



The evolution of social play in songbirds, parrots and cockatoos - emotional or highly complex cognitive behaviour or both?

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ABSTRACT

Social play has been described in many animals. However, much of this social behaviour among birds, particularly in adults, is still relatively unexplored in terms of the environmental, psychological, and social dynamics of play. This paper provides an overview of what we know about adult social play in birds and addresses areas in which subtleties and distinctions, such as in play initiation and social organisation and its relationship to expressions of play, are considered in detail. The paper considers emotional, social, innovative, and cognitive aspects of play, then the environmental conditions and affiliative bonds, suggesting a surprisingly complex framework of criteria awaiting further research. Adult social play has so far been studied in only a small number of avian species, exclusively in those with a particularly large brain relative to body size without necessarily addressing brain functions and lateralization. When lateralization of brain function is considered, it can further illuminate a possibly significant relevance of play behaviour to the evolution of cognition, to management of emotions, and the development of sociality.

1. Introduction

It was once thought that very few animals play and that pets, such as domestic dogs, continue to play in adulthood only because they were encouraged to do so by their human families (Trut, 1999). This process of paedomorphosis, the perpetuation of juvenile traits into adulthood, placed play behaviour in adult animals into some kind of medical aetiology (Packer, 2018). However, although the process of domestication of dogs, cats (Bradshaw et al., 2015) and even rats (Pellis et al., 2019) showed some very dramatic behavioural and genetic effects (Trut et al., 2004; Packer, 2018), adult play has also been documented in adult wild wolves and coyotes (Bekoff, 1974; Cordoni and Palagi, 2012). Indeed, it was soon discovered that many non-domesticated animals play and do so in adulthood (Cordoni, 2009; Palagi, 2023).

Today, play behaviour in animals has been well-documented in a very wide range of mammals (Fagen, 1981; Bekoff and Allen, 1998; Bekoff and Byers, 1998; Palagi, 2023), and even in fish, amphibians and reptiles (Burghardt, 1998, 2015; Dinets, 2015). However, the most extensive research of play behaviour has been conducted with rodents (Pellis et al., 2019; Cooper et al., 2023), great apes (Fagen, 2002; bonobos, *Pan paniscus*: Palagi, 2006; chimpanzees, *Pan troglodytes*: Palagi et al., 2004a; Mielke and Carvalho, 2022; mountain gorillas, *Gorilla beringei beringei*: Mirville et al., 2020) and other primates: white-headed

langurs, *Trachypitecus leucocephalus*, found in China (Yang et al., 2022), and macaques (Ciani et al., 2012). Studies in social play have also seen a substantial increase in the last few decades and produced many insights that have helped formulate a range of theories on the potential functions of play, including enhancement of brain development (Achterberg and Vanderschuren, 2023). However, the focus of studies in play behaviour, be this in animals or humans, has largely been on child/juvenile/ and adolescent stages and, in that developmental framework, has often been based either on the 'social skill hypothesis' (Baldwin and Baldwin, 1974; Pellis et al., 2010) or 'the motor training hypothesis' (Byers and Walker, 1995; Nunes et al., 2004b). Most studies of rodents and primates fit into either one of these hypotheses or a combination of both (Gallo et al., 2021).

By contrast, studies on play behaviour in birds have appeared later and are nowhere as numerous as studies on rodents and other small mammals.

In fact, studies on many aspects of cognition in birds have thrived in the last decades and have done so without once mentioning play behaviour. Studies on avian cognition, for instance, have often relied on assessing pallial neuron numbers, and while these cannot reliably predict all cognitive performance traits, neuron numbers may predict learning speed and the ability to adjust to novel situations (Sol et al., 2022), leading to suggestions of innovativeness being related not just to

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brain size but actual neuron numbers, and also to life history criteria. Sol and colleagues further argued that "the number of pallial neurons is greater in brains that are larger in both absolute and relative terms and positively covaries with longer post-hatching development periods." (Sol et al., 2022). Another recent study found that songbird species showing more complex vocal learning are better problem-solvers and have larger brains (Audet et al., 2023). The relevance to birds as social players is palpable here: long period of development (super-altricial) and large brains are characteristics of all socially playing birds (Diamond and Bond, 2003).

As I discovered in a detailed study of over 200 species of songbirds and parrots, play behaviour and cognition are firmly linked (Kaplan, 2020). Each separate category of play (solo, object and social play) showed a distinct difference in brain size: the species with the largest brains were also the species with the most complex form of play (social play). Species that played with objects (but not socially) had smaller brains than social players but larger brains than exclusive solo players who, in turn, had larger brains than non-players (Kaplan, 2020). This direct relationship between types of play and brain size raises many questions about correlational and even causative relationships between the many abilities usually cited as complex cognition, such as learning ability, problem-solving, innovative behaviour and many other categories. Since play behaviour is expressed early in the organism's development, earlier than any forms of problem solving, learning or innovative behaviour become manifest, one could ask whether play behaviour in birds might determine brain size development and thereby cognition or even vice versa: larger brain size and higher cognition determines play. While this may be a step too far (implying causal relationships when all we know is that they covary), these results show, especially when compared to problem-solving and other advanced cognitive qualities, that social play behaviour in birds fits centrally into discussions on cognitive abilities in birds and is not a marginal issue at all.

Many vertebrate juveniles play, but social play in adult birds is a category so far not described in many species (Diamond and Bond, 2003), and it seems to be reserved for a special, cognitively complex group of birds.

Because of the strong link between large brain size, cognition and social play, this paper will therefore concentrate on social play in birds, review what is so far known, and suggest areas of future research. This is the first attempt to do so since Bond and Diamond's thorough review twenty years ago (Bond and Diamond, 2003), reflected also in their recent book on New Zealand's keas, *Nestor notabilis* (2019). Within this category of social play, the emphasis will be on adult social play behaviour because it is in this category in which most future research would most likely produce the most promising results and possibly confirm the centrality of play behaviour in discussions on the evolution of complex cognition.

2. Research context of play behaviour in birds

In birds, play behaviour has been described in ten orders (Ficken, 1977; Fagen, 1981; Ortega and Bekoff, 1987) but with less emphasis on 'honing skills' or 'motor training'. The categories used in describing forms of play in birds are the same as in other vertebrates: solo or solitary/locomotor play (such as running), object play and social play (Ortega and Bekoff, 1987; Burghardt, 2005).

While most research on play has concentrated on species belonging to the orders of passerines and psittacines, occasional evidence of play behaviour has been reported to occur in species belonging to other orders; for example, in flight (Emlen, (1957); Hedenström and Möller, (1992); e.g., acrobatic flight of vultures (Blumstein, 1990; other raptors: Simmons and Mendelsohn, 1993; gulls: Harvey and Inman, 2022; frigate birds: Diamond, 1975; Birch, 2000), or in 'play catching' of objects documented in American darters, *Anhinga anhinga* (Webber, 2021), in cormorants and various herons (Sazima, 2008), and also in pinyon jays,

Gymnorhinus cyanocephalus (Marzluff and Balda, 1992). In some, by no means all, cases it has been shown that object manipulation in juvenile birds can be related to specific prey items or foraging techniques (Greenberg, 1999), making object play functionally relevant, for instance, when preferred objects are similar in shape or colour or size to prey items, as was shown to be the case in American kestrels *Falco sparverius* (Negro et al., 1996).

By contrast to solo and object play, examples of avian social play are still relatively sparse (Skeate, 1985), whereas social play, be this in friendly or in play-fighting contexts, is prevalent in many groups of mammals, at least in juveniles (Fagen, 1981; Barber, 1991). Social play, including play-fighting, may be the most common form of play in juvenile rodents and mammals generally (Bekoff, 1984; Taylor et al., 2012; Pellis et al., 2019) but contrary to the findings in mammals, in birds, social play seems to be the least common form of play, especially in adults.

Solo play involves the largest number of avian species. Indeed, solitary play may well cover at least half of all avian orders (out of 44 orders in toto). Fewer orders and species are engaged in object play and, as far is now known, social play is present in the smallest number of species (Skeate, 1985; Ortega and Bekoff, 1987; Bond and Diamond, 2003; Kaplan, 2021b). Moreover, the number of orders including species that play socially shrinks to three: passeriformes (perching/ songbirds), psittaciformes (cockatoos, parrots and lorikeets) and bucceriformes (hornbills). Admittedly, passerines and psittacines are extremely large orders. There are 10,980 avian species (19,830 when subspecies are included), 44 orders, 253 families and 2385 genera (Gill et al., 2023) of which well over half are passerines. Among the passerines the corvoidea alone offer a rich field of study consisting, as they do of 29 superfamilies (Kaplan, 2018; Schodde, 1999, 2005) including all corvids and allies (Table 1). Psittacines may only have 101 genera (about 400 species) but are overrepresented in avian cognitive studies.

Play behaviour in birds has a less intense and investigative research history than that of mammals, especially of rats, but it has been discussed in comparative contexts. More recently, research on play behaviour in birds has shifted attention to links with life histories (Sayol et al., 2020), cognition (Ricklefs, 2004), prosocial (Kaplan, 2020; Bauer et al., 2021) and generally cooperative behaviour (Iwaniuk and Arnold, 2004; West, 2014; Gray, 2019), as well as intensive research into brain structure and function in avian species, including brain size and neural density (Iwaniuk et al., 2005; Burghardt, 2010; Franklin et al., 2014; Güntürkün and Bugnyar, 2016; Smeele et al., 2021). Before cognitive avian research gained momentum, the idea that birds could be capable of complex behaviour, given their small brain sizes, seemed impossible (Chappell, 2017). This proved to be an incorrect assumption (Vallortigara et al., 2010; Shimizu et al., 2017). Indeed, the innovative cognitive research into avian species has revolutionised the field, finding that some cognitive abilities of some avian species are on a par with those of chimpanzees (Olkowicz et al., 2016). One can add here that social play in birds is as complex and multi-layered as that of primates (and sometimes of children) may be. Bond and Diamond (2003) drew the conclusion that the occurrence of social play in birds is influenced by three key factors: large brain size, altriciality which enabled the evolution of play; sociality and cooperative breeding which promoted social play and, importantly, delayed reproduction and persistent association with other juveniles and adults (Bond and Diamond, 2003) and that is a conclusion that I would find difficult to refute.

The few examples of documented play behaviour in birds, even just among these super-families that make up the corvoidea (Table 1), provide a strong argument for not assuming that we know much about social play in birds. There are 130 species of corvidae alone and this genus *Corvus*, includes crows, rooks, and ravens, which make up over a third of the entire family of corvidae. The psittacines account for over 380 species (Gill et al., 2023). And in each cluster, we know of a few cases showing play behaviour, but it is not clear whether they are representative of all birds in the cluster. How confident can we possibly

Table 1

Superfamilies of corvoidea and incidence of play behaviour (Families marked in red have been studied in some detail; blue indicates that some very limited observations are available (referring only to play behaviour).

1. Paramythiidae (tit berrypecker and crested berrypeckers);	15. Neosittidae (sitellas);
2. Psophodidae (whipbirds, jewel-babblers and quail-thrushes);	16. Eulacestomidae (ploughbill);
3. Platysteiridae (wattle-eyes and batiss);	17. Oreoicidae (Australo-Papuan bellbirds);
4. Tephrodornithidae (woodshrikes and allies);	18. Pachycephalidae (whistlers, shrike-thrushes, pitohuis);
5. Prionopidae (helmetshrikes);	19. Laniidae (shrikes); 20. Vireonidae (vireos);
6. Malaconotidae (bush-shrikes);	21. Oriolidae (orioles, figbirds);
7. Machaerirynchidae (boatbills);	22. Dicruridae (drongos);
8. Vangidae (vangas);	23. Rhipiduridae (fantails);
9. Pityriaseidae (Bornean bristlehead);	24. Monarchidae (monarchs and allies);
10. Artamidae (Australian magpies, butcherbirds, currawongs);	25. Corvidae (ravens, crows and others);
11. Rhagologidae (mottled whistler);	26. Corcoracidae (white-winged choughs, apostlebird);
12. Aegithinidae (iotas);	27. Melampittidae (melampittas);
13. Campephagidae (cuckoo-shrikes, trillers);	28. Ifridae (ifritabirds);
14. Mohouidae (whiteheads);	29. Paradisaeidae (birds of paradise).

(Source: Kaplan, 2018–Schodde and Mason, 1999)

be that social play is rare in birds, since it has been examined in only a handful of species of those orders and fewer still within their natural environment (i.e., not as an artefact of habituation and captivity)?

In all, our current knowledge rests on fewer than 2 percent of passerine orders and, at best, on 5 percent of psittacines and, and a far lower percentage for Class Aves as a whole. There is a good deal more research to be done, preferably in observational studies in the natural environment, before we can say with confidence that a) play behaviour is part of juvenile development in a specific group of birds and b) play behaviour constitutes a part of social life in adults, belonging to specific groups or clusters of birds.

Yet, despite the dearth of information for Class Aves generally, we are at least now in the position to examine more specific questions. To be able to do so, this paper will confine itself to social play in avian species, the first attempt to undertake this since Bond and Diamond's thorough review twenty years ago (Bond and Diamond, 2003) and reflected also in their recent book on New Zealand's keas, *Nestor notabilis* (2019). Within this category of social play, I will refer only to adult social play behaviour.

3. Circumstances for play and categories of play

It is generally agreed that individuals of any species that engage in play behaviour are healthy, well-fed, not stressed, fearful or threatened (Fagen and Fagen, 2004), and have spare time. The play activities they engage in are voluntary, may be pleasurable, can be innovative and are seemingly performed for their own sake (Burghardt, 2005). At the same time, it has been recognised for some time that social play in mammals, including humans, may contribute substantially to an increase in social, emotional, and cognitive skills (Graham and Burghardt, 2010; Pellis and Pellis, 2009; Vanderschuren and Trezza, 2014).

Ortega and Bekoff (1987) divided play performance into three large categories: solo play, object play and social play to arrive at measurable behavioural units and these subdivisions are generally still applicable. However, social play is the only category in which a variety of important social and biological factors in playing adults seem to be present, be these mammals or birds: their life history data show slow development indicating substantial parental investment in time, large or exceptional

brain size compared to other avian species, advanced cognition and often at least some early expressions of prosocial behaviour (Fagen and Fagen, 2004; Kaplan, 2019b).

Social play may not just be observed in juveniles but, in some species, carries over into adulthood. Intersexual adult play behaviour has been described in primates and canids. In a number of such studies, play behaviour has been examined and explained within very specific contexts, be these associated with courtship (Fagen, 1981), access to food (Palagi, 2006: in bonobos, *Pan paniscus*) or bonding before a hunt (Fagen, 1981: African hunting dogs, *Lycaon pictus*; timber wolves, *Canis lupus*). Such link of adult mammalian play to identifiable functions has not necessarily been established in adult play of parrots or songbirds. As far as has been observed, avian adult play seems indistinguishable from juvenile play (Schwing et al., 2017), although this may refer to type of play interaction rather than frequency.

The adult forms of play in birds are of particular interest here because their existence is no longer tied to development or to benefits for the future. When occurring in juveniles, there are many conclusions that can be drawn from play being categorised as an activity that can hone skills for the future, be these social or in motor training (Sazima, 2008; O'Hara and Auersperg, 2017). However, such functions cannot be attributed to adult play and there are, as yet no specific functions identified as to whether avian adult play may occur as a unifier of the group, as in preparing for a hunt, or as appeasement around specific conflicts or courtship as some studies of primate and wild dog play behaviour have found (cited in previous paragraph).

