformes. The six genera of hornbills in Mlikovsky's (1989; corrected to accord with Sibley and Monroe, 1990) data base (including two that had been recorded as showing play fighting or social object play) showed significantly higher relative brain sizes than expected (Figure 1b; $t(5) = 15.1$, $p < 0{:}001$), supporting the notion that extensive social play in birds may generally be associated with relatively large brain sizes. Because the complexity of social play was not significantly associated with brain size when comparing among genera of parrots and corvids, however, we must infer that the relationship between brain size and play differs according to the rank of the taxon being analyzed (Harvey and Pagel, 1991; but see Byers, 1999), as Iwaniuk *et al.* (2001) discovered in a similar species-based analysis of play in mammals.

A similar, generic-level analysis of the relationship between social play complexity and age of first reproduction, in contrast, showed a statistically significant difference ($W^{+}(8,9) = 37$, $p < 0{:}001$), with the complex social play species taking considerably longer to reach maturity (Figure 1c). The residual age of first reproduction for the complex play group was also significantly greater than zero ($t(8) = 9.19$, $p < 0.001$), while that for the simple play group was not ($t(7) = 0.52$, $p > 0.6$). Parrots and corvids that exhibited simple social play thus showed an age of maturity that was entirely in line with what would be expected of an average bird of their body size, while those that exhibited more complex social play showed a greater age of first reproduction than expected. This suggests that complex social play may be functionally distinctive from simple social play and that it may have evolved in association with a later age of first reproduction. Our findings are consistent with analyses of play in mammals that have demonstrated a strong association between play complexity and the length of the juvenile phase, even when the data are corrected for body size effects (Joffe, 1997; Pellis and Iwaniuk, 2000).

Discussion

The phylogenetic distribution of social play in birds suggests that fully realized play fighting, play invitation, or social object play has evolved separately in at least four different lineages, including parrots, corvids, hornbills, and Eurasian babblers. Of these, only parrots and corvids currently provide a sufficient sample of playing species to allow for tentative interpretations of the pattern of evolution of the behavior. Social play appears to be widely distributed among the Psittacidae, occurring in at least some form even in species as ecologically and taxonomically distant as budgerigars and hyacinthine macaws. In addition, many of the characteristic action patterns of *Nestor* social play, including rolling over, hopping, bill fencing, and wing flapping, are displayed in similar forms and contexts across some species in both the Australasian and the South American radiations (Smith, 1975; Sibley and Ahlquist, 1990; Christidis *et al.*, 1991). It is possible that social play behaviors may be phylogenetically primitive in the Psittacidae, and that parrot species that have not been recorded as showing social play either may have lost the behavior secondarily or may not yet have been observed under appropriate environmental or developmental circumstances.

The phylogeny of social play in corvids appears to have taken a different course. The form of the behavior is readily distinguishable from that in parrots. Social object play is significantly more frequent in corvids and, with the exception of the cooperatively breeding Australian species, play invitations appear to be less common. This suggests that the selective factors that led to social play in corvids may have differed from those in parrots. Corvids show more foraging innovation than parrots and more tool use (Lefebvre *et al.*, 1998, 2001, 2002), suggesting that exploratory or playful object manipulation is a more common feature of corvid behavior, and its incorporation into their social play may have parallels to the evolution of social object play in keas.

Our analyses of the effects of relative brain size and age of first reproduction suggest that social play in birds has evolved in response to a range of causal factors operating at different taxonomic levels. Higher-level taxa that include socially playing species (corvids, parrots, and hornbills) have significantly larger relative brain sizes than would be expected of an average bird of similar body size, confirming the suggestions of previous authors (Fagen, 1981; Ortega and Bekoff, 1987). Brain size is only one component of a larger adaptive complex, however. These avian groups are also characterized by altricial development, and altriciality has also been found to be associated with both higher incidence of play behavior (Ortega and Bekoff, 1987) and larger relative brain size (Bennett and Harvey, 1985b).

The fact that we found brain size to have no predictive value with respect to the complexity of social play within taxa, however, suggests that its causal associations with social play are rather remote (Iwaniuk *et al.*, 2001). At the ordinal or family level, differences in relative brain size are probably best viewed as part of a large-scale life history variation in birds. In more altricial species, greater post-hatching parental investment is associated with smaller clutch sizes and larger adult brains (Bennett and Harvey, 1985a, b; Ricklefs and Starck, 1998). Large relative brain size and altricial development may, thus, be considered preconditions for the evolution of play behavior, rather than direct causal factors (Table 3; Harvey and Pagel, 1991).

