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## **Combinatory Actions During Object Play in Psittaciformes (Diopsittaca nobilis, Pionites melanocephala, Cacatua goffini) and Corvids (Corvus corax, C. monedula, C. moneduloides)**

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# Combinatory Actions During Object Play in Psittaciformes (*Diopsittaca nobilis*, *Pionites melanocephala*, *Cacatua goffini*) and Corvids (*Corvus corax*, *C. monedula*, *C. moneduloides*)

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The playful (i.e., not overtly functional) combination of objects is considered a potential ontogenetic and phylogenetic precursor of technical problem solving abilities, as it may lead to affordance learning and honing of mechanical skills. We compared such activities in 6 avian species: 3 psittaciforms (black-headed caiques, red-shouldered macaws, and Goffin cockatoos) and 3 corvids (New Caledonian crows, ravens, and jackdaws). Differences in the type and frequency of object combinations were consistent with species' ecology. Object caching was found predominately in common ravens, which frequently cache food. The most intrinsically structured object combinations were found in New Caledonian crows and Goffin cockatoos, which both stand out for their problem solving abilities in physical tasks. Object insertions prevailed in New Caledonian crows that naturally extract food using tools. Our results support the idea that playful manipulations of inedible objects are linked to physical cognition and problem-solving abilities.

**Keywords:** object play, exploration, tool-use, combinatory behavior, avian cognition

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The playful manipulation of inedible objects may be an ontogenetic and phylogenetic precursor of functional behaviors such as extractive tool use and physical problem solving (Graham & Burghardt, 2010). During development, object play may inform individuals of typical object affordances (i.e., "an object's intrinsic and contextual properties that determine the number of ways it can be used" see Diamond & Bond, 1999, p. 77) and hone their skills for goal-directed problem-solving later in life. Phylogenetically, the presence of such tendencies in a species' repertoire, regardless

of their adaptive origin, may increase the likelihood of a descendant species acquiring a tool-using trait, or simply more goal related object manipulation (Bateson & Martin, 2013). For these reasons, species with higher rates of functional object behavior, or species that perform well in tasks that require motor skills, are also expected to play intensely with inanimate objects when no obvious immediate goal is pursued. Play behavior is generally defined as being spontaneous, intrinsically motivated (self-rewarding), exaggerated, and repetitious, occurring only in the absence of stress

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(e.g., Bateson & Martin, 2013). Within it, “object play” refers to divertive interactions with inanimate and inedible objects, including exploratory manipulations (e.g., Fagen, 1981). Here, we focus on combinatory actions, in which different objects are brought into direct contact with each other, as this is considered a particularly informative trait of physical cognition in nonhumans (Hayashi, Matsuzawa, 2003; Hayashi, Takeshita, & Matsuzawa, 2006; Kenward, Schloegl, Rutz, Weir, Bugnyar et al., 2011; Pepperberg & Shive, 2001; Takeshita, 2001) and is relevant to the development of tool use in human infants (Connolly & Dalgleish, 1989).

Children start combining two free objects when they are ~8 months old (Connolly & Dalgleish, 1989; Greenfield, Nelson, & Salzman, 1972; Piaget, 1952; Rat-Fischer, O’Regan, & Fagard, 2012). At 10 months, infants start combining objects with elements from their environment, such as inserting objects into cavities or stacking rings on a pole. After their second year, infants start to use an object as a tool to obtain a desired goal (Connolly & Dalgleish, 1989; Rat-Fischer et al., 2012). Object-object combinations have so far been studied most extensively in nonhuman primates (e.g., Hayashi & Matsuzawa, 2003; Hayashi et al., 2006; Takeshita, 2001; Torigoe, 1985). A survey across 74 primate species found that only capuchin monkeys and great apes showed complex motor actions and combinatorial behaviors in their object play (Torigoe, 1985). Both groups stand out among primates, not only for being habitual tool users in the wild, but also for repeatedly showing flexible tool-oriented behaviors in experimental contexts (see Shumaker, Walkup, & Beck, 2011 for a summary). Torigoe’s survey (Torigoe, 1985) further suggests that operative object actions, such as flexible tool use, are not predicted by the general diversity of object-related behaviors within a species’ play repertoire, but by the extent of complexity in which objects are brought into relation with each other.

Numerous reports of avian play behaviors are also comparable to those of mammals (Graham & Burghardt, 2010). Birds, particularly corvids and parrots, engage in social and/or locomotor play (e.g., Diamond & Bond, 2003; Diamond, Eason, Reid, & Bond, 2006; Heinrich, 2007; Ortega & Bekoff, 1987), as well as object play (see Burghardt, 2005 for an overview; Bugnyar, Schwab, Schloegl, Kotschal, & Heinrich, 2007; Diamond & Bond, 1999). Among corvids, ravens (*Corvus corax*) exhibit especially pronounced social and object play behaviors. Young ravens, particularly during their first years of life, are neophilic and manipulate objects such as sticks and stones for long periods without being motivated by hunger. However, responsiveness to nonedible objects declines rapidly with age (Heinrich, 1995, 2007). Ravens also extensively play-cache and retrieve inedible objects, a behavior that may foster learning about potential competitors for food caches (Bugnyar et al., 2007). Kenward and colleagues (2011) hypothesized that combining objects with substrate properties, such as cavities during play-caching, may have promoted the evolution of tool use in another corvid, the New Caledonian crow (NCC, *Corvus moneduloides*). NCCs are habitual tool users in the wild (Hunt, 1996; Shumaker et al., 2011). Kenward and colleagues (2011) compared the ontogeny of object play in ravens and NCCs until 6 weeks after fledging and found striking qualitative similarities in noncombinatorial object manipulations between the two species. However, object-object combinations increased uniformly in NCCs whereas they peaked and subsequently declined in ravens. Kenward et al. (2011) hypothesized that the high motivation

of juvenile NCCs to combine objects may boost their development and refinement of tool-oriented behaviors.