Play in some songbirds and in psittacine species is part of the behavioural repertoire of adulthood and can be lifelong (Table 1). However, there seems to be a difference between songbirds and psittacines in incidents of adult play behaviour. In songbirds it may diminish in adulthood (Pellis 1983), but in some free-ranging parrot species playfulness and readiness to play solo, object and social plays may well be maintained at a high rate in adulthood but this needs to be confirmed (Diamond et al., 2006; Skeate, 1985). Solo play, object play and social play as well as play fighting, itself a social pursuit, are useful and robust research categories that have largely remained so over the years.

Bond and Diamond (2003) have distinguished between 1) play invitations, 2) play chasing, 3) aerial play, 4) social object play and 5) play

fighting. These sub-categories are very useful because the simplest forms (2+ 3) may be spontaneous, involve little cognition and are similar in execution across species but social play may be highly sophisticated, suggesting cognitively complex abilities. Whether or not there are differences in the presence and magnitude of adult play in birds compared to juvenile play incidents cannot be shown at this time because of the dearth of quantitative developmental studies of play in birds.

Play chasing may involve chasing each other and trying to either overtake the other or reach the tail of the first and hold on to tail feathers- play chasing seems to be widespread across species, including humans (Boulton and Smith, 1992).

Aerial play is similar in style to play chasing: chasing another bird and trying to reach the tail feathers. Indeed, this category of aerial play seems to be relatively consistent across species, showing little differentiation between the description offered by Diamond and Bond (2001) on kea aerial behaviour and similar behaviour in other species, be they passerines or psittacines.

Note that Schwing et al. (2017) subdivided play behaviour in terms of type of play but not by number of players involved. Except for their category 'social ground play' which according to the authors, always consists of two or more players and therefore corresponds to the category 'social play' used here, the other categories they describe mix object play with social play ("one or more birds repeatedly tossing the same object into the air"). The same goes for their classification of aerial play (also one or two birds). These different classifications could lead to very different results from those reported by Diamond and Bond (2003) and by Kaplan (2021b). For these reasons, it seems important to continue with the subdivisions used by Bond and Diamond (2003) that keep a sharp distinction between social and non-social play forms as representing different phenomena.

4. Rationale for the focus on social play behaviour among adult birds

There are three main reasons for wanting to pursue adult social play on its own. First, adult play cannot be folded readily into the existing ontogenetic hypotheses stating that play is a developmental process to enhance motor skills and to learn about food sources, risks, and social rules. Alternative functions of play in adult birds have not been fully explored to date, with notable exceptions. Social play in birds, such as in keas and ravens, was included in studies on emotional states in animals (Mendl and Paul, 2020) and particularly in studies of joyful emotions in non-human animals (Nelson et al., 2023). "Playfulness", as a distinct characteristic of some species (specifically in parrots), has also been explored in various mammals (Pellis and Pellis, 2009; Mendl and Paul, 2020; Nelson et al., 2023).

Second, the question is whether species retain social play behaviour in adulthood as a means of strengthening affiliative bonds, as allogrooming might do (Radford, 2012; Morales Picard et al., 2020), or whether play behaviour in adults, particularly in corvids and parrots, is a way of testing or reconfirming complex social relationships (Boucherie et al., 2016; 2019). Or are there entirely unrelated reasons for maintaining play behaviour in adulthood? such as having fun (Emery and Clayton, 2015). And/or what can adult play contribute to the individual and to the social group? For instance, is having fun together (Emery and Clayton, 2015) a way of forming closer ties, leading to cooperative behaviour or even prosocial acts?

Third, is the matter of cooperation and competition. Natural selection implies competition so it has always been a challenge to explain cooperation in animals, which would require demonstrating specific cases of cooperation within a competitive model for survival (Nowal, 2006). I am not referring here to cooperative breeders or helpers at the nest which is a separate issue (see below; Lin et al., 2019). There have been countless attempts to explain vertebrate collaboration in evolution generally, including game theory, be these cooperative and non-cooperative models (Dugatkin and Reeve, 2000; Leimar and

McNamara, 2023), although the examples tend to confine themselves to incidents of helping in defence against predators (Olendorf et al., 2004; Krams et al., 2008), very rarely refer to food sharing (jackdaws, *Corvus monedula*: De Kort et al., 2006; parrots already mentioned: Brucks and von Bayern, 2020) and generally do not extend to within-group benign play behaviour. The literature on birds and primates has also identified multilevel societies, consisting of groups hierarchical nested within each other in which alliances and supportive behaviour can even be more difficult to unravel, as is the case in the cooperatively breeding superb fairy-wrens, *Malurus cyaneus* (Camerlenghi et al., 2022) but such species may not necessarily be social players.

At least in the Australian context, psittacines (parrots, lorikeets and cockatoos) are perhaps best described as forming fission-fusion societies, changing composition and alliances and even partners (Chen et al., 2022). Most of the cockatoos, except for some corellas that seem to 'divorce' at a regular rate (Smith, 1991), are socially monogamous and some, as in cockatoos, pair-bond often for decades or a lifetime. The idea of a family, with male and female raising their young together (and often equally) is an evolutionary development specifically of avian species (over 95% of birds do so, while only 5% of mammals can lay claim to this form of parenting, Clutton-Brock, (1991). One further step in 'family living' is for offspring staying close to parents (Covas and Griesser, 2007). In cockatoos, other avian species, and great apes the long-term association by offspring with parents or an extended family is also mirrored in delayed sexual maturity of juveniles and sub-adults. The advantage is a further and extensive period of accumulating experiences and/ or learning and ample opportunities for forming alliances and developing affiliative relationships to unrelated individuals. Like great apes, the psittacines usually enjoy a wide network of family, friends, allies and a range of neutral heterospecifics that may share feeding spaces but whose alliances and tolerances may change in and out of breeding seasons (Bradbury and Balsby, 2016). Clearly, one way of spending time with friends is to engage in play behaviour.

Parrots, particularly well-known in keas and, in their case studied in detail in the natural environment, tend not to have a rigid social structure but quickly adapt to changes in social and environmental contexts (Diamond and Bond, 1999; Bond and Diamond, 2019). Importantly, keas and some other avian species have layers of alliances and affiliations, very much as do humans: in the centre ring is the family unit of male, female and offspring, then a layer of extended and inter-generational family, and then, in the outer rings, may be friends, befriended families, closest unrelated allies and occasional social associates (Rowley and Chapman, 1991; Smith-Vidaurre et al., 2020; Penndorf et al., 2023). Similar observations on social life have been made in common ravens, *Corvus corax* (Fraser and Bugnyar, 2010; Braun and Bugnyar, 2012; Stocker et al., 2016; Boucherie et al., 2019). In some species, as in rainbow lorikeets, *Trichoglossus moluccanus* (see Section 8.2 below), social organisations may be more hierarchical, be this in linear and non-linear forms, or at least far more complex than has been believed so far (Mettke-Hofmann et al., 2002; Hobson et al., 2014a, 2014b; Klump et al., 2021).

How do these different kinds of social relationships relate to play behaviour and has play something to do with with keeping specific social ties, with strengthening bonds or with cooperative behaviour in different contexts? There are even more questions for which we do not yet have answers, and these are concerned with the effects of changing environments on the behaviour of birds.

Survival might well have depended on forming social allegiances, and strong social bonds because the ancient lineages evolved in a forever fickle continent. East Gondwana / Australia was and is not so much known for strong seasonal changes as for flood, fires and drought and complex forest environments. And most parrots are largely herbivores, feeding on pre-dispersed/unripe seeds (50–70%); flowers (10–30%), other plant parts, (10–20%) fruit pulp (2–10) and arthropods (1–5%) (Bradbury and Balsby, 2016), and thus they are especially susceptible to plants that are high in toxicity and otherwise well-armed and growing

unpredictably. In terms of type of food, location, and timing, these are generally deemed to be complex environmental conditions which are meant to require large memory banks and cognitive skills to navigate through such difficult terrains. In a positive sense, subtropical and tropical forests can also be called rich environments, both in plant diversity and in diversity of animal species generally.

The evolution of substantial cognitive abilities and their similarity between primates, cockatoos and parrots is likely explicable by ecological factors. Primates are largely a sub-tropical and tropical order, with about 90% of all primate species found exclusively in subtropical and tropical forest regions of Asia, Africa, and the Neotropics (Mittermeier, 1988). Parrots evolved in the same type of complex forest environments. Today, at least 70% of all parrots worldwide are forest dependent and live in tropical and subtropical Southern hemisphere regions (Forshaw, 2010; Vegara-Tabares et al., 2020).

Play behaviour may well also depend on the way social practices evolved. Interestingly, Palagi suggested, and I agree with her theoretical proposal even if it was geared more towards primates, that adult social play may be "favoured by natural selection in those species characterized by high level of social tolerance and/or by the need of others' cooperation to reach a goal", especially when facing unpredictable, novel situations and in overcoming stressful experiences (Palagi, 2023).

Some of the innovations minimizing unpredictable and dangerous situations may include significant practical and social inventions, such as the innovation of nesting in trees or caves; secondly, the invention of biparental care to which 95% of modern songbirds and all psittacine species still subscribe. And finally, for further protection, raising offspring with the help of others to keep offspring safe. Worldwide only 2% of birds breed cooperatively but, amongst Australian birds, there are 22% of cooperative breeders and as Cockburn pointed out, if one considers only its ancient lineages, the percentage of cooperative breeders rises to over 50% of all modern Australian songbirds, suggesting perhaps that cooperation was once even the dominant form of parental care (Cockburn, 1996; 2006). This is a very high percentage compared to extant mammals whose mean formation of shared bi-parental care is around 5% (as against 95% among birds (Úbeda, 2008). In short, these kinds of credentials may be significant contributing factors, ultimately impacting the way species may have adapted socially to hostile conditions.

Another reason for concentrating on adult social play concerns brain processes. We already know that some corvids and parrots are useful models for comparative brain research because of their exceptional cognitive skills (Kaplan, 2018, 2021a; Rössler and Auersperg, 2023) with large brains relative to their body size and high density of forebrain neurons (Olkowicz et al., 2016), and they are generally good, and even cooperative, problem solvers (Péron et al., 2011; Torres Ortiz et al., 2021). For the most, parrots and corvids showing complex play behaviour also tend to live in complex social groups (Fraser and Bugnyar, 2010; Hobson et al., 2014a, 2014b; Boucherie et al., 2019). Despite their high metabolism, they tend to have extended developmental periods and long lives (Iwaniuk et al., 2005; Wirthlin et al., 2018). Finally, parrots have evolved a telencephalic-midbrain-cerebellar circuit similar to that in primates, suggesting that these pathways are key to understanding the evolution of complex cognition in parrots (Gutiérrez-Ibañez et al., 2018) and, as is argued in this paper, directly relevant to play behaviour.

Concentrating on adult birds has the advantage that one can exclude many changes in brain processes that are due to development. In adulthood, playing and non-playing species could be compared and, as a future research suggestion, this might reveal whether adult play triggers or is a consequence of brain processes (neural, hormonal) that cannot be confused with developmental processes.

These developmental processes can be quite different from one species to the next, dependent also on the type of reproduction as either altricial or precocial. Unlike brains of precocial hatchlings (Starck, 1993; Rogers, 1995), the brains of altricial hatchlings, to which all oscines and

psittacines belong, do not resemble those of adults. The brain of hatchling budgerigars, *Melopsittacus undulatus*, has poorly differentiated neurons (Iwaniuk and Nelson, 2003). A lack of myelination and poor cellular differentiation are present in the hatchling Java sparrow, *Lonchura oryzivora* (Iwaniuk and Nelson, 2003). Both the budgerigar and the Java sparrow also possess relatively large proliferative zones, clearly indicating that the bulk of telencephalic neurogenesis occurs post-hatching. By prolonging post-embryonic growth, species can develop a relatively larger brain through longer periods of neuron growth, myelination, synaptogenesis, and neurogenesis, thus allowing altricial species to be shaped more readily by the environment.

5. Some factors that may affect play behaviour

There may be many factors that contribute to play behaviour and perhaps even special factors for play behaviour in adults, some of which will be summarised below but there are some that have not been explored and are mentioned here to foster future research projects. Vocal learning and vocal ability might not strike one as relevant to play behaviour at first but there may be factors important to consider. Vocal learning and abilities have been studied in much detail in songbirds, and that well over the past 100 years (Baker, 2001).

5.1. Is vocal behaviour contributing to play behaviour?

The latest taxonomical evaluations have reconfirmed parrots and songbirds as sister groups (Selvatti et al., 2022). In terms of abilities, cognition, parental care and sociality generally, there are indeed broad similarities.

The two groups also have some broad similarities in vocal behaviour, chiefly, that they can learn it. Yet their feeding and vocal apparatus is quite different. Songbirds have short or long but straight and pointed beaks, all parrots have recognizably distinct curved upper and lower mandibles. Parrots do not sing at all, but they chatter and have many different calls (Pidgeon, 1981). Parrots are attractive as companion animals because most of them learn to speak and learn human words, sentences and may even go beyond mimicry by learning words which may constitute meaningful replies (Pepperberg, 2007). However, there are very few records of parrots mimicking in the wild and the few records we have may be inconclusive, while some songbirds, largely males, incorporate mimicked sounds into their repertoire.

In vocal mimicry, there are interesting differences between songbirds and parrots. Australian songbirds (Kelley et al. 2008), for instance, have a surprisingly high practice of mimicry in the wild. According to Chisholm (1948), there may be a third or even half of all Australian songbirds capable of mimicry. Some of them copy snippets of sounds of other species and for such mimicry no function has ever been identified, although Ritters and colleagues have suggested that song can be a form of play (Ritters et al., 2022) and adding new notes and snippets from other birds may, indeed, be playful.

But there are songbirds for which mimicry has a vital function- as in lyrebird males whose song consists of strings of mimicry of other birds and whatever sounds it finds to incorporate into a courtship song. The lyrebird is probably the foremost mimic in the world, luring females with stunning displays, including dance, wing shaking and dazzling song consisting of mimicked sounds (Robinson and Curtis, 1996; Dalziel and Magrath, 2012; Backhouse et al., 2022). The Australian magpie, another remarkable mimic, just as tonally perfect as the lyrebird (Kaplan, 1999), however, does not use such mimicry in a courtship song as the lyrebird but, remarkably, for no identifiable purpose. Magpies are territorial and have a special set of territorial calls and have no courtship rituals involving song. Indeed, outside the breeding season, the singing magpie with its distinct tonal, warbling song sits by itself, just singing and doing so sometimes for hours which, perhaps, could be called solo play (Kaplan, 2008). One would certainly think that it is a pleasurable or at least enjoyable experience.

By contrast, parrots do not sing- so the question to this day is: why has the parrot brain been equipped with a song control system that is by and large the same as in songbirds? And why do parrots have an additional shell song control system, i.e. have brain structures meant for song even more complex than in songbirds (Chakraborty and Jarvis, 2015)?

We do know that parrots, as adults, have sizeable vocal repertoires (Saunders, 1983; Zdenek et al., 2015; Wright and Dahlin, 2018). Vocal production in parrots has been established to work quite differently from that of songbirds, however. Songbirds have two relatively independent syringeal sound sources to create their vocalizations (Nottebohm et al., 1976; Vicario and Nottebohm, 1988; Deng et al., 2001; Suthers et al., 2011), while parrots, like humans, have to produce their sounds from a single sound source (Beckers et al., 2004; Bradbury and Balsby, 2016; Larsen and Goller, 2002; Nottebohm, 1980). Interestingly, unlike most songbirds, parrots can remember, use, and increase their repertoire of human vocabulary as well.

