

Development of Object Permanence in Food-Storing Magpies (*Pica pica*)

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The development of object permanence was investigated in black-billed magpies (*Pica pica*), a food-storing passerine bird. The authors tested the hypothesis that food-storing development should be correlated with object-permanence development and that specific stages of object permanence should be achieved before magpies become independent. As predicted, Piagetian Stages 4 and 5 were reached before independence was achieved, and the ability to represent a fully hidden object (Piagetian Stage 4) emerged by the age when magpies begin to retrieve food. Contrary to psittacine birds and humans, but as in dogs and cats, no “A-not-B error” occurred. Although magpies also mastered 5 of 6 invisible displacement tasks, evidence of Piagetian Stage 6 competence was ambiguous.

Object permanence, the ability to understand the continuing existence of objects temporarily not visible, is a fundamental cognitive skill that provides a basis for many elaborate cognitive processes. In humans and nonhuman higher vertebrates, including birds, object permanence develops in a staggered manner. Studies on ring doves (Dumas & Wilkie, 1995); pigeons and mynahs (Plowright, Reid, & Kilian, 1998); kakarikis (Funk, 1996); Illiger macaws, parakeets, and cockatiels (Pepperberg & Funk, 1990); and grey parrots (Pepperberg & Funk, 1990; Pepperberg & Kozak, 1986; Pepperberg, Willner, & Gravitz, 1997) have demonstrated interesting parallels but also marked differences between avian species in terms of the performance level achieved and the timing of development. For example, in a comparison of pigeons and mynahs, Plowright et al. predicted better performance of mynahs on visible displacement tasks for ecological reasons. The results of their tests confirmed the predictions.

In principle, two main factors can account for variability between avian species on object-permanence tasks. First, constraints on the development of capabilities can be shared by species of common phylogenetic origin, and differences between species are then caused by different phylogeny, as it is also discussed for monkeys and apes (De Blois & Novak, 1994; De Blois, Novak, & Bond, 1998). Second, skills of a particular species can reflect adaptation to certain ecological conditions, as suggested in several recent avian studies, as an account for the capabilities of particular species (Funk, 1996; Plowright et al., 1998) or as a general

selective pressure in the evolution of object permanence. As a paragon of the latter, several authors have referred to the memory-based caching and retrieval behavior of food-storing birds (Etienne, 1984; Pepperberg & Funk, 1990; Pepperberg & Kozak, 1986; Plowright et al., 1998).

The present study is the first explicit investigation on object permanence in a food-storing bird. It is also the first systematic study on the development of object permanence in a passerine bird. Hence, this study provides the first data set for a nonpsittacine bird. Although the findings on a single food-storing passerine species cannot answer with regard to each component of the development of object permanence to what extent it is shaped by ecological or phylogenetic factors, some clear predictions can be made that allow testing of the idea that feeding ecology plays an important role in the evolution of object permanence.

In the two psittacine species investigated so far, the grey parrot (*Psittacus erithacus*) and the kakariki (*Cyanoramphus auriceps*), most stages of Piagetian object permanence are achieved by almost the same age (see Figure 2B, presented later in this article), despite large differences in the duration of development to independence, which is reached by 8–9 weeks of age in kakarikis and by 14–16 weeks of age in grey parrots (Robiller, 1997). The only major exception from this shared developmental trajectory is that Piagetian Stage 4 is achieved about 5 weeks earlier in kakarikis. If, as suggested by Funk (1996), remembering hidden objects is important in the feeding behavior of this species, the timing of achievement of Piagetian Stages 3, 5, and 6 might reflect a standard pattern of psittacine birds, whereas the earlier onset of Stage 4 might be due to earlier independence. In psittacines, Stage 4 seems to be reached with or shortly after independence.

In magpies, the requirements on object-permanence capabilities achieved by independence can be expected to be different: Before we outline this in more detail, a brief excursion into relevant aspects of magpies' behavior, juvenile development, and development of food storing is appropriate. Black-billed magpies (*Pica pica*) are not only passionate food hoarders but also a curious and exploratory species. Because of magpies' tendency to spontaneously approach and handle objects of interest, object-permanence tests can exploit natural retrieving behavior and can be carried out with minimal intervention by the experimenter. Moreover, the

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ecology (Birkhead, 1991) and food-storing development (Prior & Schwarz, 1999) of magpies are well-known. This background allows researchers to investigate how the development of object permanence relates to the development of other behaviors. In addition, a large body of data from studies on the ecological determinants of food storing, its neural basis, and cognitive performance under laboratory conditions in passerine food-storing birds has accumulated during the past two decades (cf. Clayton & Krebs, 1995; Shettleworth, 1995). This body of data provides a background for understanding the development of object permanence in magpies within a wider context.