Combinatorial actions also appear during object play in psittaciforms. Pepperberg and Shive (2001) report that a single juvenile African grey parrot (*Psittacus erithacus*) used its beak to combine up to three objects by placing them side by side, stacking them on top of each other, or putting a smaller object into a bigger one. Such actions parallel observations in nonhuman primates and human infants (Greenfield, 1991; Langer, 1986; Piaget, 1952). Another parrot in which extensive object play has been found is the New Zealand kea (*Nestor notabilis*) (Diamond & Bond, 1999). In captivity, kea playfully combine up to three items, fit objects into other objects, and insert objects into substrates (Gajdon, Lichtnegger, & Huber, 2014). Diamond and Bond (1999) suggest that the principal benefit of this behavior lies in detecting potentially functional object properties. Kea may thus develop generalized skills and opportunistically accumulate knowledge about their physical environment that they can flexibly recall at later times. Of interest to the authors, although no evidence exists for their use of tools in the wild, kea use different types of tools in captivity (Auersperg, Gajdon, & Huber, 2010; Auersperg, Huber, & Gajdon, 2011; Gajdon, Lichtnegger, & Huber, 2014).

Relative to their body size, parrots and corvids have similar forebrain sizes as the great apes (Emery & Clayton, 2004; Iwaniuk & Nelson, 2003; Lefebvre, Whittle, Lascaris, & Finkelstein, 1997) and perform comparably in cognitive tasks to mammalian taxa of similar relative brain volume (e.g., MacLean et al., 2014). The high rates of innovative foraging behaviors observed among parrots and corvids are also strongly correlated with residual brain size within the respective families; more so than in other birds (Lefebvre, Reader, & Sol, 2004; Timmermans, Lefebvre, Boire, & Basu, 2000). For these reasons, parrots and corvids are frequently used as avian models for the study of physical cognition (van Horik, Clayton, & Emery, 2012; van Horik & Emery, 2011).

In the present study, we profile unrewarded object manipulations across several parrot and corvid species, including one parrot and one corvid species that have previously demonstrated advanced physical cognition and capacities for complex tool innovation. It is not possible to obtain individuals from a large number of different species that have controlled and comparable developmental backgrounds, but we approximated this ideal by restricting differences in individual histories as much as possible. Subjects in this study were required to have minimal experimental history, including no participation in studies on object play, and being housed in social groups containing at least some individuals of less than 2 years of age.

We tested three psittaciformes and three corvids. Within psittaciformes, we used three species. Two were New World parrots, red-shouldered macaws (*Diopsittaca nobilis*) and black-headed caiques (*Pionites melanocephala*) (Juniper & Parr, 1998; Schulenberg, Stotz, Lane, O’Neill, & Parker, 2007). Both New World parrots are renowned in the pet industry for their conspicuous play behavior. The third parrot species, the Indonesian Goffin cockatoo (*Cacatua goffini*), exhibits intensive and persistent object exploration and, similarly to the kea, is an outstanding performer in tasks involving physical cognition and has displayed several types of tool innovation in captivity (Auersperg, Kacelnik, & von Bayern, 2013; Auersperg, Szabo, von Bayern, & Kacelnik, 2012). Within corvids, we tested a tool-using

species, the New Caledonian crow (Hunt, 1996); a food caching and pilfering species, the common raven (Heinrich, 2007); and a species that does not rely on food caching or tool use, the jackdaw (*Corvus monedula*).

All subjects were presented with a similar set of objects, with only slight alterations in the dimensions of some objects relative to the body size of the subjects. We used the same ethogram and trained observers for recording behaviors across all species. We aimed to record (a) free object-object combinations and (b) combinations of objects with fixed structures, such as inserting, caching, or ring-stacking. Based on previous experience, we expected all of these species to engage in spontaneous object manipulation and exploration, with more play in younger subjects (Groos, 1898; Hall, 1998). Differences in morphology, dexterity, perception/attention, motivation, and ecological niche help to explain differences across all species tested. We expected young animals of species with high technical capacities, such as the NCC or the Goffin's cockatoos, to show higher rates and diversity of object combinations during play. We further expected the object choice and the types of combinations used to reflect ecological specializations, for example, elevated play caching in food storing species such as the raven and preferential interactions with elongated objects involving probing and inserting combinations in the habitually tool using NCCs.

## Method

### Subjects

**Psittaciforms.** Ten juvenile (8 hatched in 2010 and 2 in 2011) and 4 adult Goffin cockatoos (2 hatched in 2007 and 2 in 2008), 4 juvenile red-shouldered macaws, and 4 juvenile black-headed caiques (all hatched in 2010) participated in this study (see Table 1). All parrots were hand-reared and kept on an ad libitum diet (fresh and dried fruits and vegetables, minerals, a mixture of cooked and uncooked seeds, scrambled egg, and fresh drinking water) in single species, enriched groups. All Goffins were kept as a group at the "Goffin Lab" of the Department of Cognitive Biology (Vienna,

Austria) in a large aviary with an outdoor area and an indoor section that was kept close to 20°C (see Table 1 for measurements). The macaws and caiques were kept indoors (see Table 1) at the Avian Cognition Lab, School of Biological and Chemical Sciences, Queen Mary University of London, United Kingdom (QMUL) under 12:12 light:dark cycles.