Parrot's vocal articulation might more closely resemble human speech production in the sense that both make extensive use of the tongue as a vocal articulator, and both are sensitive to very fine formant differences. However, the arising ability is not altogether the prerogative of parrots. Many songbirds can mimic other species and human words. Even zebra finches can distinguish between words such as 'wit' and 'wet' (Ohms et al., 2012). The ability of parrots to mimic sounds and human words is well-known, although this seems to occur largely in captive parrots held as pets (Benedict et al., 2022). In the wild, vocal communication in parrots is generally thought to be extensive (but not necessarily consisting of mimicry), again suggesting that much learning would take place by nestlings and fledglings, processes that add to the complexity of brain development. Crows and ravens, not generally noted as the most remarkable and melodious songbirds, sometimes also have a remarkable repertoire. Torresian crows, *Corvus orru*, for example, were found to have over 200 sound syllables (McCaig et al., 2015).

In songbirds, there are also important differences between the size of song repertoires which has been a question that was pursued quite rigorously in the 1980s. Studies showed that repertoire size, number of syllable bouts per song, say, of the brown thrasher (*Toxostoma rufum*) that may produce some 2000 different songs, the sedge warbler (*Acrocephalus schoenobaenus*), nightingale (*Luscinia megarhynchos*) and others known to have large repertoires (Catchpole and Slater, 2003), are indeed significantly correlated with the size of the high vocal centre (HVC) in a songbird's song control system. However, no matter how large the repertoire, there are no differences in size, or changes in size in another important song nucleus (Area X) and, outside the song control system, there is no evidence, say, in the hippocampus, which is one area involved in memory, of any increases in volume (Devoogd et al., 1993).

These findings strongly suggest that song repertoire is not a measure that has any influence on cognitive ability. Hence, song or song complexity does not appear to be a marker for complex cognitive ability. Equally, it is unlikely that there is an association between repertoire size and play behaviour. One can make this assertion since previous findings have shown that play behaviour in birds is associated with large brains (Kaplan, 2020).

However, song learning was considered a possible candidate for improved cognitive abilities in birds, but experiments have likewise shown that their results do not support the hypothesis that learned aspects of song suggest cognitive ability (Anderson et al., 2017) and hence would be poor predictors of play behaviour occurring.

Cockatoos and most parrots are lifelong learners while many songbirds have sensitive periods for learning song (Mooney, 1999; Bottjer, 2004; Mello, 2014) and then largely only in males (MacDougall-Shackleton and Ball, 1999; Ball and Balthazart, 2020). Relatively little is known about sex differences in parrot behaviour (Scarl, 2009; Eda-Fujiwara et al., 2016).

That leaves one with the question whether open or lifelong vocal learning is related to cognition and this question has not been fully explored. There is some evidence that lifelong vocal learning, including

the ability to produce new call combinations (Suzuki et al., 2016), may be related to cognitive abilities (Walsh et al., 2019). Many birds, such as European starlings (*Sturnus vulgaris*), American mockingbirds (*Mimus polyglottos*), or Australian magpies (*Gymnorhina tibicen*) are superb mimics and lifelong learners, and so are all cockatoos and many parrots.

However, one needs to be careful in all these assumptions because both the environment and the brain are dynamic, and each component interacts with many others. Bolhuis and Macphail (2001) warned many years ago, that it would be arbitrary (and ultimately unscientific) to assume that different song formats would engage different memory mechanisms, or that one behavioural criterion should lead one to expect difference in functional or even anatomical features in the brain to subserve cognition.

In other words, in vocal comprehension and communication, there are many untapped possibilities for research on the importance of vocal behaviour both as categories to compare with the presence of play behaviour before and during social play, as well as other acts and performances that may be potential signals for communicating a wish to start a play session (Schwing et al., 2017) or end a play bout. Comparing the two taxa, parrots may generally be the more consistent players in adulthood, although there are exceptions and some of them will be discussed later.

5.2. Altriciality and development

Psittaciformes and Passeriformes are altricial. But the hatching mode can be subdivided into semi-altricial, altricial and super-altricial following morphological characteristics of hatchlings. This may have some consequences for play behaviour as well. Semi-altricial birds hatch with feathers and eyes open, altricial birds hatch with some feathers, but eyes closed, and super-altricial birds hatch without feathers and eyes closed (Botelho et al., 2014). Psittacines, and a wide range of songbirds, are super-altricial (Botelho and Faunes, 2015).

The topic is relevant to play behaviour in adults in so far as the consequences of any adverse incidents or prolonged stress experienced by nestlings can have serious and life-long negative ramifications. In both, songbirds and parrots, super-altriciality carries enormous risks because of the extreme dependency on appropriate nourishment and protection, the length of time needed for full development and known costs to feed the growing brain. Cockatoos take a long time to raise offspring and they are also known as some of the smartest extant birds. The hatchlings are blind, helpless, and extremely sensitive to weather conditions.

On the other hand, super-altriciality has the distinct advantage that the newly hatched, especially its sensory organs, can continue to develop for longer periods than precocial or less altricial birds outside the egg, and that development importantly includes the brain. Indeed, more than half a century ago, Sutter (1951) had noticed that, during a lifespan, the brain of nest-bound (nidicolous) vertebrates expands eight to ten times from its initial post-hatch/ post-birth size; while those that leave the nest early or immediately post hatching (nidifugous), can expect brain growth to be just 1.5–2.5 times the initial size. Energy consumption in the brain, at least in mammals, including humans, accounts for over 20 per cent of total oxygen metabolism (Watts et al., 2018). Neurons use up ten times more energy than the cells of the body (Yu et al., 2014) and consume 75–80 per cent of energy produced in the brain (Hyder et al., 2013). Such growth also requires relevant supportive tissue and ongoing restorative processes as, for instance, attending to synaptic energy depletion. Brain gangliosides (Sipione et al., 2020), which have been demonstrated to function even in teleost fish, are thus an ancient and well-established part of the ontogeny of vertebrate brains generally (Seybold and Rahmann, 1985).

Because the nutritional value of food determines how much can be diverted into the growth of the brain (Watts et al., 2018), this form of altricial reproduction is a gamble. In years of low food availability or only of relatively non-nutritious food, growth may well be stunted and,

importantly, the individual may show cognitive impairments in adulthood. There is no evidence to date that an adult, growing up with nutritional deficits, can 'catch up' physically or cognitively. In a study of zebra finches, *Taeniopygia guttata* (Bonaparte et al., 2011), comparing juveniles raised on poor versus nutritious food showed convincingly that there was a significant difference between the two test groups in adulthood. The well-fed birds, well-fed in terms of protein rich seeds, were larger in body and in head size than the protein poor group, and adult song of males on poor diet as nestlings was shorter and less accomplished (Bonaparte et al., 2011).

A detailed study of pied babblers (*Turdoides bicolor*), a cooperative breeding songbird in the Kalahari Desert of Southern Africa, found that high temperatures alone during nestling stages were associated with 'worse' learning performance in adulthood, with foraging deficiencies and lower reproductive success (Soravia et al., 2022). These results strongly suggest that climate change could have permanent deleterious effects on cognition, overall health, reproduction and possibly on a range of other behaviour, if this change be expressed in higher temperatures (Blackburn et al., 2022), including play behaviour, whether expressed in sub-adults or adults.

In other words, super-altricial species tend to need the longest period of parental support and they are also the ones that develop the largest brains and that, in turn, seems to correspond with developing the most elaborate forms of play behaviour.

5.3. Ecological factors, parental care and longevity

Finally, in this comparison of passerines and psittacines, location is of some importance. Parrots are largely a product of the Southern Hemisphere and the equatorial belt to this day while songbirds, originating in Gondwana, exclusively in the Southern Hemisphere, are now spread throughout the world and the most studied species tend to live in the higher latitudes of the Northern Hemisphere with strong seasonal changes. In terms of parental care, there is an important difference between the Northern and Southern Hemispheres: in Northern Hemisphere birds, parental care for offspring often extends to just 2–3 weeks post-fledging (in about 60% of all species). Then their offspring are on their own, often requiring immediate departure on a long migration southward to overwintering places (Sillet and Holmes, 2002). By contrast, more than 60% of Australian avian parents give their fledglings support for at least another 3 months after having left the nest and often even considerably longer (Russell, 2004). In an iconic songbird, the Australian magpie, *Gymnorhina tibicen*, offspring have at least 7 months post-fledging in their natal territory where they are protected by their parents and have access to uncontested food. Some offspring may even stay longer as helpers for the next breeding season and, in some extreme cases, magpies staying for as long as 4 years in the natal territory have a near 100 percent survival rate (Veltman and Carrick, 1990). In cockatoos, such parental protection can last substantially longer than a year and is often aided by several close-knit families moving locally, roosting and travelling longer distances together (Noske, 1980; Westcott and Cockburn, 1988; Dahlem and Collins, 2021). It seems that length of parental care and protection, often indirectly supported by several other families nearby, provides time and circumstances for the development of play behaviour. That it is carried over into adulthood in many parrots suggests that the group formations in parrots may offer better and safer conditions for play behaviour than is achievable in many songbirds that are out on their own, be this as migrants or as pairs. Another important point, often mentioned, is the degree of prosocial and cooperative behaviour that can develop when the social unit may be larger than the immediate family (Decety et al., 2016).

Notably, lifespans in Australian birds with extended parental care may be 2–4 times longer than birds of similar weight classes in the Northern Hemisphere. The Psittaciformes are the longest-lived birds for their body size (Prinzinger, 1993). Cockatoos (Cacatuidae) have higher maximum longevity than parrots (Psittacidae and Loriidae); mean

maximum ages 39.5, 22.7 and 17.0 years respectively. Cockatoos, both families, *Calyptorhynchus* and *Cacatua*, have the longest lifespans (Heinsohn et al., 2009), very conservatively placed at mean maxima of 46.0 and 39.5 years respectively (Munshi-South and Wilkinson, 2006). However, although some of the older ages reported in the literature, of more than 80 years, are difficult to substantiate, such records do exist, both from private households and zoo records (Brouwer et al., 2000). At San Diego Zoo, a galah died aged 80 and a salmon-crested cockatoo, *Cacatua moluccensis* (called 'King Tut'), had served as San Diego's greeter for 64 years and was estimated to be at least 67 years old (Abrahamson, 1990). A pink cockatoo, *Lophochroa leadbeateri* was still alive aged 63 years (Brouwer et al., 2000). In relation to juvenile play behaviour, the extended period of immaturity and the extraordinary lifespans of some avian species all combine to suggest that such life history data give unprecedented opportunity for learning, developing prosocial tendencies (Decety et al., 2016; Duque et al., 2018) and using some of that time in expressing play behaviour both as juveniles and as adults.

5.4. Criteria of play behaviour in birds and life history characteristics

Because play is a diverse and dynamic behavioural category, five criteria for identifying play across separate contexts and species have been proposed (Burghardt, 2005; Burghardt and Pellis, 2019). In brief, play behaviour 1) is not fully functional in the form or context in which it appears; 2) it is spontaneous, voluntary, and/or pleasurable, seemingly performed for its own sake; 3) it is incomplete, exaggerated, or precocious insofar as it is structurally or temporally different than its normal functional counterpart; 4) it is repeatedly and variably performed; 5) it is initiated when animals are in relatively good health, and not highly stressed or facing competing demands.

Finally, and of direct relevance here, is the high level of cognitive abilities shared by some lineages of passerines as well as psittacines that has astounded researchers in the last 20 years (summarised in: Kaplan, 2018; Kaplan, 2021a). To test any association between cognitive ability, brain size and play behaviour In social play of Australian birds, for instance, I found a significant association of specific categories of play behaviour with brain size (tested in passerines and psittacines separately; Kaplan, 2021b). Social players consistently have the largest brain and solo players significantly smaller brain sizes than social players, as said before. Every play category adds to brain size, even solo playing shows larger brain size compared to species that do not play at all (Kaplan, 2021b).

Some passerines and parrots have a range of qualities in common and it is worth summarizing them here because of the implications for play behaviour and complex cognition:

- 1) bi-parental care
- 2) their reproductive rate tends to be slow (slower in psittacines and only some songbirds)
- 3) their bi-parental care is far longer than in world-wide average,
- 4) they tend to bond with their partner for life and this often includes shedding obvious sex differences in plumage
- 5) they have a well-established network of allied families
- 6) many of them act and even live cooperatively
- 7) relative to their body size they have very large brains (and pallial neurons of similar number to those of much larger primates)
- 8) are cognitively complex
- 9) many psittacines and some songbirds have a much above average life-expectancy compared to other avian species
- 10) both passerines and psittacines (incl. also some hummingbirds) have acquired the capacity for extensive vocalizations, but it is more pronounced in psittacines, that are excellent vocal mimics

The identification of characteristics of large-brained and socially playing birds has led to a plethora of comparative research not just

between primates and birds but, notably, between birds and humans (Kirsch et al., 2008; Clayton and Emery, 2015). Despite the substantial evolutionary distance between the two classes, some 300 million years of the last common ancestor, the avian brain has become an important model for discussions on primate and also human evolution and brain function (Reiner et al., 2004; Jarvis et al., 2005; Güntürkün and Bugnyar, 2016; Vernes et al., 2021).

Australian and New Zealand species are good examples to use because it is now acknowledged that all modern songbirds first evolved in East Gondwana based on some surviving lineages post the mass extinction event of 65 million years ago and psittacines are entirely of Cretaceous Gondwanan origin (Cooper and Penny, 1997; Cracraft, 2001; Edwards and Boles, 2002; Clarke et al., 2005; White et al., 2011) and have largely remained in the Southern hemisphere. And, of course, as we know since Darwin's explorations, physical features of the environment impact species and may shape the overall social structure and social organization of animal populations (He et al., 2019).

Also, the specific features of an environment and the degree of complexity it presents in terms of securing a sufficient food supply (that may be difficult to secure, find, manipulate and disarm), in turn, influences the complexity of organisms and groups as a result of rising to specific challenges (Bradbury and Balsby, 2016). Based on such criteria, Dunbar proposed the 'social brain hypothesis', arguing that social complexity is the primary driver of brain size evolution (Dunbar, 1998; 2009). 'Complexity' can of course be a rather loose term and can be a basket for just about anything. However, the link between general complexity and cognitive complexity has sparked substantial animal research in various disciplines. In an exhaustive study of parrot-specific changes in genetic conserved regulatory sequences they found that these were overwhelmingly associated with genes that are linked to cognitive abilities and also confirm heightened longevity (Wirthlin et al., 2018). Hence, the link between social and cognitive complexity and even longevity also invites comparisons between play behaviour and cognition (Miller et al., 2022), and such a link was established in social players and to a lesser extent, but still significant, in object players (Kaplan, 2021b).

6. Cognition and play behaviour

Having established the evolutionary history of modern birds (in passeriformes and psittaciformes) as a set of Gondwanan events and its key characteristics in the life histories of extant birds, one can perhaps better appreciate the complexities involved in talking about play behaviour, particularly in adults. Judging by research results so far, play behaviour in birds, particularly social play, as already mentioned, has been linked to cognition, prosocial (Kaplan, 2017; Duque et al., 2018) and generally cooperative behaviour (Woolfenden and Fitzpatrick, 1990; Cockburn, 1996) and, most decidedly, as also said before, to length of parental care (Russell et al., 2004; Uomini et al., 2020), to friendship networks, and flock sizes (Westcott and Cockburn, 1988). Bearing in mind that both passeriformes and psittaciformes are potentially prey species, alliances among animals, mammalian and avian species alike, has been found to enhance group status and survival generally (in primates: Harcourt, 1988; Harcourt and de Waal, 1992; in birds: Silk et al., 2014).

The evidence that neuroscience has produced in the last two decades, overwhelmingly confirms that birds, even though without the mammalian type of neocortex on which we once believed all intelligence hinged (Güntürkün and Bugnyar, 2016), could find alternative ways to achieve remarkable cognitive abilities, some of them quite abstract.