Within these altricial taxa, the evolution of social play appears to be promoted in families or genera that show higher levels of sociality, of associations or relationships between multiple individuals that persist over time (Table 3). Skutch (1987) provides a number of examples of social play in cooperatively breeding species, including Australian corvids, ground hornbills, and babblers, all of which were cited in our lit-

Table 3. The occurrence and complexity of social play in birds is influenced by different causal factors at different taxonomic levels

Taxonomic level	Life history variable or factor	Occurrence/ Type of play
Order/Family	Larger brain size/Altriciality	Enables evolution of play
Family/Genus	Sociality/Cooperative breeding	Promotes social play
Genus/Species	Delayed reproduction/Persistent association of juveniles with adults	Selects for complex social play in taxa in which social play is relatively common

erature survey (Table 3). Parrots do not breed cooperatively, but many of them are highly gregarious, particularly outside of the breeding season, with fledged young forming persisting associations with parents or other juvenile birds (Rowley, 1990; Munn, 1992; Collar, 1997; Juniper and Parr, 1998; Diamond and Bond, 1999). Similar social attachments are exhibited in many of the larger corvids, as well (Kilham, 1989; Ratcliffe, 1997). Sociality does not compel the evolution of social play, however, even in taxa that are well-represented with playful species. Cooperatively breeding corvids in North America have been studied intensively for many years (*e.g.* Woolfenden and Fitzpatrick, 1984, 1990; Brown, 1987; Skutch, 1987; Marzluff and Balda, 1992). These studies have yielded some suggestions of solitary play (Skutch, 1987; Marzluff and Balda, 1992), but no unambiguous instances of social play have been noted.

Within avian taxa that show social play, the behavior appears to acquire a more complex, differentiated form in species in which delayed reproduction is accompanied by persistent associations between juveniles and adults (Table 3). Delayed maturation alone is not sufficient, as there are numerous avian taxa in which young birds require years of experience prior to beginning breeding, but from which no instances of social play have ever been documented (*e.g.* Pelecanidae, Ciconiidae, or Procellariidae; Gaillard *et al.*, 1989). The addition of a persisting association between conspecifics and post-fledging juveniles appears to be crucial in promoting complex social play. For example, juvenile keas and kakas engage in complex social play when they aggregate with adults at feeding sites. Complex social play in apostlebirds occurs between juvenile helpers within a cooperatively breeding family group. In Arabian babblers, complex social play is observed among juvenile birds remaining in their parental group over a subsequent breeding season. The factors that facilitate the occurrence of simple social play—play chasing

and play fighting—are less evident, but the fact that only complex social play shows an association with age of first reproduction suggests that these two behavioral categories may be functionally and evolutionarily distinct.

The association between delayed reproduction and complex play could simply reflect the consequences of a release from the evolutionary constraints that apply to young animals trying to make their own way in the world. Social play is potentially hazardous and, of necessity, it is generally accorded lower priority than predator avoidance, foraging, or intraspecific aggression (Fagen, 1981; Power, 2000). However, the combination of a prolonged nonreproductive phase with at least adventitious custodial care by adults may provide the necessary protective environment that would allow selection for social play to operate (Diamond and Bond, 1999). In this view, juvenile birds that exhibit complex play may be experiencing a social environment that is similar, in many ways, to that of juvenile mammals. Social play in the most playful species of birds certainly rivals that of carnivores and possibly that of primates (Fagen, 1981; Ortega and Bekoff, 1987). Yet play is broadly distributed among mammals and, in contrast, relatively limited among birds (Iwaniuk *et al.,* 2001). There are undoubtedly many reasons for this striking difference between the vertebrate classes, but it is worth noting that long, protected juvenile phases with extended parental care are characteristic of mammalian social development and generally rare among birds (Ewer, 1973; Pagel and Harvey, 1993). If social play occurs primarily where there are persisting custodial associations between juveniles and adults, the conditions necessary for its evolution may be met with more often among mammals than among birds.

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