**Corvids.** Eight juvenile jackdaws (hatched in 2011), 8 subadult ravens (hatched in 2010 and 2011), as well as 9 juvenile, and 10 adult NCCs participated (see Table 1). All jackdaws and six of the ravens were hand-raised. All NCCs were wild caught in 2010. The subadult NCCs had not yet become independent from their parents, and were estimated from their gape coloration to have hatched in 2009 (as the breeding season for wild NCCs starts in October/November they were less than 2 years old at the time of testing; Holzhaider et al., 2011). All corvids were provided with food twice a day (minced beef heart supplemented with dried insects and curd, eggs, noodles, rice, vitamins and minerals, mealworms, as well as fruit, nuts, and cereals) and fresh drinking water available ad libitum. Ravens and jackdaws were kept in social groups in enriched, outdoor aviaries, each containing several shelters. Ravens were kept at the Haidlhof Research Station, an outdoor lab of the University Vienna and University of Veterinary Medicine, Vienna, Austria. Jackdaws were kept at the Avian Cognition Lab by the Department of Zoology (Oxford University) hosted by the Max Planck Institute for Ornithology (Seewiesen, Germany; see Table 1 for aviary measurements). NCCs were kept in pairs or family groups (five groups containing two to five individuals) in enriched outdoor aviaries with lit and heated (20°C) indoor rooms (see Table 1) at the Avian Cognition Lab by the Department of Zoology hosted by the Max Planck Institute for Ornithology. All subjects were individually marked with colored leg bands for identification.

### Experimental History

The Goffin cockatoos (Goffins thereafter) had previously participated in a means-means-end task featuring an artificial fruit apparatus with multiple sequential locks (Auersperg, Kacelnik, &

Table 1

*Subject Details: Family/Order, Species, Sex (M = Male, F = Female), Age Class (Juvenile/Subadult/Adult), Rearing History (Hand-Reared or Parent-Reared), Housing (Group/Pair), Keeping Location, Observer (AA, JvH = See Author List; AL = Agatha Lievin-Bazin, MS = Martina Schiestl), Aviary Size (OD = Outdoors, ID = Indoors), and Time Frame in Which Data Were Collected*

Species	Sex	Age class	Rearing	Housing	Where	Observer	Aviary size	Time frame
Goffin cockatoo	7 M, 7 F	4 adult, 10 subadult-juvenile	Hand	Group	Goffin Lab, Austria	AA	ID: 45 m <sup>2</sup> , 2–6 m high OD: 150 m <sup>2</sup> , 2–5 m high	July–Aug. 2011
Red-shoulder macaw	3 M, 1 F	Subadult-juvenile	Hand	Group	QMUL, UK	JvH	ID: 2 m <sup>3</sup>	March–May 2012
Black-headed caique	4 M,	Subadult-juvenile	Hand	Group	QMUL, UK	JvH	ID: 2 m <sup>3</sup>	March–May 2012
NCC	9 M, 10 F	9 juvenile-subadult, 10 adult	Parent	Pair/family	Avian Cognition Lab, Germany	AL	Average ID: 7 m <sup>2</sup> , 2 m high OD: 20 m <sup>2</sup> , 2 m high	July–Aug. 2011
Jackdaw	4 F, 4 M	8 juvenile	Hand	Group	Avian Cognition Lab, Germany	AL	OD: 120 m <sup>2</sup> , 2, 5–3 m high test aviary 15 m <sup>2</sup>	July–Aug. 2011
Raven	4 M, 4 F	8 subadult-juvenile	2 parent 6 hand	Group	Haidlhof Research St., Austria	MS	OD: 200 m <sup>2</sup> , 3–4 m high	Oct.–Nov. 2011

von Bayern, 2013) as well as in an experiment on Piagetian object permanence (Auersperg, Szabo, von Bayern, & Bugnyar, 2013). The red-shouldered macaws and black-headed caiques (hereafter macaws and caiques) had participated in means-end horizontal string pulling tasks, innovative foraging tasks and serial reversal learning tasks (van Horik & Emery, 2014). The ravens had been tested on social cognition and vocal studies (Massen, Pasukonis, Schmidt, & Bugnyar, 2014). Likewise, jackdaws and NCCs had participated in sociocognitive experiments. None of the subjects had been tested in the context of object play, or previously presented with the objects used in this experiment.

## Ethics Statement

All animals are permanently kept (before and after the experiment) in well-established groups at the respective research institutions and are housed in accordance with Austrian, British, and German Law. As our experiments are strictly noninvasive and based purely on behavioral observations, they are not classified as animal experiments in accordance with the Austrian, German, and British law (Austria: §2. Federal Law Gazette No. 501/1989; Germany: §7 Bundestierschutzgesetz; United Kingdom: Animal, Scientific Procedures Act). All animals are closely monitored on a daily basis; no elevated levels of stress or aggression could be detected throughout our testing period.

## Apparatus

We presented subjects with wooden objects of three color categories clearly distinguishable within the avian spectrum (Varela et al., 1993): Yellow, red, and blue (painted with childproof, nontoxic, water-based acrylic paint), of up to five different sizes (see Figure 1, and electronic supplementary material, ESM Section B for size descriptions), and of four distinctive shape categories: Sticks, rings, cubes, and balls (see Figure 1). Subjects were also presented with four different “activity plates” with different diam-

eter holes and tubes to correspond with the sizes of the wooden objects. The activity plates were comprised of: (a) four horizontal tubes, (b) four vertical tubes, (c) a 30 mm thick plate with four holes drilled into the wooden base, and (d) four dowel poles of different diameters (see Figure 2 and ESM Section B for dimensions).