6.1. The dynamics of play in birds

The various forms of play are quite distinct and easily recognisable as play behaviour. To repeat: they fall into solo (locomotor), object and social play. Object play will not be considered further here other than in

the context of social interactions. However, it is worth pointing out that object play could be an interesting and perhaps even important topic to investigate separately. Objects may be chosen spontaneously and indiscriminately, i.e., holding no intrinsic value (emotional indifference) but objects can also become toys and even favourite toys. There is ample evidence of the welfare benefits of providing toys to companion and domesticated animals (Ahloy-Dallaire et al., 2018). This can also apply to birds. Budgerigars have favourite toys and so do ravens. This can be any object, such as a stick or stone (Skaife, 2018) or a human artefact. A favourite toy may be defended against conspecifics and such action may then be misconstrued as social object play or play fighting.

Another facet of play behaviour is its variability, ranging from simple spontaneous brief incidents to complex play which may engage brain and hormonal activities differently. The former may require a moment's attention and memory activation of something learned in the past at best, at the other end of the scale, the interaction may presuppose a degree of social cooperation, and signify complex cognitive processes. For a long time, the assumption has been that our most immediate ancestor, the chimpanzee, was also our nearest cognitive ancestor, fitting in well with the *scala naturae* but this idea had to be abandoned when birds showed abilities, similar to those of chimps, as also of ravens, and other avian species (Emery and Clayton, 2004; Pika et al., 2020).

We have not discovered yet whether brain processes differ according to the complexity of play, although the role of basal ganglia in controlling movement have been well described (Medina and Reiner, 1999). Very recently, it was also discovered in birds that in both in the ventral pallidum (VP) and the ventral tegmental area (VTA), neurons change their tuning and provide a gating mechanism for movement representation in limbic circuits which, according to Chen and colleagues (2021), are commonly associated with reward and performance evaluation (Chen et al., 2021). It is thus not improbable to suggest that the responsiveness in areas such as the VTA and VP and possibly in other areas, different neurons are actively involved in different forms of play and discovering what these are might help in deciphering cognitive and/or emotive contributory elements in play behaviour.

6.2. Play invitation behaviour

A play invitation is made with reference to a future event. The idea that a future event can be negotiated at a time when the desired behaviour by one party has not yet occurred, is remarkable. This is exactly what had been shown in studies of various cooperative babbler, *Turdoides bicolor* (Bell et al., 2010; Mocha et al., 2019). Such examples suggest a cognitive ability usually associated with "theory of mind", often considered the highest cognitive level, which only humans and, to some extent, great apes had reached (Premack and Woodruff, 1978; Graham et al., 2019; Tomasello, 2023). Importantly, it is the individual recipient of the invitational gesture by another who needs to attribute intention to the other. Intentionality has also been tested in African grey parrots (Péron et al., 2010) in ravens (Pika et al., 2020) as well as in dogs (Schünemann et al., 2021; Völter et al., 2023) and Norway rats, so the idea of intentionality in non-human animals is no longer controversial (Heesen et al., 2017; Warren and Call, 2022), nor is the idea of higher cognitive abilities in birds (Zorina et al., 2022).

Social play in birds can start in various ways, and some of these may be different from play initiations in other vertebrates (Hayaki, 1985; Ward et al., 2008). It may be ritualised and happen by signalling mutual agreement to play or by invitation extended by one party to another. Acts of invitation (play initiation by one party) may indicate that there is an intention to play, and that the decision is deliberate and planned. By contrast, spontaneous changes from solo play to social play may rely on social contagion, following suit and imitating the solo player (Dakin and Ryder, 2018), thus turning an individual act into a social play situation or it can start by one bird parading an object that another then desires, leading to social object play.

A play invitation itself is quite varied both in the signals used and in

the extent to which play readiness is expressed. Pellis (1981a), in his studies on play behaviour in Australian magpies, for instance, reported that one approaching bird, prior to play commencement, may emit a long, low frequency guttural call not heard in contexts other than in play initiations, or an approaching bird may adopt an 'unnatural' stiff-legged gait, or the initiating bird may approach a potential play partner with a half-open beak (Pellis, 1981a). Kakapos, *Strigops habroptilus*, New Zealand's large flightless and slow-moving parrot, and keas 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 (Bond and Diamond, 2003). Also observed in keas, the play initiating bird adopts a stiff walk; or, as described by Keller (1975) –however in a zoo, not in the natural environment– the play initiating birds would put their heads in-between their legs and look at the potential play partner from this contorted position.

Most cockatoo species have a very pronounced crest which is used regularly in communication with others. The sulphur-crested cockatoo, *Cacatua galerita*, and galah, *Eolophus roseicapilla*, two of the cockatoo species with a pronounced crest, use the crest (in a very specific position) and their body posture to indicate play readiness. A bird that has already indicated play readiness generally then does not require a special invitation, however.

Thus, a play invitation is called so because, in some cases, it is intentional, mutually agreed and can be formal. Reported here for the first time, little corellas, *Cacatua pastinator*, have two forms of overt invitations- one is a spontaneous, 'rough and tumble' kind of invite that is not mutually agreed. The other is a quiet bowing directly in front of the other who then accepts or declines.

Agreeing on a future activity is acknowledging a recognition of understanding what another is thinking. In Fig. 1 A below, the bird on top of the obelisk has just dislodged another bird occupying the obelisk by flying full speed into the back of the occupying bird. The bird, thus roughly dislodged, had several choices: respond angrily and pursue the offender; simply fly away and the third option, most often taken, is that the dislodged bird will try to gain control of its own flight, then fly a circle back to the obelisk, flying full speed at the bird now sitting on the obelisk and the two birds even shrieked in anticipation of a timely avoidance of the onslaught of the other. This play interaction was repeated several times.

The most common form of a play invitation that I have observed in little corellas, is the gentle approach of one bird facing another and then slowly and deliberately bowing to the other (Fig. 1 B). When the second bird accepts, the two birds may fly off a short distance and engage in whatever play of their choosing. The latter is not too dissimilar to kakapo and kea play initiation behaviour (Diamond et al., 2006). Both New Zealand parrot 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 (Bond and Diamond, 2003).

In juvenile Australian magpies (Fig. 2 below) such invitation tends to take the form of standing close to each other, facing and perhaps slightly nuzzling each other with the beak -accompanied by some low-level vocalisations. However, the latter was only observed in juveniles, and has not been seen as occurring among adult magpies.

6.3. Solo play converts into social play

The reasons for this occurring may be manifold. One of the ways to start play is for an individual to do something, and for others to begin interacting with the initiating bird. Such play may fall into several sub-categories but, by whatever means a second individual or even a group is being drawn into play by some form persuasive action.

The simplest form is contagion, another mimicry, and a third enticement via competitiveness. The literature has rightly distinguished between behavioural, emotional, and social contagion (Dakin and Ryder, 2018). An example of behavioural contagion is the copying of the self-same behaviour of the other being watched, such as preening, lifting a wing, head-bobbing, or it may be by enticing movements or actions to get others involved. Winkler and Bryant (2021) argued that cooperative individuals facilitate social contagion but, in play, it could surely also be the other way around: social contagion facilitates cooperation.

One form of behavioural contagion and directly relevant to play behaviour, has a competitive edge. In little corellas, *Cacatua sanguinea*, one of the most daring feats of solo motor play is to attempt hanging from a branch or electricity overhead wire by the beak alone and then try and swing. Such attempts never go unnoticed by other corellas. Within seconds of the solo attempt, the single bird will be joined by another and typically then several more will arrive and will attempt the same swinging task by the beak and try to maintain it.

Emotional contagion impacts behaviour just as behavioural contagion does (Palagi et al., 2020). It has been suggested that emotional contagion may be an important indicator of prosociality, i.e., show a sensitivity to another individual and sometimes express this in behaviour that benefits another (Vonk, 2019). In positive stimuli, such as observing play or specific calls during play, this can lead to play readiness and synchronised play behaviour in others (Osvath and Sima, 2014), but not necessarily repeating identical movements or actions. Schwing and colleagues (2017) showed this convincingly in several playback experiments in keas. The researchers had already established all the call types of keas in previous field studies (Schwing et al., 2012) and had identified a call that was often used in conjunction with play. They found:

Upon hearing the play call, many birds did not join in play that was already underway, but instead started playing with other non-

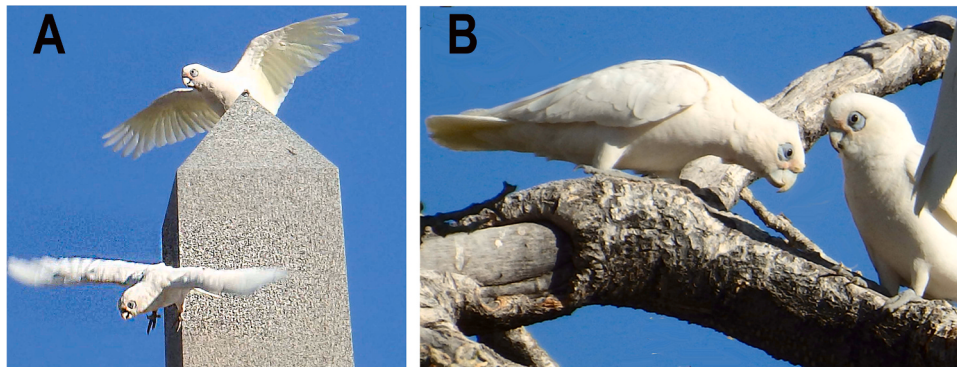


Fig. 1. Play Invitations A -little corella sitting on top has dislodged the play opponent (flying); B-a play invitation by the bird on the left bowing to the bird on the right- both birds left together and then played, swinging together on an electric overhead wire.(Photocredit G.Kaplan).



Fig. 2. Play invitation Two juvenile Australian magpies inviting each other to play. The magpie on the right is vocalising softly. Both birds are "beaking"- gently nuzzling each other's beaks. Juvenile play is not discussed in this paper. The image is shown because beaking and foot holding are also part of adult play in this species. Hence these signals have some significance for play initiations. (Photocredit G.Kaplan).

playing birds, or in the case of solitary play, with an object or by performing aerial acrobatics. These instances suggest that kea weren't 'invited' to play, but that this specific call induced playfulness, supporting the hypothesis that play vocalizations can act as a positive emotional contagion. (Schwing et al., 2017).

One would expect that play behaviour ranks among positive emotional experiences, but this assumption may be misleading (Adriaense et al., 2019). Even in play engagements not involving fighting, there may be highly stressful aspects, as in complex hide-and-seek games in juvenile magpies (Kaplan, 2019a) which can be measured observationally because emotional valence is largely conveyed by the number of vocal expressions (such as shrieks) and by avoidance, approach or imitation behaviour (Kauschke et al., 2019).

7. Social play and social object play

7.1. General

The category of social play is a long-established and workable category at least since the publications from the 1980 s onwards (Fagen, 1981; Bekoff and Byers, 1998). Diamond and colleagues (Bond and Diamond, 2003; Diamond et al., 2006) added social object play as a separate category. It is not clear whether the characteristics of social play (at least two individuals playing together) or two individuals having at least one object between them, changes the level of engagement although it may lengthen the timeframe of the engagement. Social play can occur among two individuals or in groups playing with each other or next to each other. 'With each other' seems to be a category largely reserved for humans in that such activities are highly structured, rule-governed, and often complex. The purpose of such human social games is competition (Avrahami et al., 2005). However, playing 'next to each other' is probably the most common form of group play in birds. For instance, a number of reports have been published that describe several keas or ravens flying uphill or to the top of a snow-covered roof and tumbling down together or literally 'skiing' on their feet (Eklow, 1988; Heinrich and Smolker, 1998; Brazil, 2002).

7.2. Uneven play partners

Some aspects of social play have so far not been raised in the avian literature: one is an adult playing with a juvenile and the other is cross-species playing behaviour. The latter tends to occur usually between companion/pet dogs and wild birds. Such encounters are not as rare as one might think. Jack Russel dogs, particularly when they are the only household pet living in the backyard may, at times, be seen engaging in romps of play with Australian magpies (pers. observ.). What we make of such alliances has not been established, but what can be concluded without anthropomorphising is that animals share and use heterospecifically understood signals indicating their play readiness.

The second form of uneven play partners, and biologically more relevant, is play behaviour between a juvenile and an adult (parent) bird. So far, although documented in some mammals, there has been no scientifically researched evidence of such play behaviour between an adult and a juvenile bird, other than in anecdotal reports. Juveniles of dogs, wolves (Lord, 2013) lions (Schaller, 1972) and other mammals, may have sub-adult play circles, but may also test the limit of parental patience when juveniles jump on an adult, pull or chew tails. The parent may of course not actively engage (Chick et al., 2012). In some primates (Hamadryas baboons, *Papio hamadryas*), mixed-age playing is often expressed in play-fighting (Leresche, 1976).

The play behaviour I observed between an adult Australian magpie and a juvenile occurred relatively frequently from one season to the next and in different territories, but exclusively when the juvenile was the only offspring that the pair had raised that season, and no other juveniles were within easy reach. The parent is sitting (i.e., no intimidation) and the juvenile lies on its back- quite often, in play, magpies will lie and roll around on the ground (Pellis, 1981a). The play interaction in such a case largely consists of the adult gently pulling on a foot of the juvenile and the juvenile exerting pressure with its leg against the beak of the adult—then the adult releases the pressure and the juvenile dangles the foot in front of the beak of the parent and another foot tussle begins. On other occasions, the parent might pick up a toy (be this some human toy or a clump of grass) and offer it to the young but then does not release it when the youngster begins to pull.

The question in unevenly aged play partners may also hinge on the species' hatching system, i.e., whether it is based on synchronous or

asynchronous hatching. In juveniles of synchronous breeders, an age difference is usually not tolerated amongst nestlings and juveniles. In magpies, the older one (older often by as little as 4 days) will move into fighting mode causing physical harm.

7.3. Complex play

Complex play has so far not been considered as a separate category in the literature but has generally been subsumed under social or social object play. I would like to add this sixth category to social play behaviour because, it seems to me, that it signifies highly important cognitive differences to other forms of play.

Complex play may involve an object, but it has several ingredients that simple social object play may not have. Playing a tugging game with a piece of moss or any firmer structure by two birds requires physical strength and concentration but little in terms of cognitive skills. Complex play is the kind of play that invariably involves cognitive elements. I shall give two examples, both of which I recorded and studied in detail, and both were observed only in Australian magpies.

The first example (see Fig. 3 below) involved three magpies, one adult and two sub-adult magpies (the sub-adult magpie is 10 months old- first moult and sexual puberty occur at 12 months of age). The behaviour was observed and recorded in a suburb of Melbourne. Magpies have well adapted to human company and occupy a wide range of suburban spaces in cities and towns of Australia. If the house owners are non-threatening, magpies can become quite tame but are not pets. Magpies generally tend not to be fearful of humans and will often use any structure, implement, or object for rest, play and even nest material (Kaplan, 2019a). In Fig. 3, one magpie is hanging from a towel that was drying on a hoist and two magpies stand on the ground on either side, entirely focussed on the task. One bird pulls on the hanging bird's foot and gently pulls it by its beak in its own direction and then lets go - this starts a modest swinging action. The other magpie stands waiting for the backswing and, at exactly the right moment, gives the body of the swinging magpie a push forward with the beak. In short, the precise timing of the pull and push actions by the two magpies makes the magpie hanging on the towel swing. This form of play relies on some knowledge of gravity, velocity, and the force needed to increase the height and speed of the swing and the actions require coordinated

timing. As the swinging momentum became more pronounced, each standing magpie stepped backwards a little in anticipation of the wider swing. In the literature on pre-school children, much is made of the valuable physics lessons that can be learned from a swing. Fox (1997) argue and I quote:

"Swings, as life-sized pendulums, provide three-, four-, five-, and six-year-old children opportunities to experiment with balance, force, gravity, resistance, and resonance. Findings of this study indicate that through play on swings young children accommodate and assimilate the physics principles associated with pendulums." (Fox, 1997)

Presumably, the magpies had understood these principles already, even the sub-adult had, because on the backswing the magpie did not have to get out of the way in the last second. The magpies had anticipated the greater distance of the swinging object. By contrast, toddlers and pre-school children standing by often have to be dragged to safety by adults in order not to get hit by the swing coming back. The 'knowing in advance' what will happen as a direct consequence of pushing or pulling the swinging object is a cognitive ability. Noticeably, this play took a good deal longer than play chases, social object play-bouts and any forms of object play.