The length of time from hatching to fledging is about 4 weeks in magpies ($M = 27$ days; Birkhead, 1991). After about 3 weeks, magpies start to move about the nest. A few days before fledging, they increase their range and climb twigs that are close to the nest. After fledging, young magpies are protected and fed by their parents for another 6 weeks. They commence independent feeding at an age of about 10 weeks after hatching (Redondo & Carranza, 1989). From that time, the ability to "buffer" temporary shortages of food supply by means of food storing is of particular survival value.

In captive magpies, food storing begins at an age of about 32 days, shows a large increase in quantity up to Day 45, and appears to be fully developed at an age of 55 days, that is, 1–2 weeks before independence (Prior & Schwarz, 1999). When storing behavior is fully developed, birds put the food item that they carry in the front part of their beak with a fast and fluent movement into a hole or a cleft or under a leaf they have lifted previously. Subsequently, they make a couple of hammering strikes with the tip of their bill onto the stored item before they finally cover the site with a leaf or debris. Magpies are scatter hoarders that store single items in many different places. Contrary to jays and nutcrackers, they are short-term storsers that retrieve their caches on the same day or within days, rather than after a couple of months (Birkhead, 1991; Vander Wall, 1990). During cache retrieval, magpies approach the location of the hoard, remove possible covers, and then take the item with the tip of their beak.

If object permanence plays a critical role in food storing and memory-based food retrieval, several predictions can be made regarding how and when object permanence should develop in magpies. First, magpies should achieve competence on Piagetian object permanence up to at least Piagetian Stage 5 (visible hidings at different places). The requirement for the ability to represent completely hidden objects, as achieved in Piagetian Stage 4, appears to be rather obvious because successful food storing does not depend so much on the ability of the birds to remember places where they have been but on the capability to remember hidden food items at particular places (Clayton & Krebs, 1994). Well-developed Stage 5 capabilities are to be expected because a feat of paramount importance in successful scatter hoarding is the ability to continuously update the record of which places contain food and which cache sites have already been used or found empty. This ability of updating is essentially what distinguishes Piagetian Stage 5 from Stage 4. Because magpies are scatter hoarders, there should be little limitation due to an increasing number of places. In terms of Stage 6 competence, no specific predictions based on the magpies' feeding ecology can be made because it is not clear what specific advantage the representation of invisible displacements has in feeding and food-storing behavior. Stage 6 competence may

be a by-product of high demands on object permanence in general. Second, because of the important role of food storing in the survival of magpies (Birkhead, 1991), magpies should achieve Stage 4 and Stage 5 competence by an age of 9–10 weeks at the latest, that is, before they feed on their own.

This prediction of a considerably faster development of object permanence than that reported for grey parrots and kakarikis implies only that competence of these stages is necessary before the critical age. It does not mean that speed of development per se is indicative of the ecological importance of object permanence. For example, faster development of early stages of object permanence in apes as compared with humans does not mean that apes show better overall object permanence. Third, the time course of object-permanence development should correlate with development of food-storing behavior. For example, by the time magpies begin to retrieve hidden food by themselves, they should be capable of "simple object permanence" (Piagetian Stage 4).

We recognize that a more general test of the hypothesis that adaptive specializations related to food storing are relevant to the performance level and developmental timing in object permanence would ideally include at least two independent comparisons, that is, two pairs of food-storing and nonstoring birds from different families. Nevertheless, a single-species study on magpies is justified for several reasons. First, our study on magpies starts from clear predictions that can be falsified. Therefore, the heuristic value of our approach goes beyond the evaluation of post hoc correlations. Second, in the case of food-storing passerines, a host of data on the behavior in captivity and in the wild, as well as on the behavioral and brain development of the investigated species and related species, is available (cf. Clayton & Krebs, 1995; Sherry & Healy, 1998; Shettleworth, 1995), providing corroborative support for behavioral findings. Species comparisons that included both phylogenetic and ecological differences have led to important insights (Brodbeck, 1994; Brodbeck & Shettleworth, 1995; Hampton & Shettleworth, 1996; Plowright et al., 1998). Third, because our study in magpies is the first study in a nonpsittacine species, any clear difference from the psittacine data will be helpful in understanding object-permanence development in birds and in designing future studies.