## Experimental Setup and Procedure

The activity plates were positioned on the aviary floor in a rectangular arrangement at approximately 50 cm distance from one another for ravens, NCCs, jackdaws, and Goffins. Because of smaller aviary sizes, the activity plates were positioned 30 cm apart for the macaws and caiques (as in Figure 2). The position of each activity plate varied randomly across sessions. To control for neophobia toward the plates and to familiarize subjects with the testing materials, the plates were placed inside the aviary (without the wooden objects) until each individual bird was observed approaching and touching them at least once before testing started (this phase varied from two days for Goffins and caiques to several weeks for macaws and ravens because of different levels of neophobia/neophilia). The objects were spread randomly across the aviary floor around the plates before testing at approximately 50 cm distance from the activity plates (10 cm for macaws and caiques). Because separating individuals from their social group causes stress and this may influence play behavior, we decided to test all subjects within their normal housing conditions and group contexts. This decision reflects a compromise between losing independence of individual observations and avoiding the more serious alternative of testing stressed animals.

Each group was tested for 15 30-min sessions, and all species except for caiques and macaws were tested in outdoor aviaries. The objects were present only during sessions. To maintain interest in the objects, subjects were tested at 2 or 3 day intervals. The ethogram used to record object-related behaviors (see ESM Section A) was consistent across species (see Table 2) and observers received the same training. Object actions (action addressed toward an object) were recorded on a voice recorder, starting from the moment the first object was touched by any subject. The observers mainly stood outside the aviary at approximately 2 m distance from the arrangement of the activity plates. A proportion of the data (the complete data set from caiques, macaws, and ravens) was additionally filmed, with the camera focused on the activity plates. To keep the birds’ attention engaged on the objects rather than on the experimenters, the latter stayed outside the aviary. The NCCs were housed in five different groups and, therefore, recordings were made separately for each group.

## Analysis

The Goffins (see Table 1) and NCCs included two age groups, adults and young subadults. As we found pronounced differences between the two age groups in NCCs, they were treated as different entries in the analysis. We focused our analysis on a selection of actions as summarized in Table 2. We used the mean frequencies of the respective object action, as recorded across subjects, for each species. For interrater reliability testing, part of the video data (Sessions 11–15 of each, caiques, ravens, macaws, and ravens) was independently rated for object-object and the three object-

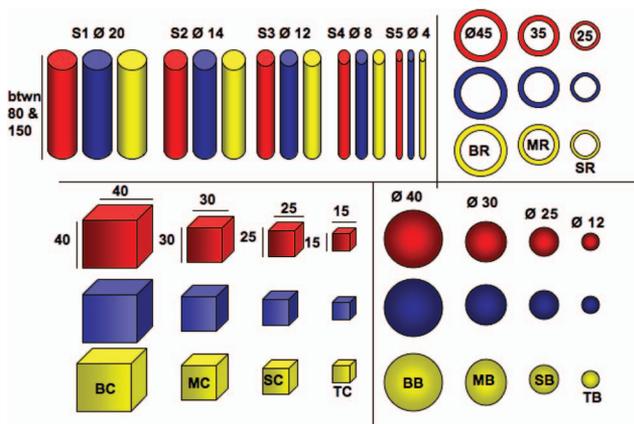


Figure 1. Wooden toy objects used (dimensions in millimeters); Sticks (S1-S5); Cubes: Big Cube (BC), Medium Cube (MC), Small Cube (SC), Tiny Cube (TC); Balls (BB-TB); and Rings (BR-SR). Sticks (S1-S5) were between 8 and 15 cm long depending on species’ body size: 8 cm for macaws and caiques, 10 cm for Goffins and jackdaws, 12 cm for NCCs, 15 cm for ravens. See the online article for the color version of this figure.

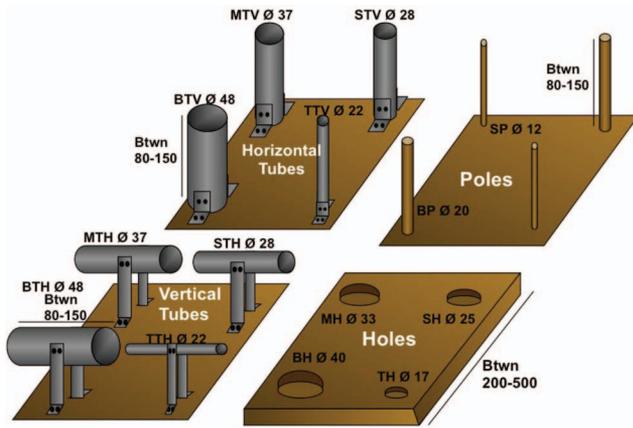


Figure 2. Activity plates (dimensions in millimeters unless specified): tubes and poles (length 80 to 150 mm depending on the respective species' body height: 80 mm for macaws and caiques, 100 mm for Goffins and jackdaws, 120 mm for NCCs, and 150 mm for ravens); vertical tubes: big tube vertical (BTV), medium tube vertical (MTV), small tube vertical (STV), tiny tube vertical (TTV); horizontal tubes (BTH-TTH); poles (BP and SP); holes (BH-TH). BTH, BTV, and BH fit all objects except big rings, MTH, MTV, and MH fit all objects except for the big rings cubes and balls, STH, STV, and SH fit all objects except for big and medium rings cubes and balls. TTV, TTH, and TH fit tiny cubes tiny balls and sticks from size S2–S5. See the online article for the color version of this figure.

substrate interactions by three raters (JvH, AA, & M. Schiestl for caiques and macaws; AA & M. Schiestl as well as an independent observer, M. Domansegg for ravens): Intraclass correlation coefficients were as follows: for ravens between raters 1 versus 2 = 0.91 for ravens 2 versus 3 = 0.95, for ravens 1 versus 3 = 0.89; for caiques 1 versus 2 = 1; for caiques 2 versus 3 = 0.97, for caiques 1 versus 3 = 0.97; for macaws 1 versus 2 = 1; for macaws 2 versus 3 = 1, for macaws 1 versus 3 = 1.