The second example of social play is called 'Hide and Seek', a familiar children's game that was played by sub-adult magpies and I observed repeatedly. The term 'game' is used here advisedly rather than 'play'. Play is a generic term while game has set rules known by all those that enter it and while it often imposes limitations (rules) it makes the game possible because these create the conditions for the game. The rules are simple: Participant 1 (P1) has to close its eyes so that Participant 2 (P2) can hide, then P1 has to find P2. If the game is played honestly, P1 really does not know where P2 is and has to search. In this magpie game, P1 had looked away and P2 had taken the brief opportunity to hide but P1 had probably seen the bird disappear in a given direction. When P1 discovered the hiding place, or P2 suddenly reappeared, P1 usually shrieked. They often played this game several times.

Very little research has been conducted of children's performance in this game, but one study had tested children and they showed that only by the age of five years could most children successfully play this game (Peskin and Ardino, 2003; see also Kaplan, 2015 for a detailed

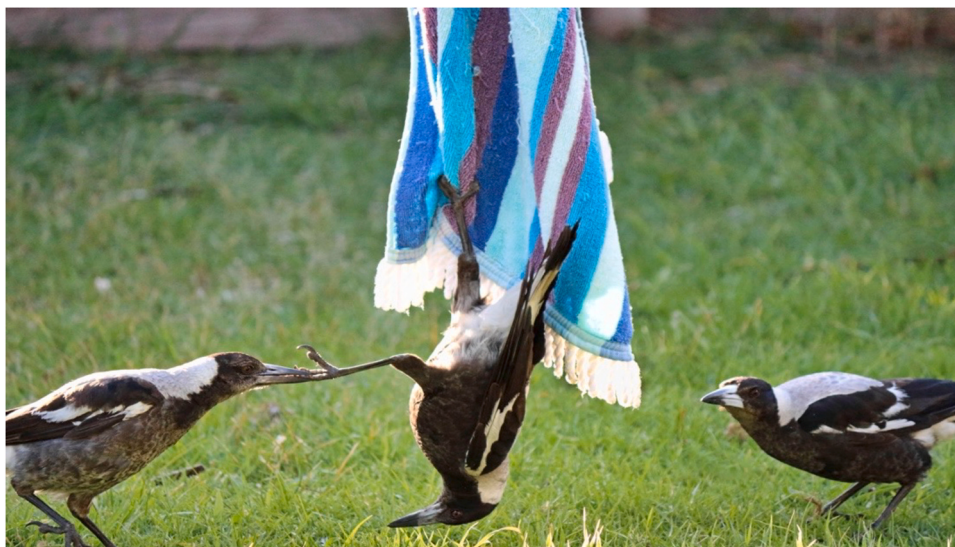


Fig. 3. Complex swinging group activity. Magpies causing the hanging magpie to swing, Left and hanging magpie are juveniles, on the right: adult female. Juveniles are readily identifiable by grey chest and abdominal scalloped grey feathers, adult dark and not scalloped. On the right: adult female: females of several sub-species in the southern part of Australia (*Gymnorhina tibicen telonocua*, *G.t. tyrannica* and *G.t. hypoleuca*) have light grey feather on the back while those of males are white (see Kaplan (2019a), Schodde and Mason, (1999) (Photocredit: Danielle "The Magpie Whisperer"- with permission-link to her photo gallery: <https://www.shop.themagpiewhisperer.com/pages/photo-gallery>).

discussion).

It is not difficult to see why the successful performance of 'hide and seek' leads to discussions of cognition on a par with the performance of 5-year-old children (Peskin and Ardino, 2003). At the very core of the game is the disappearance or partial disappearance of one party from the visual field of another.

Such behaviour is quite a complex because 'hide and seek' may involve two different cognitive processes of interpreting the 'disappearance' of part or the whole of a body. One is referred to as amodal completion- the ability to conceive of the entire body of a partially visible or disappearing object. It is the ability to conceptualize the entire body of a partially visible object to still appear whole (Fig. 4) or, expressed differently, the process of forming mental images of objects in the absence of direct visual sensory input due to their occlusion (Thielen et al., 2019).

Some avian species have been tested for this ability. Precocial birds seem to be able to do it nearly from day of hatching (Regolin and Vallortigara, 1995).

A second and different form of hiding is not partial occlusion but complete (temporary) disappearance, i.e., no partial image can be seen by the observer, but the subject is momentarily hidden but still there, termed object permanence, which is developmentally fluid and, according to Piaget, goes through six stages (Zewald and Jacobs, 2022). So far, studies of this ability seem to have concentrated on birds belonging to corvoidea or psittacidae, such as African grey parrots, *Psittacus erithacus*, Australian budgerigars, *Melopsittacus undulatus*, and cockatiels, *Nymphicus hollandicus* (Pepperberg and Kozak, 1986; Pepperberg and Funk, 1990), as well as carrion crows, *Corvus corone* (Hoffmann et al., 2011), European black-billed magpie, *Pica pica* (Pollok et al. 2000), Eurasian jays, *Garrulus glandarius* (Zucca et al., 2007), and azure-winged magpies, *Cyanopica cyanus* of the Iberian Peninsula and Far East (Wang et al., 2021), also found in four species of tits (Paridae ssp.) in the context of predator recognition (Tvardíková and Fuchs, 2010), but rock pigeons, *Columba livia*, are relatively poor in amodal completion tasks (Ushitani and Fujita, 2005; but see also Zentall and Raley, 2019).

'Complex' play behaviour, just by observing the players in their natural environment, can reveal complex cognitive elements. It has conceptually difficult features that need to be known and understood by all participants, if the game is going to work. Interestingly, these complex games also tend to last much longer than solo or object play sessions. The former may usually not exceed 2 minutes while a complex social game such as 'Hide and Seek' may go on for 5 minutes or more.

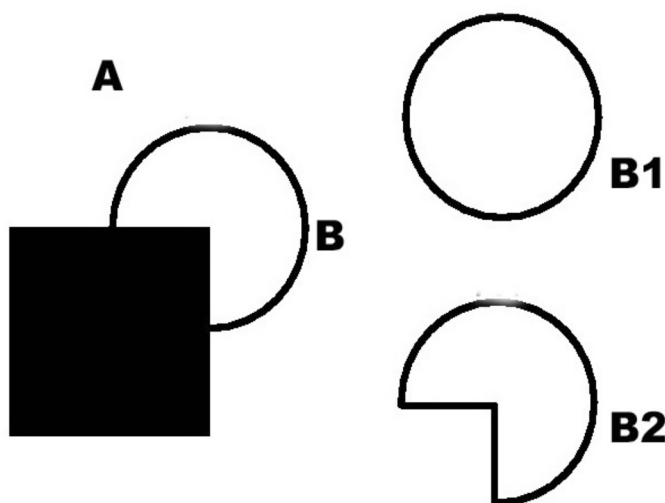


Fig. 4. Amodal completion. A: an object/person/animal partially hidden behind an object. Does B still equal B1 or has it become B2? Amodal completion requires the answer to be B1.

One notes also that the seeker tends to shriek when the hiding bird suddenly reappears. As in children, there is a moment of shock and possibly even fear accompanying the reappearance of the playmate. In some human variants, this moment of reappearance is accompanied by a vocal expletive. In the magpie game, the reappearing bird may amplify its reappearance by outstretched wings (Kaplan, 2019a).

The switch from unstructured and spontaneous social play to a structured game, at least in Piaget's model of cognitive development (Piaget, 1953), has been seen as a substantial step forward in explaining cognitive abilities. Whether this is the case in birds, has yet to be fully investigated. The question is whether this understanding of physical principles is part of a 'core knowledge' (Spelke, 2000, Vallortigara et al., 2010) or part of a cognitive development in some altricial and super-altricial birds is yet to be established (see Shettleworth, 2009), although the importance of play in juvenile magpie development (Pellis (1981b) and their cognitive abilities as adults would suggest that Piaget's model may well apply to some avian species (Hanfstringl et al., 2019).

7.4. Aerial acrobatics and chases

Aerial games that Diamond and Bond (2003) described in keas often happen just half a meter to two meters above ground, skipping rather than flying up briefly or making a low flying round before landing in the same spot the bird had just left. Many juvenile birds may engage in this behaviour. Juvenile southern ground hornbills (*Bucorvus leadbeateri*) engage in fast aerial chases, bill wrestling, jumping on or over each other (Kemp, 2001). Australian magpies and keas are renowned for rather sophisticated and vigorous flights in groups, but they never collide. Schwing and colleagues (Schwing et al., 2017) aptly described aerial acrobatics as "sinusoid, spiral, loop or other flight paths with high levels of spatial movement without apparent gain in distance or elevation; performed at high relative speeds". Aerial acrobatics in adult birds is rare and if and where it occurs, as in some birds of prey, such acrobatics are usually part of courtship displays, such as the daring cartwheeling flights by some raptors (Debus, 1978; Simmons and Mendelsohn, 1993) and ravens (Heinrich and Smolker, 1998). However, Rowley (1974) rightly observed that courtship displays need to be seen in the context of their bonds. He noted that the general paucity of courtship displays in Australian corvid species (he surveyed Australian ravens, *Corvus coronoides*, and little ravens, *C. mellori*) suggested that "the need for elaborate performances is very much less in long-lived birds maintaining a long-lasting pair-bond than in those with more temporary liaisons". This seems to hold for all avian species that are monogamous. Galahs and corellas appear to be the only cockatoos that engage in aerial and trapeze acrobatics as adults (galahs: Rowley, 1990; corellas: pers. obs.).

8. Play-fighting

As many researchers would agree, investigating animal sociality lies at the heart of animal social ecology and evolution (He et al., 2019). The sociality of mammals and birds refers to social relationships among individuals, expressed in social activities such as competition, cooperation and dominance (Whitehead, 1997; Silk et al., 2003; Farine and Sheldon, 2015; McDonald et al., 2017; Yang et al., 2017). Play behaviour can form an important part of those social relationships but not always so. Among nearly seventy primate species Pellis and Iwaniuk investigated, in more than a third, adult-to-adult play was not present (Pellis and Iwaniuk, 2000a, 2000b).

8.1. General play-fighting patterns

Play-fighting is a particularly interesting category (Pellis, 1988), which was recently called 'the most iconic form of social play' (Nolfo et al., 2021) presumably because play-fighting may reflect and incorporate all three social relationships (competition, cooperation and

dominance). Play-fighting is present in all (juvenile) primates and is a play form that has had extremely wide coverage over the greatest number of vertebrate species (Cordoni, 2009; Cordoni and Palagi, 2012). There is a substantial literature now on play-fighting in small mammals, largely of the order Rodentia, including ground squirrels, hamsters, and prairie dogs (Nunes et al., 2004; Cooper et al., 2023) and especially rats (Pellis and Pellis, 2007), with the occasional reference to some marine mammals, of which dolphins are probably the most playful (Kuczaj and Eskelinen, 2014; Hill et al., 2017; Matrai et al., 2022). However, relatively little attention has been paid to play-fighting in birds even though it exists. This is surprising since play-fighting in birds has a good deal in common with play-fighting in mammals - and not just in terms of the rules of play-fighting but in terms of social aspects (Pellis et al., 2023).

The categories of play fighting used by Nunes et al., (2004) for squirrels could be directly transcribed and applied to birds. Their categories, however, include real fighting with face-to-face orientation and biting (biting and pecking in birds), seeking out vulnerable parts of the body and being able to inflict real harm but this is usually not implied in the term play-fighting, although in rare occasions play-fights can turn into real fights.

Playfighting is distinguished by some clear ground rules that harm should not be inflicted and that, whatever action is taken, the mock action will not cross the line and the players will know where this 'line' is.

A play-fighting bout in birds may take the form of wrestling face to face on the ground and trying to push the other over, or as tackling bouts jumping or pouncing on another bird, usually from a running start; or as mock sexual behaviour including mounting. A calmer wrestling version

is played exclusively on the ground: the play initiator and play partner lie on their sides on the ground and just engage in leg wrestles (on all see Nunes et al., 2004). Australian magpies have a clear way of indicating victory over another bird, when the victor stands tall, spreading wings with stretched neck, and the opponent 'volunteers' to adopt the total submission posture, lying on its back and defensively raising its legs and feet (Fig. 5).

Many of the play-fighting actions are conducted in total silence but at certain highlights in the game there may be expletives such as shrieks or loud cries, but these do not end the game, unless the vocal signal is a distress call.

In corella species, as well as in other cockatoos, it may be difficult to tell whether the playing parties are subadults or adults for several reasons. First, juveniles look like adults after the first year or even before, but do not reach sexual maturity until about 5 years of age or, in some species, even later. They can form pair bonds well before sexual maturity and will then often stay together and become a pair (Beeton, 1985; Smith, 1991, Kaplan, 2019b). The only way to test whether both juveniles and adults play would be to sex them surgically as nestlings, then band them for identification, and follow them for at least five years. Corellas of any species, at least those that exclusively occur in Australia and not on adjacent islands, are flocking cockatoos and they play-fight. These include the long-billed corella, *Cacatua (Licmetis) tenuirostris*, western corella, *Cacatua (Licmetis) pastinator*, the little corella, *C. (Licmetis) sanguinea*, the latter by far the more common throughout most of Australia. The Tanimbar corella, *Cacatua (Licmetis) goffiniana*, from the Tanimbar Archipelago, close to and northwest of Australia is also known as the Goffin's cockatoos is a little smaller than the other corellas and a little paler in the colour patches around the beak, but is



Fig. 5. Play fighting: Victorious magpie with outstretched wings at the end of a playfight. The vanquished bird lies on its back, raising its legs defensively so it will not be pecked. Seconds later, the victorious bird tucks in its wings and the vanquished bird jumps to its feet, unharmed. Note that magpies, once they have been expelled from their natal territory, form bachelor flocks and may roam in these for up to 5 years (sexual maturity is reached after 1 year) and in this context play fighting is most often observed (Kaplan, 2019a; Photocredit G. Kaplan-distracting background removed,GK).

almost indistinguishable from Australia's widely dispersed 'little corellas' (Beeton, 1985; Dabb, 1996). Because Tanimbar cockatoos have been used in an Austrian research institute, a good deal is known about their cognition (Auersperg et al., 2014; O'Hara et al., 2015; Bobrowicz et al., 2021), while next to nothing is known about the behaviour and abilities in wild cockatoos (Smith, 1991), unless they are endangered, as most black cockatoos are.

