Journal of Comparative Psychology
2009, Vol. 123, No. 3, 295–303

0735-7036/09/$12.00 DOI: 10.1037/a0016303

The Development of Caching and Object Permanence in Western Scrub-Jays (*Aphelocoma californica*): Which Emerges First?

Lucie H. Salwiczek
University of Cambridge

Nathan J. Emery
University of Cambridge and Queen Mary University of London

Barney Schlinger
University of California at Los Angeles

Nicola S. Clayton
University of Cambridge

Recent studies on the food-caching behavior of corvids have revealed complex physical and social skills, yet little is known about the ontogeny of food caching in relation to the development of cognitive capacities. Piagetian object permanence is the understanding that objects continue to exist even when they are no longer visible. Here, the authors focus on Piagetian Stages 3 and 4, because they are hallmarks in the cognitive development of both young children and animals. Our aim is to determine in a food-caching corvid, the Western scrub-jay, whether (1) Piagetian Stage 4 competence and tentative caching (i.e., hiding an item invisibly and retrieving it without delay), emerge concomitantly or consecutively; (2) whether experiencing the reappearance of hidden objects enhances the timing of the appearance of object permanence; and (3) discuss how the development of object permanence is related to behavioral development and sensorimotor intelligence. Our findings suggest that object permanence Stage 4 emerges before tentative caching, and independent of environmental influences, but that once the birds have developed simple object-permanence, then social learning might advance the interval after which tentative caching commences.

Keywords: Western scrub-jay, object permanence, sensorimotor intelligence, caching development, cognition

Many questions in comparative psychology derive from studies of human behavior and cognition (Etienne, 1984). Much attention has been paid to Piagetian object permanence, namely the cognitive capacity to understand that objects are separate entities, which are independent of the observer and his or her actions, and which continue to exist after moving or disappearing from sight (for overviews in primates see Tomasello & Call, 1997; for nonprimates see, e.g., Etienne, 1984; for birds see Dore & Goulet, 1998). In his seminal studies on child development, Piaget (1936, 1954) described infant cognitive growth during the preverbal phase (0–2 years) as a stepwise development of five closely interconnected cognitive abilities (sensorimotor intelligence, object permanence, time, space, and causality) that all develop at the same rate (Dumas & Dore, 1991). Piaget distinguished six substages, each of which reflecting a specific way of interacting with the environment (Berk, 1993).

Uzgiris and Hunt (1975) standardized Piaget's informal tests of infant development in cross-sectional studies, and subdivided the Piagetian six-stage framework more finely to facilitate interindividual as well as interspecies comparisons (Dore & Dumas, 1987). Object permanence has been studied so far only in mammals and birds (for reviews see Dore & Goulet, 1998; Etienne, 1994; Tomasello & Call, 1997). All tested species progress through a fixed sequence that for many species follows the pattern described for human infants (Piaget, 1954). Species were found to differ only in concrete timing, proficiency, and final accomplishment (see Table 1).

Although all animals experience the disappearance of physical or social objects, several authors have discussed the particular importance of object permanence for food-caching birds (Bugnyar, Stoewe, & Heinrich, 2007; Etienne, 1984; Pollok, Prior, & Güntürkun, 2000; Zucca, Milos, & Vallortigara, 2007). It has been suggested that hidden objects can only be retrieved when the birds

Lucie H. Salwiczek, Department of Experimental Psychology, University of Cambridge; Nathan J. Emery, Subdepartment of Animal Behaviour, University of Cambridge and Senior lecturer at Queen Mary University of London, School of Biological and Chemical Sciences; Barney Schlinger, Department of Physiological Sciences, UCLA; Nicola S. Clayton, Department of Experimental Psychology, University of Cambridge.

This research was funded by a Biotechnology and Biological Sciences Research Council Grant and the University of Cambridge. Nathan Emery was supported by a Royal Society University Research Fellowship.

We acknowledge the support of Julia Parker, Director of the Wildlife Care Network, Santa Barbara, California, and the volunteers for their cooperation in providing us with scrub-jay young for this study and everything concerning food and advice on hand-raising scrub jays in the lab. We cannot thank Petra Wise enough for her assistance in feeding the birds and the experimenter, for her moral and mental support, and finally for analyzing videos to calculate interobserver reliability. We are also extremely grateful to Vladimir Pravosudov and Selvino de Kort for advice and discussion, to Rory Spence who kindly lent us the testing room we needed to conduct this study and to Wolfgang Wickler for comments on earlier drafts of the manuscript.