The data for each individual were divided into three blocks of five sessions each (Block 1 = Session 1–5, Block 2 = Session 6–10, and Block 3 = Session 11–15). We conducted two Generalized Linear Mixed Models (GLMM). Included in the model, as independent variables, were only those species that showed more than one of the respective object action categories (adult NCCs and macaws never combined two free objects or objects with substrate features more than once, as described in Table 2). A first model was run with species (caiques, Goffins, jackdaws, young NCCs, and ravens), sex, session block, interaction species\*sex, interaction species\*session block, and interaction sex\*session block as fixed

factors, subject as random factor, and number of combinations of two free objects as the dependent variable. A second model with species (Goffins, jackdaws, young NCCs, and ravens), sex, session block, type of object-substrate combination (inserting, caching, ring-stacking see Table 2), interaction species\*type of object-substrate combination, interaction species\*sex, interaction species\*session block, interaction session block\*type of object-substrate combination and interaction sex\*type of object-substrate combination as fixed factors, subject as random factor, and number of object-substrate combinations as dependent variable.

As our data did not meet the requirements for parametric evaluation we used nonparametric dependent and independent samples tests for all post hoc analyses. All results were corrected for multiple pairwise comparisons using the Bonferroni-Holms method.

## Results

### Free Object-Object Combinations

Neither adult NCCs nor macaws could be included in this analysis because the former never combined two objects and the latter did so only in a single occasion. All adult and young Goffins (the only other species for which we had more than one age class) combined at least two objects (mean number of combinations/session young =  $4.6 \pm 2.27$  CI; adults =  $1.7 \pm 1.77$  CI). Although the scores between adults and young Goffins were different, the disparity was because of one adult female that did not interact with the objects. Because both age classes made a large number of object combinations, we pooled the two age categories of Goffins for subsequent analyses.

There were significant differences in the frequency of object combinations between species (caiques, Goffins, jackdaws, young NCCs, and ravens;  $F = 5.027$ ,  $df = 4$ ,  $p = .001$ ; see Figure 3). Young NCCs and Goffins combined two free objects more frequently than ravens (Mann–Whitney test:  $N_{NCC} = 9$ ,  $N_R = 8$ ,  $Z = 2.985$ ,  $p = .002$ ;  $N_R = 8$ ,  $N_G = 14$ ,  $Z = 3.142$ ,  $p = .001$ ) and jackdaws (Mann–Whitney test:  $N_{NCC} = 9$ ,  $N_J = 8$ ;  $Z = 3.468$ ,  $p < .0001$ ;  $N_G = 14$ ,  $N_J = 8$ ,  $Z = 3.384$ ,  $p < .0001$ ). Post hoc analysis of caiques versus other species was not possible because of the small sample size ( $N = 4$ ). However, they made free object-object combinations at moderate rates relative to young NCCs and Goffins (see Figure 3). The remaining  $p$  values resulting from object-object combinations between species were below chance expectation (after Bonferroni-Holms correction).

Only young NCCs and Goffins combined three free objects repeatedly, NCCs did so more often than Goffins, but this differ-

Table 2  
Subjects' Actions With the Experimental Objects That Were Used for Analysis: Object Actions and Factors Were Compared Within and Between Species

Object actions	Factors
Free object-object combinations	Combinations of two objects Combinations of three objects
Object-substrate combinations (activity plates/aviary features)	Insertions (inserting, dipping, or probing) Ring-stacking Caching (objects are brought out of sight, behind, underneath, or into aviary features other than activity plates)

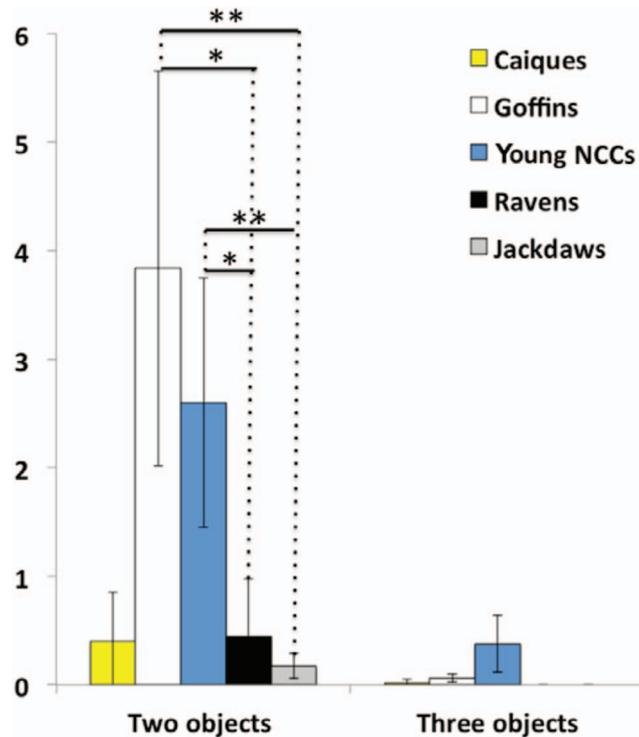


Figure 3. Mean ( $\pm 95\%$  CI) number per session and individual of free object-object combinations of two and three objects per session for each species. \* Significantly above chance expectation after Bonferroni-Holms correction; \*\*  $p < .0001$ . See the online article for the color version of this figure.

ence was on the margins of conventional significance (Mann-Whitney  $U$  test:  $Z = 2.01$ ,  $p = .053$ ).

### Object-Substrate Combinations

We did not observe any combination of objects with the activity plates or other aviary features in macaws. A single instance of insertion was observed in both adult NCCs (small yellow cube into tube) and caiques (small yellow ball into tube of a similar diameter). One caique also stacked a yellow ring onto a tube. Because of the small number of such observations, macaws, caiques, and adult NCCs were not included in any further analysis. With the exception of the observation in caiques described above, Goffins were the only species to stack rings on tubes or poles (see Figure 4). They frequently used the beak in coordination with one foot while stacking rings. As all adult and young Goffins inserted (mean/session young =  $2.05 \pm 0.78$  CI; adult =  $1.3 \pm 1.2$  CI) and cached objects (mean/session young =  $0.22 \pm 0.16$  CI; adult =  $0.1 \pm 0.11$  CI) and stacked rings (mean/session young =  $1.16 \pm 1.09$  CI; adult =  $1.3 \pm 1.6$  CI) a substantial number of times, and there were no significant differences, we pooled them in the analysis.