Little corellas certainly play-fight but, as in all parrots and cockatoos, they do not engage in play chases - play chases on the ground seem to be a prerogative of avian species with a good walking gait, as have songbirds, that none of the psittacines possess. Hence, their play-fighting is usually confined to ground wrestles (Figs. 6 and 7 below). Unlike most songbirds, cockatoos that use their feet to manipulate food are also able to use their feet like hands effectively in other contexts such as clasping, even fist making, in such ground wrestles. The function of these games has not been fully identified in cockatoos but one of the hypothesis Pellis and Iwaniuk proposed (2000a), (2000b) about adult-adult play behaviour was to suggest that play-fighting is a way of socially assessing a member of another family group. In some cases, in sulphur-crested cockatoos (*C. galerita*) for instance, ground-confrontations may not get beyond the symbolic tussle and, while these interactions may look fierce (Fig. 6), they rarely develop into a full play-fighting interaction, let alone real fights, yet these encounters may very well be a sizing up of social status and other features. Thus, in sulphur-crested cockatoos, play fighting tends to be brief and largely symbolic.

In contrast to play fighting, all actual fights happen in-situ, i.e. in trees or other surfaces, usually in competition for nest sites. They are swift, energetic, and uncompromising. Full foot or leg amputations happen rarely but leg injuries are common and may even prove fatal. Such interactions usually take seconds rather than minutes and are clearly distinguishable in terms of viciousness, speed, and location from play-fights.

8.2. Aggression, gregariousness and play-fighting

Kummer and Kurt (1965) were perhaps the first who distinguished various types of play-fighting, subdividing it into wrestling, (inhibited) biting, chasing and being chased (but see also Nunes et al., 2004 for an extension of this list).

Play-fighting in adults may not always be feasible or ecologically sustainable, however. To give just one example of the social behaviour of the widespread Australian rainbow lorikeet (*Trichoglossus moluccanus*; subfamily Loriinae), one of 55 species: Rainbow lorikeets have been described as aggressive, especially toward other birds using the same food sources or entering their territory (Bruce, 1973). They have been observed to dominate over miners *Manorina* spp., red wattlebirds *Anthochaera carunculata*, little wattlebirds, *A. chrysoptera*, friarbirds *Philemon* spp., New Holland honeyeaters *Phylidonyris novaehollandiae* and scaly-breasted lorikeets, *Trichoglossus chlorolepidotus*, but red wattlebirds can also dominate over rainbow lorikeets (Chapman, 2005).

They will certainly defend nest sites, even against their own flock members and will behave competitively when food sources are scarce. However, the claim of aggression, which is supposedly a hallmark of this species, is doubtful and my personal observations do not support this claim. Aggression is a dysfunctional behaviour and, in psychology, regarded as a multifaceted disorder (Frau et al., 2019; Haller, 2022), as in an unprovoked attack that neither benefits the instigator nor to the recipient. However, in coastal New South Wales, where my observations were made, food sources are abundant.

Rainbow lorikeets are nevertheless also very gregarious and small alliances of 10–50 birds will often share every activity (Porter, 1992; Lamont and Burbidge, 1996). Their social organisation may be best described as a fission-fusion society. Yet play behaviour in adult rainbow lorikeets is extremely rare and so is play-fighting, although an instance of play fighting has been observed in captivity (pers. communication).

One might ask, why mention the social organisation of rainbow lorikeets in a paper on play? First, lorikeets are parrots, have socially complex relationships, have been shown to be highly adaptable to changes/deterioration in their environment by partly switching from nectar (Emura et al., 2011) to foods that are available (Cannon, 1984), even as extreme as meat (Gillanders et al., 2017). So why have they not been observed playing, since they are known to be gregarious and even playful (Cannon, 1984)? Parental care is also extensive as it is in other parrots and this species seems to meet all or most of the criteria that explain the occurrence of play behaviour in adult parrots.

There is a plausible explanation for the near absence of play and play fighting in wild adult rainbow lorikeets. From my extensive observations it seems that rainbow lorikeets may have a rigid dominance hierarchy (yet to be confirmed), like that first identified in chickens as a pecking order (Strauss et al., 2022).

Described here for the first time, the evidence of their behaviour suggests that social life in this species is structured as a linear hierarchy, one bird at the apex with a few body-guards next to the lead bird. Their social life is guided by a high level of symbolic interactions, reconfirming the dominant bird in its position by deferent actions and body postures of the birds around the dominant bird. Such symbolic gestures seem to be enough to avoid fights of any kind. Agonistic signals to one another are plentiful and are expressed whenever they congregate socially and even during feeding. The symbolic signals fall into several categories that are usually expressed sequentially, each step containing a more direct threat display than the one before, giving another bird plenty of warning to retreat or stop engaging in a specific behaviour and thus avoid escalation into an actual fight. These threat postures seem to express subtleties of degree and often all four non-vocal signals are consistently displayed in sequence:

- 1) elongating body and erect head posture (may indicate dominance),
 - 1a) variant, possibly a stronger message: as (1) above but including an open beak display
- 2) arched head forward (may indicate annoyance);



Fig. 6. Little corellas play-fighting - almost all fighting is done with the feet. Victory is achieved when the opponent is pinned down. Note that the right foot of the victor holds the left foot of the defeated. Outstretched wings may intimidate but they also tend to be used to maintain balance (Photocredit Bobbi Marchini).



Fig. 7. Sulphur-crested cockatoo males (dark brown eyes-females have reddish eyes) posturing and mock-fighting showing each other their fearlessness. Less than a minute later they were foraging quietly together. (Photocredit: G.Kaplan; Bobbi Marchini).

- 3) arched head forward and raised feathers on neck (may indicate rising anger);
- 4) arched head turned to one side and feathers raised on back and nape of neck, close to attack.

These various gestures, as shown in Fig. 8A-C below, may either be displayed sequentially or may be arrested at any point of the sequence. If an incorrect response is given by a subordinate, the punishment may be a swift peck or, more severely, a bite on the foot or leg. Apart from the head, the bare legs and feet are the most vulnerable parts of a bird's body, as mentioned before.

Appeasement gestures by nearby conspecifics tend to set in at level 2 of the warning - consisting of mock allopreening or of lowering the head in submission. Subservience follows very similar bodily expressions seen in mammals: holding head down (importantly: lower than that of the dominant bird), immediate attempts or offers of preening the dominant one.

My records show that one or two birds guarding the dominant bird always respond to incoming birds and checking them before they can get to the dominant one - the series of images below best demonstrate such symbolic gestures (Fig. 8 A-C below). In my observations, there was never any biting or actual fighting, and these short symbolic acts were sufficient to avoid open conflict and injury.

With closely related species, the same symbolic interactions, and the open beak display, as well as stretching the neck, seem to have become a reliable signal not only for group members but also for heterospecifics, judging by their retreat, here shown in the interactions of a rainbow lorikeet with a scaly-breasted lorikeet (Fig. 8 C). Note that these interactions take a few seconds but may be repeated several times within each minute for as long as the individuals are close to each other. These ritualistic movements and intense bouts of mutual observation prevent the two 'bodyguards' from feeding altogether. They remain with their heads submissively bent downwards (Fig. 8A, top left 1B).

Note that rainbow lorikeets are monomorphic. Hence it is impossible to discriminate the sexes by sight. Waiting for the breeding season to start and see who mounts whom is also not a failsafe method because same-sex sexual behaviour/mounting is quite frequent in birds since males have no intromittent organ (only flightless birds and waterfowl have a penis) - even the sex organ is unisex (the cloaca). Female-female (sexual behaviour) occurs most frequently in socially monogamous species but rarely in species that display obligate polygamy (MacFarlane et al., 2006). Hence it is impossible to tell in un-banded, wild birds whether the dominant individual is male or female. However, since adults tend to be paired it is most likely that flocks, even small ones, will consist roughly of equal numbers of males and females. In almost all raptors but also in a number of parrots that I have observed, the female is the more aggressive partner and will readily punish the male if he does not perform in a manner the female seems to expect (observed in wild budgerigars, *Melopsittacus undulatus*, princess parrots, *Polytelis alexandrae*, and the South African love birds).

Discriminating between individuals, however, is possible in so far, as

the amount of yellow and red colouring on the belly and close to the green back and wings tends to show slight variations, making it possible to identify individuals and observe patterns in behaviour and confirm the dominance hierarchy.

However, one element is missing from the social organisation of this species and that is equality. Rainbow lorikeets are monomorphic both in plumage and weight as many parrots, cockatoos and Australian songbirds indeed are, indicating that overt sex differences have been discarded and that such differences are no longer a basis for mate choice (Kaplan, 2019). This 'unisex' style may lead one to be misled into concluding that the social organisation is likewise egalitarian and that may be so in other parrots although information is scant on this point, and the little we know stems from captive birds. The information gained from captive birds may also be misleading, because captivity introduces variables not found in the wild (Hobson et al., 2014a, 2014b; de Souza Matos et al., 2017). The social organisation of rainbow lorikeets is not egalitarian within their own ranks and gregariousness means that they often meet and move in large congregations. Lin and Schank (2022) concluded from their model that small group size promotes more egalitarian societies, and this may be well worth investigating in birds in future.

Dominance hierarchies in birds tend to develop in a variety of ways. One of them is the result of hatching asynchrony - the first hatched is larger and claims first rights to being fed and therefore grows faster than the last hatched (Valderrábano-Ibarra et al., 2007). Another has to do with the female depositing more testosterone into one egg than another and the hatched bird will be more assertive in securing food from the parent, hence grow larger, as has been shown in zebra finches (Gil et al., 1999) or stress in the maternal bird before egg laying causes inequalities in hatchlings (Hernández et al., 2022). However, rainbow lorikeets, like chicken (Chase, 1974, 1982; Strauss et al., 2022), are synchronous hatching and, like chicken, rainbow lorikeets form dominance hierarchies and so do other avian species (e.g. monk parakeet, *Myiopsitta monachus*: Hobson et al., 2014a, 2014b; rock pigeon, *Columba livia*). A recent paper suggests that birds tend to form transient dominance hierarchies (Tibbetts et al., 2022). We know far too little yet about certain social factors and their relationship to potential play behaviour.

In well-studied mammals with dominance hierarchies, at least the young play. In spotted hyena (*Crocuta crocuta*) society, for instance, a matrilineally organized social group, the first-born of the highest-ranking female inherits rights and privileges (Hofer and East, 2003; Benson-Amram and Holekamp, 2012). In wolves, play also reflects their dominance relationships (Cafazzo et al., 2018). Hence, since their social hierarchies tend to be stable, group and individual energies can be diverted elsewhere but there is evidence that, as Cordoni and Palagi put it, "hierarchical steepness" inhibits social play as they observed in adult wolves (Cordoni and Palagi, 2016) and one could therefore surmise that if the social hierarchy is even more rigid, play behaviour in adults may cease altogether, as is the case in rainbow lorikeets.

There have been many studies on sociality and cooperation in animals, but they have been largely confined to primates (Dugatkin, 1997;

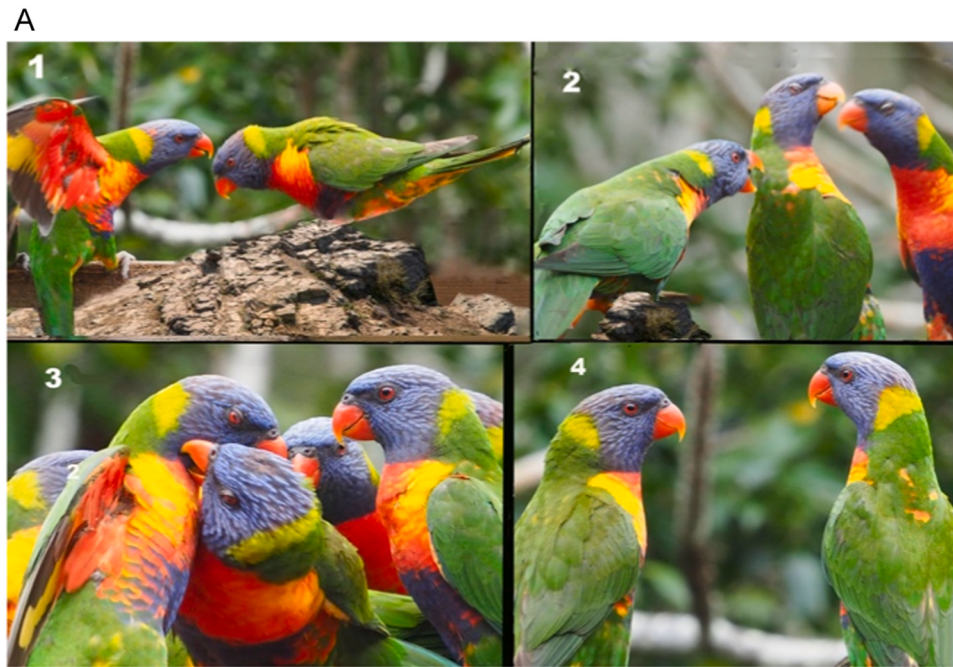


Fig. 8A. **Frame 1:** A is the dominant bird and all others ensure that its head is positioned above that of any others surrounding it. **B-** is one of the 'bodyguards' and it maintains the lowered head position in submission for the entire length of the observation period (5 minutes) after which the birds flew off, flight readiness indicated by Bird A. Bird C possibly the bonded partner(?) is the only one allowed to nuzzle Bird A in an affiliate gesture of gentle beak rubbing. **Frame 2:** Rising hackles in Bird A and neck turned, **Frame 3-** Bird A turning to partner (left) and this is followed by brief allo-preening on top of Bird A's head and then Bird A flattens its feathers again and lifts its head above those of the other birds. **Frame 4:** shows a scaly-breasted lorikeet (*Trichoglossus chlorolepidotus*) making a brazen entrance into the group but does so with an attentive seeking gesture of placing its right foot on the side of the back of the rainbow lorikeet partner but the request was ignored and the scaly-breasted lorikeet flew to another side of the group.

Dunbar, 2009). In bonobos (*Pan paniscus*), their society is female-dominated (Parish et al., 2006) yet they are known to play as adults (Palagi and Paoli, 2007; Palagi, 2023), but the bonobo's social system is not as hermetically closed and far more fluid than that of hyenas. Such flexibility is applied cleverly in bonobos by a system of close affiliations among females and some limited support for some males to stay in the in-group, but also by looking after members via practices of reconciliation and various forms of mutual consolation (Palagi et al., 2004a, 2004b; Anzà et al. 2021).

To my knowledge, there are no such privileges and birth rights in avian societies that are inherited. The lorikeets thus would have to negotiate each aspect of a hierarchy anew in each generation. Social ranking fundamentally shapes the social lives of animals and that may well be a factor in non-expression of play behaviour (Portugal et al., 2020; Rosa Salva et al., 2007, 2013).

Palagi undertook an interesting study when raising the question of the importance of play. She suggested that social play may be a balance between cooperation and competition (Palagi, 2006). Tensions between cooperation and competition (and the level of compliance a highly structured society like that of the rainbow lorikeets demands) could certainly be observed in the rainbow lorikeets' interactions. It would be of interest to investigate such questions in avian and other species with similar and dissimilar social organisation. For instance, one noticeable feature in the case of cockatoos is their prosocial/other directed behaviour and this usually would not indicate dominance hierarchy. Chance (1967) put it well when he argued (of primate society) that the social behaviour in groups of primates is organized in part by an underlying "attention structure"—and to quote:

"Dominance relations reflect the degree to which animals dominate the attention of others. The dominant animal therefore may be said to dominate the attention of others at most, if not all, times, and usually without specific actions to do so." (Chance, 1967, p.509)

This description fits the social organisation of lorikeets very well. Their behaviour would indicate that their dominance hierarchy is indeed based on the degree of attention one individual is afforded over others and, compared even to the number of glances a primate would lavish on one individual, the behaviour of these lorikeets may certainly represent a most extreme form of attention given to the dominant bird by the subordinate members of the group.