Correspondence concerning this article should be addressed to Professor Nicola S. Clayton, Department of Experimental Psychology, University of Cambridge, Downing Street, Cambridge, CB2 3EB, United Kingdom. E-mail: nsc22@cam.ac.uk

Table 1
Avian Species (With Respective Reference) Tested on the Object Permanence Task As Developed by Uzgiris and Hunt (1975)

Stage	Species	Literature
4	Pigeon (*Columba livia*)	Plowright, Reid, & Kilian, 1998 [tested for visible displacement only]
	Ring doves (*Streptopelia risoria*)	Dumas & Wilkie, 1995
	Domestic chick (*Gallus gallus*)	Regolin, Vallortigara, & Zanforlin, 1994
5	Mynah (*Gracula religiosa*)	Plowright et al., 1998 [tested for visible displacement only]
6	African grey parrot (*Psittacus erithacus*)	Pepperberg & Funk, 1990; Pepperberg & Kozak, 1986
	Illiger mini macaw (*Ara maracana*)	Pepperberg & Funk, 1990
	Budgerigar (*Melopsittacus undulatus*)	Pepperberg & Funk, 1990
	Golden-crowned parakeet (*Cyanoramphus auriceps)*	Funk, 1996
	Cockatiel (*Nymphicus hollandicus*)	Pepperberg & Funk, 1990
6	Eurasian jay (*Garrulus glandarius)*	Zucca et al., 2007
	Ravens (*corvus corax)*	Bugnyar et al., 2007
	Magpie (*Pica Pica)*	Pollok et al. 2000

Note. Stage: Ultimate stage of Piagetian object permanence mastered by a given species.

possess a mental representation of an invisible object (Stage IV of Scale 1). Development of object permanence in corvids has been studied so far in black-billed magpies (Pollok et al., 2000), Eurasian jays (Zucca et al., 2007), and ravens (Bugnyar et al., 2007). All species achieved Piagetian Stage 6 of Scale 1 and followed the known stepwise development. Newly hatched corvid young are blind. In the first days after their eyes open, individuals still do not show a search response to moving items (Stage I). However, they soon begin to track an items' movement (Stage II). After leaving the nest, young birds are able to recover a partially (Stage III), then a fully (Stage IV) occluded item. Finally, they may retrieve an item that has been visibly (Stage V) and invisibly (Stage VI) displaced from previous hiding locations (for details, see Uzgiris & Hunt, 1975).

Western scrub-jays have become a model species for studying animal cognition (e.g., Clayton & Dickinson, 1998; Correia, Dickinson, & Clayton, 2007; Dally, Emery, & Clayton, 2006; de Kort et al., 2005; Emery & Clayton, 2001; Raby, Alexis, Dickinson, & Clayton, 2007). They are omnivorous and opportunistic scatter-hoarders that hide primarily seeds, but also insects or animal parts for later consumption. Scrub-jay young fledge at about Day 20 posthatch (Curry, 2002). They begin to forage actively about 20 days after fledging and are food independent at the age of 6 weeks, but are still fed by their parents until at least 55 days posthatch and as long as 3 months after hatching, when they finally disperse from their natal territory.

Little is known about the development of caching in corvids (but see Clayton, 1992, 1994, for studies on the development of caching in food-storing titmice). Bugnyar and coworkers (2007) have described only recently the development of food-storing behavior in ravens, in particular the relationship between caching development and object permanence. In ravens, food caching improved in a stepwise fashion that was dependent on age but irrespective of the type of object provided. First, young ravens pressed items under or toward large objects, although these remained at least partially visible. Then, the ravens stuck items into small crevices and holes in solid structures so that the objects were completely invisible. Next, the ravens repeatedly showed head movements that are critical for orientation and spatial memory in food-storing birds (Clayton, 1993). Finally, ravens consistently picked up surrounding substrate (e.g., leaves, twigs, soil) and used it to cover their caches. Thus, at about 2 months postfledging, the "juveniles showed all the elements of adult-like caching (manipulative actions: sticking, touching, covering; visual behavior: checking, looking up)" (Bugnyar et al., 2007, p. 763).

Pollok and coworkers (2000) summarized the major steps in magpie development from the literature and correlated these data with their analysis of object permanence development. Young magpies leave their nests about 4 weeks after hatching, and stay with their parents for another 6 weeks until the young become independent 10 weeks after hatching. In captivity, magpies start to hide food at around 32 days old, and at the same time they also retrieve partially hidden objects (Task 3). Young magpies start to retrieve their food at age 42 days posthatch, which coincides with their ability to go to the correct corner, where food had been completely hidden, but without retrieving it (Task 4). Only at 57 days old, when food caching is fully developed (age 55 days), do young magpies also retrieve completely hidden items.

The studies that correlate the appearance of object permanence with caching development suffer from two drawbacks. The first is a concern that species solve a given task by learning rather than spontaneously (Bjork & Cumming, 1984; Dore & Dumas, 1987). To circumvent this problem, species were not tested daily, but with intervals ranging from 2 to 5 days (Bugnyar et al., 2007: every 5th day; Zucca et al., 2007: twice a week; Pollok et al., 2000: two sessions per week). Consequently, Bugnyar et al.'s (2007) statement that " "true" caching [. . .] is observed exactly at the time when ravens demonstrate Stage IV competence" is in fact only a rough estimation "with a median deviation of $\pm$5 days" (p. 763). In other words, the exact order of developing object permanence in relation to the ontogeny of caching proficiency remains an open question.