The relative incidence of object-substrate combinations differed between the four remaining species (Goffins, young NCCs, ravens, and jackdaws,  $F = 9.067$ ,  $df = 3$ ,  $p < .0001$ ; see Figure 4). We also found significant differences between the three types of

object-substrate interactions investigated (inserting, caching, ring-stacking:  $F = 54.117$ ,  $df = 2$ ,  $p < .0001$ ), a significant species\*object-substrate interaction ( $F = 27.058$ ,  $df = 6$ ,  $p < .0001$ ), and a significant sex\*type of object-substrate combination interaction ( $F = 14.68$ ,  $df = 2$ ,  $p < .0001$ ).

Goffins engaged in inserting (Wilcoxon signed-ranks test:  $N = 14$ ,  $Z = 3.182$ ,  $p = .001$ ) and ring-stacking (Wilcoxon signed-ranks test:  $N = 14$ ,  $Z = 2.633$ ,  $p = .008$ ) at the activity plates significantly more frequently than caching objects inside aviary features (Wilcoxon signed-ranks test:  $N = 14$ ,  $Z = 2.633$ ,  $p = .008$ ). Ring-stacking was not observed in any of the corvid species. Young NCCs inserted more than they cached (Wilcoxon signed-ranks test:  $N = 9$ ,  $Z = 2.314$ ,  $p = .021$ ), whereas ravens cached more objects than they inserted (Wilcoxon signed-ranks test:  $N = 8$ ,  $Z = 2.533$ ,  $p = .011$ ). All further differences between object-substrate combinations within species were below chance expectation (their probabilities were above the respective Bonferroni-Holms-corrected criteria).

Between species, young NCCs and Goffins inserted more objects than jackdaws (Mann-Whitney  $U$  test:  $N_{NCC} = 9$ ,  $N_J = 8$ ,  $Z = 3.094$ ,  $p = .001$ ;  $N_G = 14$ ,  $N_J = 8$ ,  $Z = 3.041$ ,  $p = .001$ ) than ravens (Mann-Whitney  $U$  test:  $N_{NCC} = 9$ ,  $N_R = 8$ ,  $Z = 2.851$ ,  $p = .002$ ;  $N_G = 14$ ,  $N_R = 8$ ,  $Z = 3.18$ ,  $p = .001$ ). Ravens, in turn, cached more objects than Goffins, young NCCs and jackdaws (Mann-Whitney  $U$  test:  $N_G = 14$ ,  $N_R = 8$ ,  $Z = 3.516$ ,  $p < .0001$ ;  $N_{NCC} = 9$ ,  $N_R = 8$ ,  $Z = 2.654$ ,  $p = .006$ ;  $N_J = 8$ ,  $N_R = 8$ ,  $Z = 3.398$ ,  $p < .0001$ ) and young NCCs cached more objects than Goffins (Mann-Whitney  $U$  test:  $N_G = 14$ ,  $N_{NCC} = 9$ ,  $Z = 32.32$ ,  $p = .019$ ) and jackdaws (Mann-Whitney  $U$  test:  $N_J = 8$ ,  $N_{NCC} = 9$ ,  $Z = 2.65$ ,  $p = .006$ ). The remaining  $p$  values resulting from comparisons of object-substrate combinations between species

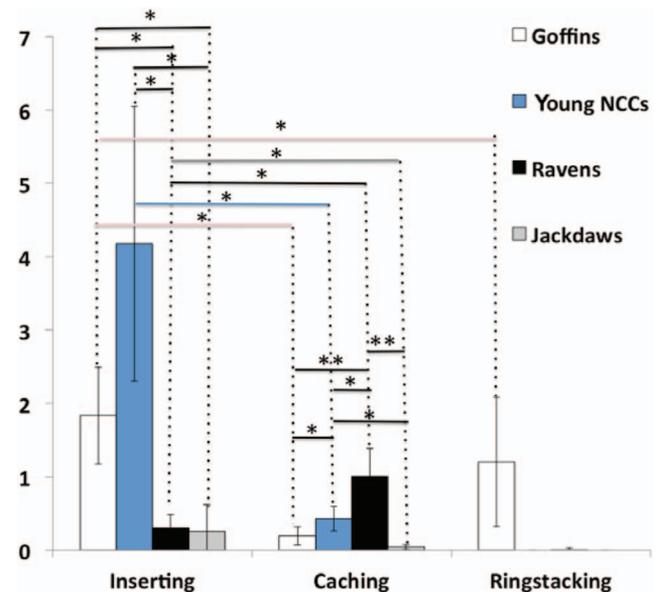


Figure 4. Mean ( $\pm 95\%$  CI) number per session and individual of inserting, caching, recovering, and ring-stacking actions per session\*, for each species. \* Significantly above chance expectation after Bonferroni-Holms correction; \*\*  $p < .0001$ . See the online article for the color version of this figure.

were below chance expectation (Bonferroni-Holms corrected criteria).

Sex differences within the three types of object-substrate combination could only be statistically assessed for Goffin cockatoos (when divided into the two sexes the sample size was not sufficient for pairwise comparisons for any of the three corvids). We found no differences between the sexes in Goffins for any type of object-substrate combination (Mann-Whitney  $U$  tests,  $p$  values  $< .05$ ).