9. Emotions, cognition, the lateralized brain and play behaviour

So far, forms of play have been discussed. Results have also indicated, as mentioned above, that social play appears to be a prerogative of large-brained birds and mammals (Iwaniuk et al., 2001). Play behaviour exemplifies particularly well the disciplinary boundaries and layers of explanation between social behaviour and neuroscience. But, when lateralization of brain function is not considered in the behaviour, this can be a substantial problem, an issue that will be addressed below. An even greater problem for the study of play behaviour is the fact that we do not actually know whether it is part of the cognitive abilities of birds, even part of theory of mind or merely a spontaneous, inconsequential outburst of emotions. It is probably both, but a good deal more research needs to be done for a variety of reasons discussed below.

Some play behaviour might readily be regarded as fitting into a theory of mind paradigm because play, in its very essence, may indicate innovativeness. This is certainly an aspect of play behaviour that Patrick Bateson pursued (Bateson and Martin, 2013; Bateson, 2014). Bateson said that play in animals may also mean playfulness going beyond the typical five point definition of play (with which the paper started). He argues that playful play, as distinct from the broader biological category of play, is accompanied by a particular positive mood state in which the individual is more inclined to behave, and possibly think, in a spontaneous and flexible way. Interestingly, Bateson further argued that playfulness may also contain or consist of rule-breaking behaviour.

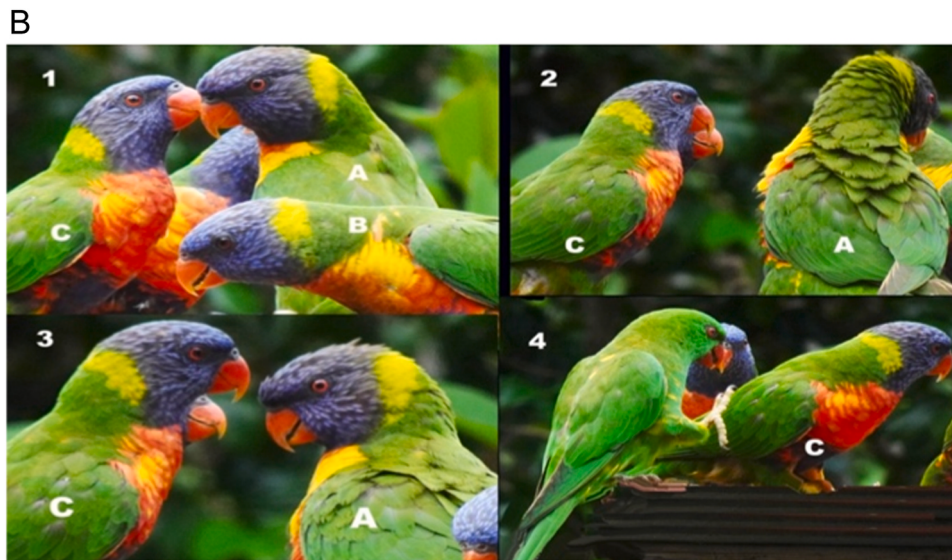


Fig. 8B. **Frame 1:** a new bird flies in and is immediately inspected and welcomed (**Frame 2**). **Frame 3:** However, conflict arises immediately when the incoming bird tries to get to the dominant bird. Agonistic signals come from behind and the front of the bird and the incoming bird makes an undignified retreat. Note the open beak display by the bird on the left is accompanied by loud screeches, from a symbolic body movement to a vocal warning signal. **Frame 4:** peace is restored (dominant bird: right).

Breaking the rules in a safe environment, which is what play can apparently do, and finding new ways of doing things (innovation) (Bateson, 2014).

At the very least, play can further illuminate a possibly significant role of play behaviour both in cognitive behaviour and in survival. Or expressed differently, as Bauer et al. (2021) reminded us concerning human development: "Imaginative play is a physical activity during which children cognitively conceive of the world differently than it really is." We cannot prove that birds play imaginatively but the paper by Bauer et al. (2021) significantly also claimed that play behaviour, at least in humans, encourages prosocial behaviour and of the latter we do have evidence from experiments with ravens (Lambert et al., 2017) and parrots in sharing food (Brucks and von Bayern, 2020), or consoling an affiliate (Fraser and Bugnyar, 2010). We thus already know that prosocial behaviour is an attribute that exists in animals, including birds (Kaplan, 2020; 2023). One could, in fact, argue that prosocial behaviour is a prerequisite for play behaviour.

9.1. Emotions and play

Emotions need to be raised in the context of play behaviour because, at times, play has been described as having 'fun' (Emery and Clayton, 2015) while some games, when accompanied by shrieks, could be interpreted as startle or fear responses. The history of describing emotions in birds has been rather patchy. In some cases, emotions were presumed to exist for which there is, frankly, little to no evidence. Friedman, for instance, writing in the 1930s believed that "greed, cruelty, fear and social emotions" were permanent instinctive emotions while "love" and "courtship" behaviour were "cyclical" in birds, i.e. temporary and presumably confined to the breeding season (Friedmann, 1934). A more traditional view subscribed to the belief that the various observed behaviours to which we attach different meanings, calling them 'emotions' of various kinds, are produced by underlying undifferentiated physiological arousal (Angell, 1916). In such a case it would be entirely unwarranted (and unscientific) to ascribe differences to visible emotional behaviour when the physiology shows no underlying differentiation between behaviours, such as fight or flight responses (Cannon, 1927; Reisenzein, 1983). By contrast, Darwin was quite explicit about the existence of differentiated emotions in animals, at

least basic emotions such as anger and fear (Darwin, 1872; Kaplan and Rogers, 2004). Davidson et al. (1990) working with human subjects, concluded after very rigorous experiments on two complex emotions (happiness and disgust) that unique central or autonomous patterns differentiate between different emotions. Kotrschal (2012) thought of emotions globally and as far more important than a few specific expressions. He said:

"affects and their conscious representations, emotions, are the central agents of social organization in humans and non-human animals. These are bio-psychological phenomena with morphological and physiological substrates, with evolutionary functions, modulated in ontogeny and conservatively preserved in evolutionary history" (Kotrschal, 2012).

Kotrschal worked with corvids for many years and while this definition and context is broad, it is applicable to birds, and raises emotions next and equal to cognition in importance. It seems, that extensive research has once and for all shown that emotional facets of an organism, including birds, may be as manifold and as essential as cognitive and social characteristics. This is quite a significant shift and one that is worth noting when investigating play behaviour (Pellis and Pellis, 2016; Pankseep, 1991).

Before asking what kinds of emotion birds might have, it is perhaps important to ask whether they have the means to generate and express a variety of emotions. After years of significant endocrinological and neuroscientific studies, it is confirmed that birds have the same complement of hormones, or their close equivalents as humans do. The HPA axis (the Hypothalamus-Anterior Pituitary and Adrenal cortex), an ancient conserved system common to all vertebrates (Smulders, 2021), controls stress, mood and emotions. Its main function is to release and regulate corticosterone in birds (cortisol in mammals) from the adrenal gland. We now know that birds have the same, or closely equivalent, sets of neurotransmitters and hormones as do humans and other mammals. Oxytocin (Tobari et al., 2022; Triki et al., 2022), serotonin (Puglisi-Allegra and Andolina, 2015) and the dopaminergic system (Silva et al., 2020) are present in birds, not just in mammals. Even prolactin, once thought to be unique to mammals, is present in birds and forms an important part in modifying parental care of birds (Smiley, 2019).

It would seem difficult to argue that play behaviour does not raise

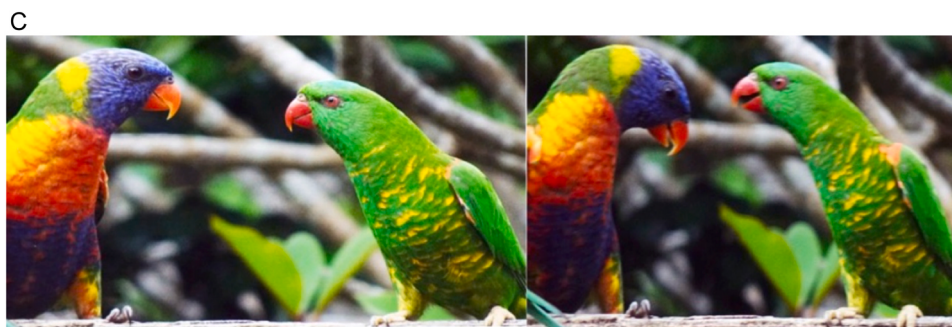


Fig. 8C. Scaly-breasted lorikeet (the same bird as in Fig. 8A, Frame 4 has landed at another location and is confronting a rainbow lorikeet head-on. Although scaly-breasted lorikeets are smaller, they are quite feisty and appear to fear no-one. Unlike rainbow lorikeets, they tend not to be gregarious and live in pairs but feed on the same range of foods as rainbow lorikeets and are therefore potentially competitors. In the second frame, the scaly-breasted lunges forward in an agonistic threat display. However, the rainbow lorikeet adopts a submissive posture immediately and the scaly-breasted lorikeet immediately stops his advances. (all images Fig. 8 A, B,C: Photocredit G.Kaplan).

any emotions or is not, at least in part, an emotional response to a social challenge or play invitation in any vertebrates and that it could also include brief periods of stress.

The stress hormone in birds, corticosterone, is the principal avian glucocorticoid produced in response to stress and it has made its entry into the literature especially via welfare studies in domestic fowl (Wang et al., 2013). It also plays a role in avian reproductive behaviour. In a study of zebra finch females (*Taeniopygia guttata*) it was shown convincingly that stressed females at the time of laying pass on elevated stress-levels to all embryos (Miltiadous and Buchanan, 2021). On the other hand, the possible advantage in stress caused within play situations is that it is short-lived and spikes in corticosterone can return to normal levels rather quickly, with possibly long-term benefits. Gregory Bateson who was one of the first scholars to discuss play behaviour (Bateson, 1955, 1956) proposed an evolutionary model (Bateson, 1963) linking stress responses to somatic change in evolution. These ideas deserve to be rediscovered as Fagen and Fagen (2004) indeed did.

In avian studies, emotions have been relatively neglected, partly because emotions are at times difficult to judge from observation alone and partly because the presence of sophisticated emotional expressions in birds have been doubted. Basic emotions such as aggression and fear have been amongst the few accepted emotions -excepting sexual motivation for copulation (Tinbergen, 1953).

Fear is indeed one of the fundamental emotions in all vertebrates. In birds, there is a centre on both sides of the brain (sub-cortical), the amygdala, that is designed to respond to such emotions. Activating the amygdala does two things: increases adrenalin and raises the vigilance level, as well as enabling memory formation of the specific event that induced the fear response. In humans, at least, the amygdala and ventromedial prefrontal cortex (vmPFC) are known to play a central role in emotion processing (Di Iorio et al., 2017; Lindquist et al., 2012) and the amygdala is a hub for threat detection and negative emotional experience (human: Cardinal et al., 2002; Adolphs et al., 2005; Anderson and Phelps, 1998; rats: Davis and Bauer, 2012; macaques: Kazama et al., 2012). Two regions were recognized as subpallial amygdaloid nuclei in birds, the nucleus taeniae of the amygdala (TnA) (Cheng et al., 1999) and the newly identified subpallial amygdala (SpA) with similarities to specific mammalian subpallial amygdaloid nuclei (Yamamoto et al., 2005). Fearful events (but perhaps also joyful events?) then get encoded in memory.

Memory formation of this kind is crucial to survival, but prolonged fear is seriously detrimental to any animate organism. Agnval and colleagues (2015) tested the relationship of fear (fear of humans, for instance) by conducting experiments for several physiological and behavioural traits in junglefowl (*Gallus gallus*), and found that in fowl with low fear, base metabolic rates were higher, feeding efficiency was greater, plasma levels of serotonin were higher and exploratory

behaviour was greater compared to birds with high levels of fear. Moreover, continuous high levels of fear keep corticosterone levels elevated and such stress exposures can be far-reaching and even lethal to the individual but can even 'infect' a group when exposed to ongoing high stress behaviour (Agnvall et al., 2015). Noguera and colleagues (2017) showed this in yellow-legged gull, *Larus michahellis*. Not only did high levels of corticosterone in some of the gull chicks result in retarded growth, poor quality plumage and cell damage, but raised the stress levels of healthy chicks and they too then carried its insidious health consequences (Noguera et al., 2017).

By contrast, the absence of fear has certain measurable health benefits and presumably makes room for positive emotions. They can act just as much as motivators as fear certainly can. The occurrence and extended practice of play behaviour might require a number of favourable environmental (Auerbach et al., 2015) and social conditions (Ikemoto and Panksepp, 1992; Vanderschuren et al., 1995), first of all, one would imagine, require an absence of fear (Zanette and Clinchy, 2019).

9.2. The role of neurotransmitters in play behaviour

The role of neurotransmitters in the context of social play behaviour can be an important barometer of mood and levels of enjoyment and/or excitement. We know from a large variety of studies on hormones and region-specific pharmacological manipulations in rats and other mammals that the nucleus accumbens, now also identified in birds (Riters et al., 2022), is an important site in regulating social play behaviour (Achterberg and Vanderschuren, 2023). Serotonin (5-hydroxytryptamine), a monoamine neurotransmitter, controls mood. In humans at least, low levels of serotonin have been associated with depression. Oxytocin (mesotocin in birds), is a neuropeptide that is synthesized in the brain, acting as a neurotransmitter and many functions have been attributed to it, among them inducing positive emotions (Tops et al., 2014). Oxytocin is involved in modulating memory, learning, cognition generally and, in humans and primates, even modulates various aspects of social behaviours such as empathy, trust, in-group preference and memory of socially relevant cues (Crockford et al., 2013). Oxytocin has also been shown to improve social performance by reducing stress (Shamay-Tsoory and Abu-Akel, 2016, but see also Jonaidi et al., 2003 finding that oxytocin induced arousal).

The dopaminergic system, often described as the 'reward' system (Baik, 2020), is named in many broad ranging executive functions, even playing a key role in partner preferences and maintenance (Wang et al., 1999) and it has been linked to cognition (Diamond, 2013; Ott and Nieder, 2019). Indeed, the significant dopaminergic innervation of the prefrontal cortex has been confirmed in studies of rats, primates (Berger et al., 1991), (rats: Kalsbeek et al., 1988), and birds. In birds, the nucleus

caudolaterale nidopallium (NCL), is regarded as the equivalent of the mammalian prefrontal cortex (Waldmann and Gu, 1993; Durstewitz et al., 1999; Von Eugen et al., 2020) and is now known to have the richest dopaminergic innervation of any area in the brain (Güntürkün, 2005).

But despite substantial and detailed studies of the functions of this apparently important dopaminergic system, there is little that is specially illuminating as to the role for opioids in birds, until very recently. Ritters et al. (2022) investigated positive emotions in birdsong, but as yet not in play behaviour in birds, although, interestingly, Ritters and colleagues regarded individual song practice as a form of play (Ritters et al., 2019). It would likely be very useful to have future studies investigate the role of any of these hormones and neurotransmitters, the location of activation of such emotions in the process and maintenance of play behaviour in birds.

There is also a large corpus of studies on the hippocampus and the pituitary adrenal system and some early studies on sex differences due to the action of hormones on social behaviour that refer to play behaviour. For instance, in rats, after neonatal exposure to medroxyprogesterone acetate, research has shown long-lasting effects on play behaviour; viz., reduced levels of rough-and-tumble play, particularly in play initiation (Birke and Sadler, 1983). A recent study by Alugubelly and colleagues (2019) found that a) the synaptic levels of GABA and glutamate increased during play, b) players had significantly raised values of neuro-transmitter activity, including the opioid, serotonin, and dopamine systems and c) an increased level of stress occurred during play.