A second problem relates to differences between studies in methods and terminology. The distinction between food storing per se (i.e., hiding food completely), and food storing with associated retrieval, is not just an issue of semantics, but is actually reflected in neuronal organization (e.g., Clayton, 1995; Clayton & Krebs, 1995; Sherry & Vaccarino, 1989). Bugnyar and colleagues (2007) described various types of "caching" in detail, with a focus on the developmental changes in manipulation during hiding food (i.e., placing an item visibly, inserting it, and finally camouflaging the cache sites). However, the time when the ravens started re-

trieving the items remains unclear. Pollok and coworkers (2000) distinguished between the onset of "food storing" (age 32) and the start of "food retrieval" (age 42), as reported in literature, but these estimates are not 'exact.' Thus, both studies only provided a rough estimate of how food storing per se and food storing with associated retrieval might be related to object permanence development, as tested in standardized retrieval tasks. Zucca and coworkers (2007) focused solely on object permanence development in Eurasian jays and demonstrated that successful mastering of trials was delayed when birds showed neophobia.

The present study therefore has three objectives. The first is to describe the development of caching behavior in Western scrub-jays. The second is to relate the development of caching with the emergence of Piagetian Stages 2 to 4, with particular interest in analyzing whether the emergence of Piagetian Stage IV precedes caching or whether experiencing the reappearance of hidden objects, as occurs when the birds have the opportunity to recover hidden caches, enhances the timing of the appearance of object permanence. The final objective is to discuss the findings within the framework of 'sensory-motor intelligence' (Piaget, 1936), which is intimately related to the object concept.

Method

Subjects and Housing

A total of 15 young Western scrub-jays (*Aphelocoma californica*) were hand-raised as a group at the University of California Los Angeles (UCLA). They were taken, with appropriate federal (OMB No. 1018–0022) and state (SC-8592) licenses, from the Santa Barbara Wildlife Care Centre in May and June 2006 as soon as members of the public handed them in. Most individuals originated from an area within 17 km distance, only three siblings (Black, Mix, and Shiny) and the oldest bird (Yellow) were from as far as 50 km away from Santa Barbara. For analysis the 15 birds were divided into two subgroups according to age (i.e., day of arrival at UCLA, independent of location of origin. Group 1, arriving May 9 through 22, comprised birds aged 19 to 30 (median: 21) days post hatch; birds in Group 2, arriving June 1 through 20, also ranged from 16 to 29 (median: 19) days of age.

Depending on their age on the day of arrival, the very young birds (age 15–19 days posthatch) were kept in artificial nests in bird cages (41 cm × 38 cm × 59 cm), and then moved with the nest into an aviary (192 cm × 152 cm × 76 cm). Older jays (>21 days posthatch) were placed into the aviary as soon as they were captured.

The aviary was equipped with six wooden perches at different heights, and its walls were lined with dark gray fiberglass screens while the floor was covered with brown paper. Hand-fed birds were given a diet of Roudybush Baby Bird Formula 3, soaked dog kibbles, dog and cat food, and various fruits (bananas, blackberries, strawberries, minced apple, or minced pear). Older birds, who had already started to feed by themselves, always had available a bowl with powdered dog kibbles mixed with powdered nuts (peanuts, pine nuts, safflowers), enriched twice a week with half a hardboiled egg. Water, provided in a plastic bowl for drinking and bathing, was available ad libitum.

The birds were kept on a 14:10 hour day:night schedule, which enabled up to 14 hours hand feeding. Every day, the experimenter (LHS) spent up to 6 hours in the birds' room: (1) every 20 to 45 minutes for hand feeding, (2) 2 × 2 hr observations of caching development, and (3) approximately 1 hour for tests of object permanence. The scrub-jays were not deprived before testing of object permanence or before exploring the room communally.

The aviary was located in a room with a total floor space of about 265 × 275 cm^2 (see Figure 1). The testing area and aviary were in the same room, which allowed physical and visual, but no acoustic isolation. The scrub-jays learned to leave and to return voluntarily to the aviary when the experimenter opened the door of the aviary at the start and the end of a session in the testing area or after observations on caching in the room respectively. The birds were identified by colored plastic leg rings, which were only removed after the birds were returned to the refuge center to be released back into the wild.

Tests on the Development of Object Permanence

As soon as the birds arrived at UCLA, they were all tested daily. The birds were presented with tasks from Uzgiris and Hunt's (1975) Scale 1 following Pollok et al. (2000). Participation in all trials was voluntary. The order in which the birds were tested varied randomly across days. Only one experimenter (LHS) administered the tests because the birds were neophobic toward unfamiliar people.