### Color/Shape Preferences

In the course of this experiment we also looked at general color/shape preferences (including behaviors in which objects were not combined). The analysis revealed that Goffins generally preferred yellow objects over red ones and red over blue; jackdaws preferred blue over red objects. Furthermore, Goffins chose sticks more than cubes and balls, and rings more often than balls. NCCs preferred balls over all other objects, and preferred sticks as well as rings over cubes (see ESM Section C for details of the respective analysis).

### Discussion

Whereas all subjects in this study showed a variety of interactions with objects, object-object and complex object-substrate combinations occurred only in a subset of the species. Both the quantity and the type of combinatory actions varied significantly within and between parrots and corvids, which may reflect their respective ecological backgrounds.

The expected greater display of object play behaviors in younger animals (Graham & Burghardt, 2010; Groos, 1898; Hall, 1998; Heinrich, 2007) was very marked in NCCs, but not in Goffins, the two species where different age classes were tested. The young NCCs in the present study were already over 1.5 years old, but NCCs have an extended juvenile period where they remain closely associated with their parents until up to 3 years of age (Holzhaider et al., 2011). NCCs may also exhibit a prolonged period of object play while remaining with their family groups. This may be confounded though because our adult NCCs had spent a smaller proportion of their lives in captivity than their offspring.

In Goffins, both age classes showed high frequencies of object-object and object-substrate combinations. Goffins are dietary generalists that pass through different habitat types throughout the course of their lives (ranging from agriculture during subadult life to various types of tropical dry forest when breeding and as juveniles; Cahyadin, Jepson, & Manoppo, 1994; Jepson, Brickle, & Cahyadin, 2001). In species that inhabit diverse or unpredictable environments, adult object play may influence general foraging skill proficiency through the exploration of new stimuli, which may represent potential food sources (e.g., Diamond & Bond, 1999; Godfrey-Smith, 2001; Graham & Burghardt, 2010; Hall, 1998).

Young NCCs and Goffins combined two objects more frequently than the remaining species. Furthermore, these species also repeatedly created triadic object combinations, which in primates have so far been only observed in habitually tool using species, such as capuchin monkeys and great apes (Torigoe, 1985). In contrast to the remaining species, NCCs and Goffins have both previously shown a capacity for complex forms of tool use: NCCs

are the only corvid species known to regularly use and manufacture different types of foraging tools in the wild (Hunt, 1996; Shumaker et al., 2011). Their tool use is innate (Kenward, Weir, Rutz, & Kacelnik, 2005). Moreover, NCCs have revealed high-level skills in numerous problem-solving tasks in several contexts, both related and unrelated to tool use (e.g., Auersperg, von Bayern, Gajdon, Huber, & Kacelnik, 2011; von Bayern, Heathcote, Rutz, & Kacelnik, 2009; Weir, Chappell, & Kacelnik, 2002; Wimpenny, Weir, Clayton, Rutz, & Kacelnik, 2009). Similarly, the Goffin cockatoo, although not a habitual tool user, has repeatedly demonstrated the capacity for innovative and flexible stick tool use in captivity (Auersperg, von Bayern, Weber, Szabadvari, Bugnyar, & Kacelnik, 2014; Auersperg et al., 2012) as well as high-level performances in problem solving tasks involving object manipulations (Auersperg, Kacelnik, & von Bayern, 2013; Auersperg, Szabo, et al., 2013). This supports previous findings in primates showing that some functional abilities are predicted by object play and vice versa (e.g., Hayashi & Matsuzawa, 2003; Hayashi et al., 2006; Takeshita, 2001; Torigoe, 1985). In birds, playful triadic object combinations have been reported otherwise only from a captive African grey parrot (Pepperberg & Shive, 2001), a species with sophisticated categorization abilities (Pepperberg, 1999). Consistent with the above, recent studies in the same species have also revealed advanced physical problem-solving skills (Pepperberg & Kozak, 1986; Pepperberg, Willner, & Gravitz, 1997; Peron, Rat-Fisher, Lalon, Nagle, & Bovet, 2011; Schloegl, Schmidt, Boeckle, Weib, & Kotrschal, 2012), including the use of tools in a self-directed context (Boswall, 1977). One clear case of establishing triadic (and more) object combinations is during nest building (Hansell, 2007). However, most parrots including Goffins and African grey parrots do not construct nest cups, as they are nest in tree hollows (Forshaw, 2001; Forshaw & Cooper, 1989).

We also observed complex object-substrate combinations in all three corvid species as well as in Goffins. Such behaviors were not observed in the two Neotropical parrot species, except for a single incident of one caique, which inserted a ball into a tube and stacked one ring onto a tube. Inserting behaviors occurred most frequently in young NCCs, followed by Goffins, consistently with their tool use capacities and their morphology, which allows for the fine-tuned handling of objects. In the case of NCCs, motor control may have been facilitated by their straight beak morphology, which allows them to accurately maneuver objects within their optimal field of binocular vision (Troscianko, von Bayern, Chappell, Rutz, & Martin, 2012). In the case of Goffins, the tool could be held between their maxilla and controlled with their flexible and strong muscular tongue (Auersperg et al., 2012). Ravens and jackdaws also inserted objects into the plates but at significantly lower rates. Not surprisingly, most caching of objects in aviary features occurred in ravens, the only frequent food cachers in our species set. This confirms that the phase in which young ravens cache inedible items extends to at least 1.5 years of age (Bugnyar et al., 2007; Jacobs et al., 2014). Goffins were the only species that, in addition to inserting objects into the activity plates, repeatedly stacked rings on poles and horizontal and vertical tubes, and they did it nearly as frequently as inserting objects. Fitting a frame over a fixed shape is likely to occur less frequently in natural situations than fitting a shape into a fixed frame and it may require a higher level of motor control. The cockatoos even stacked the rings onto, or pulled them over, free stick-shaped