Method

Subjects

Eleven young hand-raised magpies (*Pica pica*) participated. Seven of them were tested on the entire Scale 1 by Uzgiris and Hunt (1975; see the *Tasks* section below), starting in Spring 1997. Testing began at an approximate age of 35 days, with 1 bird starting at 50 days. Because successful mastering of the first tasks of Scale 1 was present at 35 days of age, 3 additional birds were tested in Spring 1998, beginning at an age of 21–22 days. One bird that began testing in 1997, together with the 7 other birds, was tested on Tasks 1–3 only. This very shy bird did not attend during sessions of Task 4 and was not tested further.

Magpies were captured with appropriate license from nests close to the Bochum University campus. After being taken from their nests, the birds were first kept in a cardboard container that was the size of a magpie nest. A few days before fledging, when magpies in the wild normally start to move about their nests, the birds were transferred to wire birdcages (120 cm long \times 60 cm wide \times 120 cm high), in which they were housed in two groups of 4 in 1997 and one group of 3 in 1998. Each cage was equipped

with six wooden perches. Freshly cut twigs from tree species (hornbeam, maple) used by magpies for nesting in the study area were provided in the cages for shelter and additional perching. The floor of each cage was made of two drawers covered with paper. The nestlings' diet consisted of finely cut meat, insect larvae, hard-boiled egg, vegetables, and some water delivered through a plastic pipette. As soon as the birds began to feed partially on their own, the diet was a mix of these foods and commercial bird food (Fett-Alleinfutter; Claus, Friedensau, Germany). In addition, a mineral and vitamin supplement with trace elements (Vitakalk; MFE, Roth bei Nürnberg, Germany) was given. The age of the birds was determined when the birds were taken from their nests at an age of 14 ($n = 7$) to 27 ($n = 1$) days. Estimation of age was based on regular observation of the nests (egg laying) as well as the developmental status of the young, as indicated by the development of feathers, length of tail and wings, and tarsus length.

The 3 nestlings investigated in 1998 were transferred to the laboratory at 21 ($n = 1$) and 22 ($n = 2$) days posthatch. They were tested from the 1st day at their new home. They were hand-raised and kept as described for the other birds and were tested only on those tasks (Tasks 1–3) for which clear evidence was lacking from the older birds.

Tasks

The magpies were presented with tasks from Scale 1 by Uzgiris and Hunt (1975). These tasks have proved to be suitable for interspecies comparisons and have been used successfully in earlier studies on object permanence in birds (cf. Pepperberg et al., 1997). Though Scale 1 has been criticized recently (see the Discussion section), we considered it a good choice for our study because this scale allows for a direct comparison with the other two avian species tested so far. Tasks of Scale 1 test for the occurrence of Piagetian Stages 2–6. The 15 tasks correlate with the Piagetian scheme, but they allow for finer subdivisions. Uzgiris and Hunt allocated their tasks to five subgroups: (a) visual pursuit of slowly moving objects (Tasks 1 and 2), (b) search for simply hidden objects (Tasks 3–7), (c) search following more complex hiding (Tasks 8–9), (d) search following an invisible displacement (Tasks 10–13), and (e) search following successive invisible displacements (Tasks 14–15). The boundaries of these subgroups and the boundaries of the Piagetian stages coincide partially. All Piagetian stages correlate with a specific subset of tasks from Scale 1. Because we mainly refer to the Piagetian stages during our discussion of our data, we have grouped the following brief description of the 15 Scale 1 tasks along the Piagetian stages.

Piagetian Stage 2 (Tasks 1 and 2 of Scale 1)

Task 1. In this task, an object (e.g., a metal or plastic ring) was fixed to a thin nylon thread and was brought in front of the bird that was perching. As suggested for human infants, the object was shaken or swung when a trial was starting in order to have the bird pay attention. Then the object was moved slowly around the bird in the horizontal plane through an arc of 180°. In addition to this standard procedure, the object was moved through a full circle of 360° as well as through several full circles in succession. The criterion for successful performance was that the bird had to continuously and smoothly follow the object through an arc of 180°.

Task 2. A moving object tied to a thin nylon thread disappeared at one side of a screen and reappeared at the opposite side. The criterion for successful performance on this task was demonstrated if the bird looked at the point where the object disappeared or, after several presentations, returned its glance to the starting point or the point of reappearance before the object reappeared.

Piagetian Stage 3 (Task 3 of Scale 1)

An object was partly hidden under a single cover. The criterion in this task was met when the hidden object was obtained by pulling it out from under the cover or by taking the object after removing the cover.

Piagetian Stage 4 (Task 4 of Scale 1)

An object was completely hidden under a single cover. The criterion performance was removing the cover and picking up the object.