On test, each subject had to sit on a metal pillar or close to it while tasks were administered. Items to be hidden in Tasks 3 and 4 were (half) wax worms and fruit pieces depending on subjects' preferences. Objects were placed on the ground approximately 50 cm in front of an individual and (partially or completely) covered by a cloth while the bird observed. Cloths varied in shape (star, triangle, quadrangle, cross, rotund, u-shape), color (yellow, orange, red, green, pink, brown, purple), and size between trials and/or days. The size of cloth (quadrangles from 6.5 × 6.5 cm^2 to 10.5 × 10.5 cm^2) was increased in relation to increasing body size of the growing young.

Several precautions were taken to reduce the chance of learning because of repeated, daily trials. First, object permanence was tested at different times of day on consecutive days between 9 a.m. and 7 p.m. before, between or after the two observational sessions (see below), and therefore the jays could not associate success (i.e., retrieval of an item) with circadian rhythms of any kind. Second, our birds could not anticipate the hidden object through the cover. More importantly, LHS did not lift the cloth in the presence of a subject once the cloth had been placed to cover a food item. Consequently, a subject that had not retrieved the hidden item (e.g., because it was not attending) was removed from the testing arena without seeing the item uncovered or receiving a reward. However, all birds received food after returning to the aviary independent of their performance.

Furthermore to avoid possible visual cuing during the task, the demonstrator left the room after administering a task waiting outside until the bird made its choice or 1 minute had passed (whichever was first). If the bird finished a trial before the demonstrator reached the door, she returned for the next trial without leaving the room. To prevent the birds from using odor cues during a given task, all the covers had been in contact with all types of food used for demonstration (fruits and wax worms), and all birds had interacted with all cloths.

Performance criteria for the four tasks in this study were similar to those of previous studies (Pollok et al., 2000; Pepperberg, Willner, & Gravitz, 1997) and are described in detail in Table 2.

Trials were scored as unsuccessful if the birds did not retrieve the partially and completely hidden item, testing was terminated and the bird was returned to the aviary. If a subject did not approach a cover within 1 minute or left the testing area ignoring the cover(s), the experimenter returned, placed the bird on the perch, and administered the task again. If a subject again did not cooperate within 1 minute, the session was scored as "not attended," testing was terminated, and the bird was returned to the aviary. To pass a task successfully, items had to be retrieved consecutively multiple times; either five times in a row on one day or twice three times in a row on two consecutive days without failures between the days. The latter criterion was necessary because some individuals did not cooperate on a task for more than three or four times, either because they lost interest or became satiated. If a bird successfully retrieved three items in a row on two successive days, the second day was counted as the day of acquiring a given Piagetian stage. All sessions were video-recorded from a distance of about 1.2 m from the subject. The recording was started by LHS when the bird was in the testing area.

The object permanence test responses were noted on a categorical scale (succeeded, failed, not attended) by the experimenter (LHS) after the tasks. Petra Wise, who was unfamiliar with the task, also analyzed 16% of all the trials (thereby at least one not attended session of each bird was included, and of participating birds, one succeeded and one failed trial) to test interobserver reliability by calculating fixed-marginal kappa coefficients (Siegel & Castellan's, 1988). This tests whether observer agreement exceeds chance levels if there are at least two observers and more than two categories. In general kappa coefficients is interpreted as an indicator of low agreement if being less than 0.4, moderate if being between 0.4 and 0.6 and high if above 0.6. (Fleiss, 1981; Habison, Slater, & Howe, 2002). The percentage of overall agreement was 95.6% and fixed-marginal kappa was 0.93, thus interobserver reliability is considered to be high.

Observations of the Development of Caching

Given that the young jays ignored trays and food when separated from the other birds, the group was released communally from the aviary into the room twice a day for 2 hours in the presence of LHS. Each bird was observed for at least 5 minutes depending on their daily and personal activity level. The sequence of birds varied randomly between the two daily sessions as well as between days. If a bird was seen to be (tentatively) caching although not the focal animal, the caching event was nevertheless noted down. During observation, the experimenter occasionally recorded videos on various caching events and social interactions. Food available for caching (peanuts, pine seeds, hard dog kibbles, and wax worms) was presented in separate bowls in the testing area. Four ice cube trays and a metal bar were filled with desert Blend lizard litter and distributed in the room.

To study the behavioral development of food caching, we recorded any exploration and manipulation of available items (edible or not), the origin of the item (floor, beak of another individual), location of action, and action alone or cooperation with other (for more details see Table 3).

Data Analysis

The age of the young jays was calculated based on growth data kindly provided by Vladimir Pravosudov (Pravosudov, Lavenex. & Omanska, 2005). The age at which the birds passed Task 3, Task 4, and first performed tentative caching, was calculated by adding to the estimated age on the day of arrival the number of days that had elapsed until the day of passing the respective stages of object permanence. For statistical analyses, we used Systat 9.2 (Systat Software, Richmond, CA) to test (1) whether the data was normally distributed (Kolgomorov-Smirnov Lilliefors test), (2) for homogeneity of variance, and (3) to compare non-normally distributed data sets (Mann–Whitney *U* test for independent data sets). All tests were two-tailed and alpha was 0.05.