objects, which is technically more challenging than if either frame or shape are fixed. The Goffins coordinated their beak with one foot to stack rings onto sticks or tubes. Parrots regularly use their zygodactyl feet to grasp objects, which are currently manipulated with beak and tongue (Luescher, 2006). Elaborate beak-foot coordination, which is not as prevalent in corvids, may facilitate frame fitting during ring stacking. The observation that Goffins displayed behaviors absent or at least rare in other species, such as stacking objects onto poles or triadic object combinations may reflect a high capacity for innovation in technically challenging situations (Auersperg, Kacelnik, & von Bayern, 2013). It is not known whether such Goffins' traits reflect adaptations to discover potentially new resources in a particularly variable or unpredictable natural environment (Cahyadin et al., 1994). The almost total absence of object combinations in the macaws is particularly surprising, as, much like the caique, this species inhabits various different habitat types and has a broad range of distribution in South America, and this may be expected to favor a high propensity for innovation (Forshaw & Cooper, 1989; Juniper & Parr, 1998; Schulenberg et al., 2007).

We additionally found some distinct color or shape preferences for the objects in some of the species tested. Although it remains unclear why such inclinations arise during object play, there may be ecological as well as morphological explanations. For example Goffins have yellow patches underneath their wings that are used for signaling, furthermore, sticks and rings may simply be easier to grab with a curved beak than cubes or balls. Surprisingly, although stick-tool users in the wild, both adult and young NCCs preferred balls over other objects in this experiment, contradicting a subsequent study on object exploration, in which sticks were clearly preferred over compact objects (Jacobs et al., 2014).

It remains possible that some of the observations were partly influenced by differences in housing conditions. Furthermore, social dynamics and tolerance levels could have played a role, given that NCCs, caiques and macaws were kept in smaller groups ( $N < 5$ ) than the Goffins, ravens, and jackdaws. As specified above, conducting the study within the normal social context was a compromise deliberately taken so as to provide a relaxed atmosphere in which play behavior could occur. Young NCCs received the objects in their family group, which represents a less competitive situation than faced by the other corvid species that were tested in peer-groups with a clear dominance rank hierarchy. Birds kept in larger groups (ravens, jackdaws, and Goffins) may also show reduced self-directed object play as they were busy protecting objects from conspecifics or paying attention to object manipulations of conspecifics (Schwab, Bugnyar, & Kotrschal, 2008). In contrast, seeing others engaged in object manipulations may also be contagious and increase the likelihood of manipulating objects in various ways (Stöwe, Bugnyar, Heinrich, & Kotrschal, 2006). However, there were no overt cases of aggression and monopolization of objects was not pronounced; individual subjects did not monopolize more than one activity plate or more than two or three toys at once in any of the species or for prolonged durations. Nevertheless, the social context of testing may have influenced the frequency or form of object manipulations.

Another consequence of the group setting is that monitoring larger groups is more demanding, although we are confident that the recorded behavioral categories were salient and not easily overlooked. Still, the number of combinations in the group-housed

Goffins, jackdaws, and ravens could be slightly underestimated, at least when filming was not possible (in jackdaws and Goffins).

In conclusion, the most complex interactions with inedible objects, that is, using objects to carry out a variety of (apparently playful) actions on other objects or the environment, prevailed in the two species that have previously shown higher performance in technical innovation and tool use (NCC and Goffins). Such findings coincide with previous findings in primates (e.g., Hayashi & Matsuzawa, 2003; Hayashi et al., 2006; Takeshita, 2001; Torigoe, 1985). Whereas combinatory object behaviors were not significantly different in complexity, frequency, and structure between young and adult Goffins, adult NCCs showed almost no interest in the objects. In young NCCs, it is possible that complex object play reflects the spontaneous emergence of tool-using behaviors, and may be lost once functional tool use is established (Kenward et al., 2011). In Goffins, object play might contribute toward general-purpose exploratory behaviors, perhaps supporting a lifelong plasticity in problem solving.

As a wider conclusion, our observations support the view that corvids and parrots, highly playful species that readily bring objects into complex spatial relationships with other items in non-foraging contexts, may be more likely to express flexible and innovative solutions to novel problems through their lives (Bjorklung & Gardiner, 2011; Emery, 2013). Using a broader set of closely and distantly related species with different ecological backgrounds, and larger tasks sets (see for instance MacLean et al., 2014; Auersperg, von Bayern, Gajdon, Huber, & Kacelnik, 2011) would seem a profitable way forward. Our findings could be further corroborated if more highly specialized corvid or parrot species could be tested regarding potential object-related behavior such as tool-use or food-caching. Investigating the performances of a habitually tool-using parrot, such as the black palm cockatoo (*Probosciger aterrimus*) (Lantermann, 1999) or the extreme food storing Western scrub jay (*Aphelocoma californica*) (Clayton & Dickinson, 1998; Madge & Burn, 1994) would be of particular interest. Furthermore, future studies incorporating the same test with small versus large group settings within each single species could help to investigate the role of social context on object related behaviors.

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### **Correction to Auersperg et al. (2014)**

In the article “Combinatory Actions During Object Play in Psittaciformes (*Diopsittaca nobilis*, *Pionites melanocephala*, *Cacatua goffini*) and Corvids (*Corvus corax*, *C. monedula*, *C. moneduloides*),” by Alice M. I. Auersperg, Jayden O. van Horik, Thomas Bugnyar, Alex Kacelnik, Nathan J. Emery, and Auguste M. P. von Bayern (*Journal of Comparative Psychology*, Advance online publication, December 1, 2014. <http://dx.doi.org/10.1037/a0038314>), the title was incorrectly set as “Combinatory Actions During Object Play in Parrots (*Psittacus erithacus*) and Corvids (*Corvus*).” All versions of this article have been corrected.

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