Piagetian Stage 5 (Tasks 5–9 of Scale 1)

Task 5. Two screens (sheets) were used. The object was hidden three times under one screen (A) and then was hidden under the other screen (B). The criterion performance here was immediate search in the place of final disappearance, namely, the second screen (B). Search under the first screen would indicate the Piagetian "A-not-B error."

Task 6. The object was hidden alternately under two different coverings. The criterion was to search under each of the covers, depending on the site of the last hiding.

Task 7. The place of hiding varied between three different screens. Immediate search under the screen where the object was finally hidden was the criterion performance.

Task 8. An object visibly presented in the experimenter's hand was passed successively under each of three screens and finally hidden under the screen where it disappeared last. Immediate search under the last screen demonstrated object permanence during successive visible displacements.

Task 9. To test the bird's persistence, an object was hidden under three superimposed covers. Criterion performance was indicated by obtaining the object after removing all covers.

Piagetian Stage 6 (Tasks 10–15 of Scale 1)

Task 10. The object was first placed into a small nontransparent container. The container was then passed under a screen, and the object was hidden under the screen. Finally, the empty container was shown to the bird. Checking the container and then retrieving the object from under the screen where the container had disappeared or searching immediately where the container had disappeared indicated criterion performance.

Task 11. Corresponding to Task 5, the container with the object was hidden under one of two screens and subsequently hidden under the other screen. A search under the second screen where the box had disappeared demonstrated object permanence during successive invisible displacements.

Task 12. The container was hidden alternately under two screens. Immediate search under the screen where the container disappeared was the criterion.

Task 13. The container was hidden under one of three screens. The criterion was the same as in Task 11.

Task 14. The object was visibly placed in the palm of the experimenter's hand, which was then closed. The hand passed under two screens (closed), and the object was left under the last screen. Then the experimenter showed his empty hand to the bird. The experimenter then withdrew his hand and moved backward. The sequences of displacements were ABC or CBA. The criterion was searching under all screens in the same order as the experimenter's hand passed under the screens and finding the object under the last screen or searching directly under the last screen after having found the object there before.

Task 15. After the bird had met the criterion for Task 14, the task was repeated similarly, but the object was left under the first screen. The criterion was searching systematically in reverse order: final screen, second screen, and first screen.

Procedure

At the beginning of a session, the magpies were transferred by hand from their home cage into the experimental room (6.0 m long \times 3.5 m wide \times 4.0 m high), where they could move around freely. Whereas the central part of the room was open, there were several objects close to the walls (e.g., a row of desks and shelves) that the birds could use for perching. Task 1 was carried out while the subjects were perching. During

the other tasks that required active search, objects and screens covering the objects were presented on the floor of the experimental room, as is the case in the wild, where magpies search for and hoard food predominantly on the ground (Birkhead, 1991). Two types of screens were used alternately: screens of crumpled paper of a size of about 20 cm × 20 cm and screens of cotton sheets of about 50 cm × 50 cm. Because the paper screens and the cotton sheets were crumpled or knitted, the hidden objects did not provide any visible cue. The objects were food and nonfood objects of different sizes (e.g., mealworms, dehusked peanuts, rings of plastic and metal, coins, spoons, and little toys).

At the beginning of a trial, the experimenter showed an object of interest to the subject. In most cases, the bird would then approach the experimental array. When the bird was paying attention (looking at the object), the appropriate manipulation (simple hiding, complex hiding) was done by the experimenter. After the object was hidden, the experimenter moved backward and remained quiet. After a delay of 4–7 s, in a few cases up to 10 s, the subject would approach the array and make its choice.

Initially, the birds received two testing sessions per week until Task 8 was mastered. Thereafter, only one session per week was administered. On a few occasions when a subject first made two correct choices and then an incorrect choice, one additional session was carried out on the following day so as not to miss the exact onset of the stage in question. A maximum of three trials of a given task per session was administered (if all were correct). A session ended after any incorrect response.

All tasks were carried out with nonfood objects and food objects (peanuts, mealworms) in a pseudorandom order. Before carrying out object-permanence tasks that required the birds to obtain the object (Tasks 3–15), we tested whether the nonfood objects that were used elicited the appropriate behavior (approaching and picking up the object). During all tests, we found no performance differences due to the use of either food or nonfood objects. The lack of a difference in performance between food and nonfood objects indicates that possible cues arising from food objects (e.g., odor) did not play a role.