Results

The 15 scrub-jays were approximately 15 to 30 days of age at the beginning of the study. One subject (hbl) was too shy upon arrival, never became tame, and thus could not participate in the object permanence study. Within the duration of the study (approximately 8 weeks), all 14 participating jays passed Tasks 1 and 2 (visual pursuit), and successfully mastered Task 3 (i.e., retrieving a half-hidden object). Thirteen birds achieved Stage IV competence (retrieving a completely hidden object), whereas the youngest bird never attended Task 4 sessions.10 individuals and hbl started tentative caching (i.e., hiding an object completely and retrieving it immediately after hiding it). The three youngest birds

Table 2
Object Permanence Tasks Following Pollok et al. (2000)

Task	Correct
1. A plastic object dangled from a transparent synthetic fiber, moving in 180° or 360° angles around the bird several times in counterbalanced clockwise and anticlockwise fashion.	The bird continuously followed the object in 180° arc or more.
2. As in task 1, but moving horizontally from one side behind a screen and reappeared on the others side. Moving directions (right-left, left-right), were counterbalanced. In addition, the fiber long enough to keep the hand out of the birds' eye sight.	The individual was looking at the point of disappearance or at the starting point of reappearance before the object actually reappeared.
3. An object was partly hidden under a single cover.	The bird retrieving the object by pulling it out or removing the cover.
4. An object was completely hidden under one of two different covers.	The individual removed the appropriate cover and retrieved the object.

Note. Task: Description of the experimenters demonstration. Correct: Criterion to pass a given task successfully.

Table 3
Recordings During Observations

Origin of object	For example, floor, beak of another bird, bowl
Actions	Taking an object into the beak
	Dropping item
	Wiping the object, for example, over the floor
	Carrying object in the beak to another location
	Placing an object on the floor, in corners, etc.
	Pecking (pounding) on item
	Retrieving an item
Item 'property'	Invisible (completely hidden)
	Visible
	Identity (dog kibble, peanut, etc.)
	Type (hard, soft)

were never seen to be involved in caching activities until the study ended.

Object Permanence Development Related to Age

All subjects passed Tasks 1 and 2 (visual pursuit) on their day of arrival including the youngest bird at 15 days of age. There seemed to be a modest tendency for birds of Group 2 to succeed on Task 3 at a slightly younger age (Group 1: 32 days old, Group 2: 28 days old; see Figure 2), whereas most jays acquired object permanence Substage 4 competence (retrieving fully occluded objects) at the age of about Day 35 posthatch (see Figure 2). The number of days between passing Task 3 and passing Task 4 did not different significantly (Mann–Whitney $U = 11.5$, $N_1 = 6$, $N_2 = 7$, $p = .171$, Figure 2). The age at which the birds passed Task 3 as well as the age when the birds passed Task 4 was not influenced by the time they arrived in our facility; earlier (Group 1) or later (Group 2).

Behavioral Development of Western Scrub-Jays

The youngest scrub-jays left their nest at the latest on Day 19 posthatch, and started to sit on perches or stand on the ground. They were not yet moving around, only waiting to be fed, cleaning their own feathers, and "nibbling" at a (foster) sibling's feathers when sitting in close contact. If during feeding, a food item dropped down, they followed the item with their eyes, however never picked it up, even when they stood on the floor and could easily reach the item. It took several days until they started to roam around and to explore the larger room. Only then did the jays become interested in interactions with objects different from eating them. A sequence of four behavioral object exploration and manipulations respectively were identified.

Pick and drop. After fledglings began to explore the room and its content, they started to pick up food and nonfood items. Often individuals took objects into their beaks and let them drop again with their head tilted such that one eye could inspect the fallen item before picking it up and starting the sequence all over again. In between such a sequence, they often wiped the item on the floor. Individuals were also interested in picking up items dropped by another group member.

Placing. With increasing mobility the young birds soon started to move things around and to place a given item in corners, along edges, or cables. Most importantly, they pecked on every hard item with increasing force (further on: to "pound"). The birds also began occasionally to defend their items and to carry them away when other birds approached. However, at other times, individuals worked together on one item. The duration of the study was too short to determine whether this was the beginning of developing relationships between cooperation partners, as shown in rooks (Emery, von Bayern, Seed, & Clayton, 2007) and jackdaws (von Bayern, de Kort, Clayton, & Emery, 2008; de Kort, Emery, & Clayton, 2003, 2006).

'Insertion'. An individual placed or dropped an item onto sandy ground, and then pecked at it until the object disappeared into the sand. Then the subject either left the location, or it investigated a different, visible object. In our group, older individuals, having been nearby, sometimes retrieved the "unintentionally" hidden item. As soon as the object became visible again, the younger bird pounded on it until the item disappeared again and so on. Although this could continue for several turns, the young bird never retrieved the hidden item by itself, but still relied on another individual to retrieve it.