The results by Alugubelly and colleagues (2019) raise important questions on the actual impact of play on the playing organism and invite further research and how a 'good feel' idea of play is reconcilable with the idea of increases in stress levels, for instance, and how emotional and cognitive processes in play might interact. Clearly, emotions play a significant role in the processing of external events and encounters. The brain of vertebrates generally, including humans and birds, has a complex neuroendocrinal apparatus and many brain regions subserving emotions, providing ways of dealing with negative and positive experiences. The prefrontal cortex, the amygdala, the HPA axis but also the sensory-motor areas (eyes and ears) contribute in some way to the regulation of emotions.

9.3. Relating behaviour to brain processes (left/right)

Research concerning the bird brain offers challenges for the simple reason that it is very small and yet manages processes that are astoundingly similar or surpass abilities of much larger brained primates and even shows important parallels to human brain function. Nieder (2017) pointed out that the best-known corvid songbirds (ravens, crows, jays and jackdaws) have a behavioural repertoire suggesting a sense of past and future (Nieder, 2017), a key 'requirement' for confirming Theory of Mind (ToM) (Shettleworth, 2009). They also have many other remarkable cognitive abilities such as episodic-like long-term memory (Salwiczek et al., 2010; Torres Ortiz et al., 2022) and social abilities (Loretto et al., 2012; Veit and Nieder, 2013; Smirnova et al., 2015), some of which are reflected in play behaviour (Brazil, 2002; Bugnyar et al., 2007).

In vertebrates, sensory specializations are usually correlated with increases in size of specific brain areas that are associated with that specialization. This correlation is called the 'principle of proper mass' indicating that the size of a neural structure reflects its processing capacity or is even a reflection of the complexity of the behaviour that it serves (Iwaniuk et al., 2000). For instance, the impressive discoveries of the larger size of the hippocampal complex in food storing birds (Sherry et al., 1989), but also its seasonal size variability (Sherry and Hoshoooley, 2010), and neural spatial representational variations (Payne et al., 2021) have shown that the brain is finely tuned and adaptable to specific needs of a species (Iwaniuk and Hurd, 2005).

There is, however, at times an element missing in the discussion on

brain and cognition: What quite often disappears in cognitive research and all-brain size measurements, is the correct location of the main activity for a particular behaviour (Yamazaki et al., 2007). Location here referred to as left or right hemisphere. This is most likely more important than has at times been given due credit, because each hemisphere controls different functions (Rogers, 1980, 2012). Where and how is problem-solving processed, where is play behaviour processed in the brain and why does it matter? And, where exactly in the brain are the various behaviours processed that we regard as play behaviour?

Neuro-lesioning and neurohormonal research is largely done by sectioning one side of the brain but, unfortunately, in many papers this is discussed without stating which side of the brain was investigated. It would be incorrect to assume that knowing processes occurring in one side of the brain could lead to valid extrapolations for processes on the contralateral hemisphere without needing further examination. One feels dissatisfied when a new behaviour or a significant hormonal action in the brain is described as a set of brain processes and locations are named but it is not clear which side of the brain takes the lead functionally.

A few major laboratories and researchers have spearheaded real advances in how the brain works by clearly stating which behaviour or sensory input activated which part and side of the brain (for instance: extensive work in the laboratories of O. Güntürkün, L.J. Rogers, and G. Vallortigara-see Refs. for specific titles). And some papers from other laboratories indicate clearly, usually in a figure, which area of the brain had been sectioned (Nieder, 2017) but often papers do not say or emphasize either, whether it is the left or right side and/or to what extent the results are applicable also to the contralateral side of the brain.

The two halves of the brain are linked in humans by a strong corpus callosum while in birds it is a much weaker and smaller commissure through which information is relayed to the contralateral side of the brain. A lateralized brain indicates that some tasks are predominantly performed by one side of the brain. Such asymmetries can often be gauged quite easily in behaviour: as right or left footedness in birds or handedness in humans, head turning right or left for visual or auditory responses and by monocular testing in birds (Kaplan and Rogers, 2021).

Both human and bird brains have a visuospatial bias towards the right hemisphere (Diekamp et al., 2005; Tommasi and Vallortigara, 2004; Rogers et al., 2004, 2013). The auditory system has not yet been investigated in as much detail as the visual system, but it too shows hemispheric specialisations (Kaplan, 2017).

The right hemisphere is largely responsible for detecting fine details; it responds to threats, and it is generally capable of strong and instant action (Koboroff et al., 2008) including attack behaviour (Rogers, 1982, 2008). In other vertebrates, fear and escape are controlled by the right hemisphere (Lippolis et al., 2005). Human faces, as has been tested in chickens, are also processed in the right hemisphere (Rosa Salva et al., 2007; Rosa Salva et al., 2013). Martinho and colleagues (2015) showed asymmetry of the pigeon visual system, meaning that visual input is processed by the right hemisphere. Auditory stimuli similarly can be measured by the turns of the head to the right or left, because, as in visual information processing, the information is processed in the contralateral hemisphere (Rogers, 2008; Kaplan, 2017).

While brain asymmetry may be anatomical, biochemical, or functional, it is the functional level that has mostly been investigated. Anatomical asymmetry has so far been described in chickens (Rogers, 1995) and pigeons (Güntürkün, 1997; Güntürkün et al., 2014) and in two nocturnal species that rely on echolocation. In those cases, the auditory projections in the left hemisphere are larger than those on the right (Rogers, 1980). The capacity for vocal learning is lateralized and shared only by humans, songbirds, parrots, hummingbirds, and some cetaceans (Doupe and Kuhl, 1999), including hemispheric lateralization for both motor and auditory processing (Köppl, 2022; Voss et al., 2007; Phan and Vicario, 2010), whilst human language and bird song processing is mostly left hemisphere dominant (Moorman and Nicol, 2015).

Broadly, the left hemisphere (LH) in birds tends to attend to routine, learned behaviour and it categorises stimuli and focusses its attention on the task being performed (Rogers, 2012). Song in birds (and, also human language) is the function of the left hemisphere based on continual interaction between secondary auditory regions and sensorimotor regions, similar to the interaction between Wernicke's and Broca's areas in human infants (LH) acquiring speech and language (Prather et al., 2017). The left hemisphere is responsible for visual discrimination learning, attention switching, peck-no peck decisions.

The right hemisphere (RH) activates the hypothalamic-pituitary-gonadal axis and controls attack and copulation, and it detects responds to novelty, processes strong emotions (distress or fear), and generally activates emergency responses (Rogers et al., 2013). Classes of objects and organisms, however, are only processed as categories in the LH and thus the left hemisphere cannot distinguish between individuals or finer points. This important task is entirely managed by the right hemisphere (Vallortigara and Andrew, 1994). Spatial memory and musical processing involve mostly the right hemisphere which also detects and remembers fine cues and notes small changes in the environment (on all see Rogers, 2012). The RH initiates withdrawal, fleeing the scene and actions agonistic responses, while the LH is noted for approach behaviour (Koboroff et al., 2008). The LH can also modify and reduce the impact of emotions generated in the RH.

The identification of specific functions of the LH versus the RH would suggest that much of play behaviour might be controlled by the right hemisphere in birds,

- a) because emotions are largely processed by the right hemisphere and
- b) recognition of familiar faces, i.e., close conspecifics and even human faces is also undertaken by the right hemisphere.

But there are complicating factors. First, the left hemisphere can modulate (inhibit) the emotional responses of the right hemisphere (Rogers et al., 2013); and the right hemisphere is also known to make a contribution to cognitive aspects of behaviour or, at least, as a study by Yamazaki and colleagues found (2007), there are cognitive dichotomies of the cerebral hemispheres in pigeons: the left hemisphere computes categories and the right hemisphere uses an exemplar strategy and relies on configuration. Further, songbirds and parrots have laterally placed eyes and so are the ears-hence input of information is different on each side, but the visual or auditory information input is not processed by the side of the input. A left eye/ear input is processed by the right side of the brain and a right eye/ear input is processed by the left side of the brain. Hence, each hemisphere receives visual and auditory input from the contralateral eye or ear. The same nuclei occur on the left and on the right side of the brain, but they are often not of equal size or function, i. e., are fundamentally asymmetrical. Because each hemisphere may have similar but not identical functions, such an organisation has been called efficient because it avoids duplication of tasks and leads to faster responses to stimuli, see for instance the fascinating experiments showing the hemispheric differences of visual categorizations in pigeons (Güntürkün and Ocklenburg, 2017). The speed with which information is transferred may decide what behaviour can follow. The interactive dynamics between the two hemispheres are also relevant to play behaviour in birds because, for instance, the left hemisphere can suppress strong emotions produced in the right hemisphere.

These dynamics of information processing and transfers yet await far more investigation especially concerning play behaviour. It would seem reasonable to hypothesise that the processing of play behaviour may be simple or quite complex both in emotions and cognition, depending on play type, and that both, emotional and cognitive expressions may be quite complex and even conflicting (for instance when a play offers both exhilarating and fearful emotions). So far, this has hardly been addressed because hemispheric lateralization and specialisations have rarely been considered. Even though in mammals the basic neural circuits needed to produce play are subcortical (Achterberg and

Vandershuren (2023), there are known asymmetries in subcortical brain regions in mammals (e.g., hippocampus, Kawakami et al., 2003; Goto et al., 2010; Karizbodagh et al., 2021; amygdala: Ocklenburg et al., 2022, midbrain: Gloveli et al., 2023). In birds there are clear asymmetries in the midbrain (Manns and Ströckens, 2014). This means that, in avian species, the lateralities are present in brain regions relevant to play behaviour.

We know that another special ability, that of vocal learning, is multifaceted (Catchpole and Slater, 2003; Carouso-Peck et al., 2021), and is strongly influenced by a range of factors, including and importantly by social experiences (Chen et al., 2016). It may require the management via the executive functions of the brain (Bobrowicz and Greiff, 2022), which includes suppressing of impulses, being flexible and, in play behaviour, getting involved in challenging as well as exciting tasks (Rogers et al., 2004, Berk and Meyers, 2013).

10. Concluding Remarks

In the past, the idea that birds could be capable of complex behaviour, given their small brain sizes, seemed impossible. It was a false assumption, be this in problem solving tasks, innovation (Griffin et al., 2014), or apparent cognitive abilities (Güntürkün and Bugnyar, 2016). Indeed, the cognitive research into avian species has revolutionised the field, finding that some cognitive abilities of some avian species are on a par with those of chimpanzees (Olkowicz et al., 2016).

Many writers begin their examination of animal play with a generalised all-embracing definition of what it is that the term 'play' means to them. Play, as outlined above (Section 5.4) should be intrinsically rewarding, pleasurable, spontaneous, voluntary and/or intentional; it must be modifiable (can be incomplete or exaggerated) relative to functional behaviours. Moreover, play forms should be identifiable from one occasion to another and animals would have to appear safe and relaxed (Janik, 2015).

We have known for some time that the context of play behaviour also plays a role. For instance, complex environments improve learning abilities (Ferchmin and Eterovic, 1982). Schank and colleagues (2023) rightly suggested that any theoretical framework on play could be dovetailed with two other variables: 1) environmental enrichment and 2) curiosity as a factor. Indeed, these are valuable suggestions. And they quoted an earlier study by Freund and colleagues (2013) which had shown, when testing mice in the same environmentally enriched context, and using only genetically identical mice, that differences in individuals emerged in adult neurogenesis as a result of different experiences (Freund et al., 2013; Paredes et al., 2016). Those with richer experiences also literally 'grew' more neurons in their hippocampus and this was a significant finding. To quote: "the key function of adult neurogenesis is to shape hippocampal connectivity according to individual needs and thereby (to) improve adaptability over the life course" (Freund et al., 2013) and presumably survival. The other suggested area to be included is curiosity and there are good reasons for this too, as Gruber and colleagues (2019) found. Curiosity and exploration in juveniles enhance hippocampal-dependent memory encoding which is related to modulations in activity in the dopaminergic circuit (Gruber et al., 2019).

By concentrating exclusively on adult social play behaviour in birds, this paper does not suggest in any way that the juvenile period is not crucially important in shaping individual responses to their environment and in variable responses to play opportunities (Mettke-Hofmann et al., 2002). However, it suggested that adult play requires also its own explanations. Very few species play as adults and those of which we so far know, such as humans, some great apes, rodents, cetaceans, elephants, cockatoos, keas, corvids, do not just have some crucial life history factors in common. They also have the largest brains in absolute terms and relative to body mass.

We know a good deal about the cognition of passerines and of psittacines now (encyclopaedic summaries: Kaplan, 2018, 2021a). The link

of play behaviour with cognitive ability, or at least between instances of social play and brain size has also been discovered recently (Kaplan, 2021b). These findings raise the question what the links between cognition and play might be and, to answer questions of this kind, it now requires that avian brain studies carefully identify the areas of the brain that are activated in play. Brain asymmetry as said before, can be quite easily assessed in behavioural studies, such as handedness (in humans, primates), pawedness (in dogs, horses), or footedness (in cockatoos); right-footed meaning left hemisphere dominant. Although emotion processing is accepted as being lateralized, the specific role of each hemisphere in processing and expressing emotions and play behaviour remains an open question and invites further investigation.

There are indeed many questions that are raised about play behaviour when the connection to hemispheric specialisation is made. Vocal and social learning are largely left hemisphere activities but play itself can raise stress levels which could impede learning and such conclusions would certainly not fit with current results. The activities in social play may require on-the spot solutions in interactive play-fighting, for instance, when split decisions can make the difference between 'winning' or 'losing', and between a positive or fear inducing experience.

As suggested throughout the paper, there is much yet to be discovered, be this for evolutionary ecologists, comparative psychologists, ethologist, behavioural neuroscientists, or endocrinologists (Angelier et al., 2010; Smiley, 2019, Smiley et al., 2022) to investigate many crucial questions yet unanswered in the play behaviour of birds generally and especially in adult social play.

One of the aspects missed so far is that social play behaviour in adults may indeed not just have to do with large brains but with emotion and social affiliation. Neuroscience has made probably the most significant contributions to our knowledge of the vocal behaviour, learning and cognition in birds, starting perhaps with Nottebohm (Nottebohm, 1980). The line of important discoveries could now include social play behaviour and answer some of the riddles about the brain activities associated with play, being mindful, however, to consider which side of the brain is more engaged and in which specific context. In object play, this should be quite simple to test. In laboratory work, object play can be quite readily induced (Auersperg et al., 2015).

In adults, the persistence and amount of social play behaviour is far more difficult to test and, at least in free-ranging birds, many other factors would have to be considered. One would need to establish their social characteristics, i.e. the level of prosocial and cooperative behaviour (Prior et al., 2020; Kaplan, 2020, Palagi, 2023) and the level of affiliative bonds. Play could be one confirmation of such bonds. In many other species, even outside the sister group of songbirds and parrots, it has been shown that pair bonds may be established well before sexual maturity (Choudhury and Black, 1994; Teitelbaum et al., 2017, Kaplan, 2019b), and one would probably include species known to be gregarious that have both the opportunity and inclination to form adult bonds with conspecifics (Tobias et al., 2016; Prior et al., 2020).

Then there is the question of group size: small group size promotes more egalitarian societies, and this may be well worth investigating in birds in future. In adulthood, playing and non-playing species could be compared and, as a future research suggestion, this might reveal whether adult play triggers or is a consequence of brain processes (neural, hormonal) that cannot be confused with developmental processes, but suggest an expansion of both emotional and cognitive dimensions of the brain of which adult play behaviour is just one of many manifestations.

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Declaration of Competing Interest

The author has no conflicts of interest to declare.

Data Availability

Not applicable.

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