'Tentative caching'. A bird placed an item onto sand, pecked/pounded on it until the item disappeared, and retrieved it immediately. This sequence was repeated many times in succession. Some individuals worked together, such that one hid the item, whereas the other retrieved the object without delay. The jays used "hard" items, that is, dry dog kibbles and nuts for tentative caching, whereas worms were eaten at once.

Development of OP in Relation to the Development of Caching

When the birds started to manipulate objects they also successfully retrieved items that were partially visible (Task 3). However, they did not show any interest in a cover that occluded an item completely. All young engaged in placing and insertion behavior, yet it took them several days after passing Task 4 (i.e., retrieving a completely hidden item) before they showed the first onset of tentative caching (see Figure 2). Importantly, the interval between

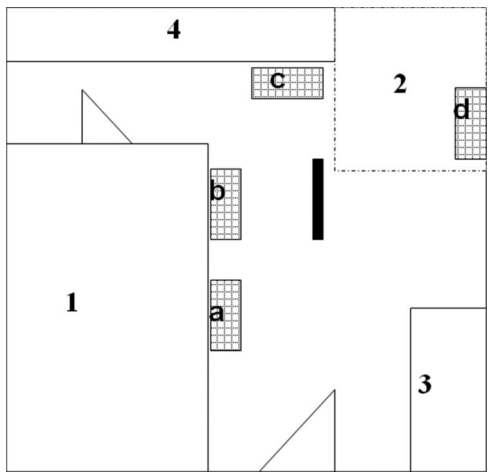

Figure 1. Schematic overview of the experimental room (1) aviary; (2) testing area; (3) location of LHS during observations; (4) board; (a–d) trays filled with lizard blend; (triangles) doors.

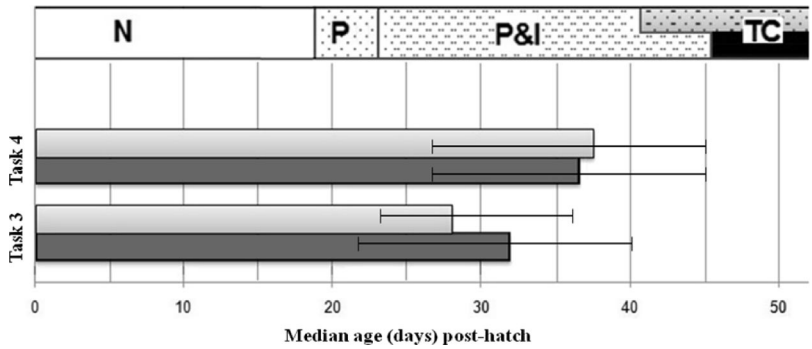

Figure 2. Developmental stages, median age (days posthatch), minimum and maximum, on day of passing Task 3, passing Task 4, and on their first day of tentative caching. Black bars: Group 1, $n = 7$, arrived in UCLA May 9 through 22, 2006. Gray bars: Group 2, task 3: $n = 7$; task 4: $n = 6$, arrived June 1 through 20, 2006. N: nestling phase; P: Pick & drop phase; P&I: Placing & Insertion phase; TC: onset of Tentative Caching.

the onset of full object concept (Stage 4) and tentative storing was significantly shorter in Group 2 than in Group 1 (Mann–Whitney $U = 20.000$, $N_1 = 5$, $N_2 = 4$, $p = .013$, see Figure 3).

Discussion

Behavioral elements of caching development in Western scrub-jays followed a linear sequence: picking up and dropping items, followed by placing the items in visible locations, which in turn was followed by insertion, and in older birds finally tentative caching. Each step of caching behavior was independent of early experiences, or time of arrival in our facilities, but depended on prior acquisition of Piagetian stages of sensorimotor intelligence and object permanence. Only after the emergence of simple object permanence (Stage 4) did social interaction seem to influence the interval after which tentative caching emerged.

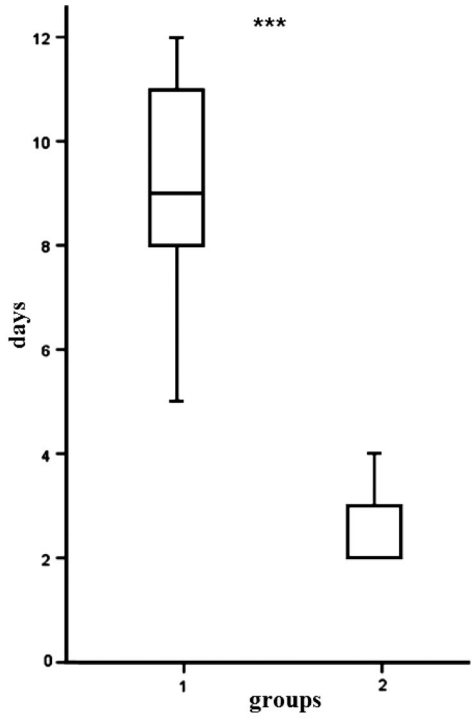

Figure 3. Interval (days) between passing Task 4 and onset of tentative caching. Group 1, $n = 5$, arrived in UCLA May 9 through 22, 2006. Group 2, $n = 4$, arrived June 1 through 20, 2006. Data are presented as median, 1st and 3rd Quartiles, minimum and maximum. Data were tested by Mann–Whitney U test, *** $p < .001$.

Caching Development Depending on Piagetian Stage III of SMI and OP

Caching development appears to be preprogrammed, because all scrub-jays progressed through the same sequence of emerging behavior. Young who just left the nest did not pick up a food item that dropped down, but waited until another bird or LHS offered this item or a new piece of food. If neither happened, the young birds either left the item on the ground or started to manipulate it; however, they did not swallow the food item. It seemed that the young birds had to learn that items lying on the floor are edible, as are items offered by their parents' beak. In Piagetian terms, this means that fledglings are in sensorimotor Substage 3 (Secondary Circular Reactions); the newly acquired knowledge that external objects can also be food items (i.e., independent of the social stimulus of the parent's beak) has still to be connected to the action scheme 'picking up object from ground.'

Even before the scrub-jays started to eat from the ground, they moved items around and placed them somewhere else, mostly visible, for a brief time. This is the time when the birds started to perform on object permanence Task 3, which all participating subjects passed successfully. Very young birds, however, did not eat the retrieved item rather than wiping them over the floor or pecking on them while older siblings swallowed them. This confirms that general curiosity might be enough to retrieve partially hidden objects (see Bugnyar et al., 2007) once birds started to explore objects on the ground even if they did not recognize them as part of a known food item.

While the birds were engaged in further manipulative interactions, including placing and inserting items into holes, they most often pounded on objects on the ground. This is different from caching in a number of ways; most importantly, the adult birds hold an item in the beak and "drill" it into the ground rather than

pounding on it. Second, adult birds only cache into a soft substrate. The pounding of youngsters, however, is highly repetitive, and is indiscriminative of whether the substrate is hard or soft, and whether the item is hard or soft, food or nonfood item. Nonetheless, such pounding may accidentally cause items to disappear particularly if they were on a soft substrate, such as sand. Initially, young scrub-jays left the scene after an object disappeared in sandy ground, even if close-by companions sometimes retrieved an object that a young bird accidentally pounded into the sand. Thus, young subjects were frequently exposed to the outcome of items disappearing and then reappearing when retrieved; they left without retrieval apparently because of a lack of understanding, rather than a lack of interest in the result produced on the external item.

Caching Development Depending on Piagetian Stage IV of Sensorimotor Intelligence and Object Permanence

With progressing to Stage 4 of Piagetian SMI, actions that have been acquired in previous stages are combined and coordinated into a new behavior. As soon as Stage 4 (i.e., simple object permanence) emerged, the scrub-jays successfully retrieved fully occluded items combining the simple object permanence concept with the actions of picking up and moving an object (i.e., the covering cloth). In other words, the bird retrieved items that they saw being covered by the experimenter, yet they did not retrieve items that they themselves made disappear by accident in sand (i.e., through pounding). It took them at least another 2 days until they displayed the onset of tentative caching, combining the outcome of two actions, hiding, and retrieving, with simple object permanence. One could argue that, after the birds understand that an object continues to exist when being out of sight, they need to learn that it is in their capacity to bring the items back into sight.

Within developmental cognition scientists seem to have accepted that human infants develop an understanding that an occluded object continues to exist, as shown in visual tasks using for example a violation-of-expectation paradigm (e.g., Baillargeon, 1986; Baillargeon & DeVros, 1991), before they have the behavioral and motoric capability to bring it actually back as required in Piaget's manual search task (e.g., Sophian, 1997; Spelke, 1988). By contrast, comparative studies still rely on Piaget's manual search tasks and consequently on concern is whether we might underestimate a young animal's understanding of occlusion events.

Social Learning Involved in the Emergence of Tentative Caching

After successful performance on object permanence Task 4, scrub-jays from Group 2 started tentative caching earlier than jays having arrived earlier in our facility. Because birds in Group 2 had a similar age range, though individuals were overall slightly younger, than Group 1, it is unlikely that they have seen caching activity before arriving in our facility. As argued above, the timing of caching development is dependent on cognitive growth (i.e., sensorimotor intelligence and object permanence). Only once these cognitive capacities had emerged did social learning play a role in the early emergence of tentative caching in Group 2. Birds in Group 1 explored all sites in the room. To explore and interact with objects did not require any conspecifics as motivators, yet the fact that the older birds spent lots of time at sandy sites increased the time that individuals of Group 2 spent close to the sandy sites, and in turn increased the likelihood that younger birds could learn that items that became invisible can still be retrieved, as well as that sandy locations are suitable caching sites (see also marsh tits, Clayton, 1992, 1994). Stimulus enhancement (Heyes, Ray, Mitchell, & Nokes, 2000), on the other hand, seems to have played only a minor role, if any, because jays in Group 1 demonstrated a preference to place and manipulate hard items, but eat soft items (e.g., worms, fruit pieces).

Tentative caching of our young scrub-jays is different from the "true" caching of adults in two respects (Clayton, 1992, 1994). Most importantly, adult birds retrieve items hours, days, and eventually even months, after caching them. Our young jays initially retrieved items immediately after the item had been hidden. Second, adults do not necessarily pound on items until they disappear, but often keep the item in their beak, digging or drilling it into the sand, and then cover the hole with wiping movements.

Comparison With Other Corvid Studies

Behavioral elements of caching development in Western scrub-jays were very similar to the behavioral sequence of caching development described for young ravens (Bugnyar et al., 2007) and young parids (Clayton, 1992, 1994; Haftorn, 1992). In addition, object permanence developed in a very similar fashion in most corvid species tested so far (see Table 4). All corvid young pass Task 3 within a week after fledging, simple object permanence emerges about 1 to 1.5 weeks thereafter, which is 4 to 5

Table 4
Comparison of the Four Corvid Species Tested on Object Permanence

Species	Fledging age (days)	Task 3 age (days)	Task 4 age (days)	Independence age (days)	Body mass (g)
Scrub jays	19	g2: 28 g1: 32	35	63	76.0
Eurasian jays	20	31	37	63	139.0
Magpies	25	32	a: 44 b: 57	75	188.1
Ravens	40	47	54	90	1051.9

Note. References are given in the text. The older jays in Group 1 (g1) passed Task 3 at an older age then Group 2 (g2). Pollok et al. (2000) report a two step development (A, B) of Stage 4 competences (Task 4) in magpies.

weeks before young birds become independent. The two jay species, the Eurasian jay and Western scrub jay, are very similar in the exact timing of caching development and object permanence. This is perhaps surprising because one would expect that Eurasian jays, which have a larger body size and a larger total brain size might develop more slowly relative to the smaller scrub-jay. That said, it should be noted that the Western scrub-jays has been reported to possess the largest total brain volume relative to body mass among the corvids studies to date (Pravosudov & de Kort, 2006).

Only Pollok and colleagues (2000) mention development of simple object permanence (Stage 4 competence) in two substeps. First, magpies return to the correct cover but do not retrieve the hidden item; hence they fail to meet the criterion (i.e., fail to remove the cover and to pick up the object) but seem to show some memory of where an item has been hidden. It takes nearly 2 weeks until the young birds meet retrieve the hidden object. Pollock and coworkers (2000) refer to Piaget's observation (Piaget, 1954) that human infants show a two-step development of simple object permanence, that is, that they initially retrieve the hidden item only if the infant observes the item to be covered when it already started moving. Our scrub jays did not show anything similar. Before passing Task 4, the young jays would not approach the cover, but look for a visible object in the room or move toward the aviary. Once they started to approach the cover, they quickly retrieved the hidden item. One question is whether we failed to see such two-stage development because we tested the scrub jays daily. This, however, is unlikely, because neither ravens nor Eurasian jays were found to show a two-step development of simple object permanence, even though these birds were tested much less frequently, only every 5th day for the ravens (Bugnyar et al., 2007) or "twice a week" for the Eurasian jays (Zucca et al., 2007). Although in magpies the first onset of simple object permanence (i.e., looking at the correct cover but not retrieving the item) occurs at the same time as in the other tested corvid species, it remains an open question as to why magpie development deviates from other corvids in the two-step emergence of simple object permanence, which causes magpies to pass Task 4 successfully (i.e., retrieving fully covered items) with a delay of about 2 weeks.

Conclusion

Various authors have discussed the validity of the Piagetian framework for comparative studies on the development of cognitive skills (e.g., Dore & Dumas, 1987; Gomez, 2005; Pepperberg, 2002), concluding that stages of cognitive development exist, and that nonhuman animals, like humans, progress through the (mostly) same fixed sequence of developmental stages, though the actual timing might differ between species. The avian studies so far have not described stages of developing knowledge about food objects (i.e., when does become an item on the ground a food item for the young bird), and might have underestimated the important distinction between the actions (i.e., that certain actions have specific consequences, such as hiding food) and object properties like continued existence while outside of perception (i.e., object permanence).

Previous studies on object permanence have used the manual search task devised by Uzgiris and Hunt (1975), that can be administered only when a subject can move around and transport objects, just as we have reported here. These retrieval-based tasks, however, do not precisely test whether an individual knows that an object exists after its disappearance, rather whether an individual understands that it can retrieve the no longer visible, but still existing, item.

Our analysis suggests that it is important to study cognitive development (e.g., object permanence) separately from behavioral development. In doing so, our data provides the first evidence that object knowledge precedes successful performance on tentative caching.

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Received November 30, 2008
Revision received April 6, 2009
Accepted April 12, 2009 ■