The number of presentations and the scoring criteria were chosen on the one hand to provide sufficient and statistically valid evidence for the onset of a given stage and on the other hand to confront each individual with a given test situation as rarely as possible to prevent any conditioned responses. Each subject received a maximum of three trials per day. If the subject did not attend to the object shown by the experimenter and did not approach the experimental array, a trial was scored as "not attended," and the experimenter did not hide the object. A trial began as the subject approached the array and looked at the object. Then the object was hidden, and any response by the subject was scored as either "correct" or "incorrect." "Incorrect" was every response not in agreement with the criterion for a given task. For example, if on a trial of Task 4 the subject "lost interest" without approaching one of the screens, one cannot tell whether there was a lack of motivation or no representation of the hidden object. If the subject performed an incorrect response (in most cases in the first trial), the session ceased for that day. After correct responses, up to two additional trials were administered. A trial was completed after the bird either had made a choice by removing a cover or had left the experimental array, for example, to perch at a place remote from the experimental array.

A task of Scale 1 was considered as mastered if the subject made three correct responses and no errors on 2 consecutive test days. The statistical significance of six correct responses within two consecutive sessions was $p < .002$ (binomial test) if three or more response options were equally likely. However, the chance probability for each of the response options could not be predicted exactly. For example, on Task 4, the three incorrect alternative solutions suggested by Uzgoris and Hunt (1975) would be expected to have different probabilities. If this is considered and a rather conservative criterion is used by categorizing the subjects' responses only as either correct or incorrect with an expected probability of .5 for each category, the significance level for six consecutive correct responses within two consecutive sessions would be $p < .02$ (binomial test).

Results

The subjects mastered all tasks of Scale 1 with a few exceptions. One exception was that performance on Task 2 was not consistent enough to meet our criterion. Another exception was that the birds continued to search behind the final screen on Task 15 (see the *Task 15* section below). Onset of competence on a given task occurred at almost the same age in all birds, whereas there were clear differences between the stages (see Table 1 and Figure 1).

Task 1

All birds ($n = 8$) tested in 1997 followed an object moving through an arc of 180° on the 1st day of testing (Day 35 for 7 birds and Day 50 for 1 bird). If the object was moved in a complete circle (360°) around the birds, they made a volte-face jump on the perch after the object had moved 180° and by doing so followed the object through a complete circle or for several circles in succession. In all birds ($n = 3$) tested in 1998, the criterion was achieved in the first test session at an age of 21 days (1 bird) or 22 days (2 birds). Thus, the magpies mastered Task 1 at an age of 3 weeks posthatch or younger.

Task 2

The magpies showed the correct response to watch the point of disappearance or, alternatively, to estimate the point of reappearance for a number of times (on about half of the trials), but none of the 11 magpies that were tested achieved the criterion of three correct responses in a row during two consecutive sessions. This was the case in young birds (25 days or older) as well as in adults. The birds would follow a moving object until it disappeared behind the screen. Often they looked to the place of presumptive reappearance, but equally often they started other activities shortly after the object had disappeared. Therefore, the criterion for successful Task 2 performance was not met, although the general behavior of the birds suggested a quick shift in attention rather than a lack of task-specific abilities.

Task 3

In those birds that began testing at the age of 35 days, Task 3 was mastered in the second session on Day 38 or Day 39, which was the first session in which the birds were presented with this task. In the bird tested from Day 50, the task was mastered in the first test at Day 53. In the birds tested starting at 21–22 days, Task 3 was mastered on Day 31 or Day 32, which was the fourth or fifth test for the birds. This finding indicates that Task 3 competence was achieved by the magpies at an age of 4.5 weeks. In incorrect trials, the younger birds did not try to retrieve the partially hidden object.

Task 4

Successful retrieval of a completely hidden object occurred after 6–8 weeks. Stage 4 competence emerged in two steps. The birds simply lost interest and did not search for a hidden object before Day 44 ± 3.6 (mean \pm standard deviation). After 44 days, they started to go to the correct cover, but initially they did not remove the cover and retrieve the object. It took another 13 ± 1.6 days

Table 1
Age When Achieving Criterion or Partial Solutions on Scale 1 Tasks

Task of Scale 1	Piagetian stage	Number of birds ^a			Performance ^b	Age (in days) ^c
		Session	Attended	Mastered		
1	2	11	11	1	Criterion	(≤50)
				7	Criterion	(≤35)
				1	Criterion	≤21
				2	Criterion	≤22
2	2	11	11	0	Criterion not met	5.5–18 months
3	3	11	11	1	Criterion	(≤53)
				7	Criterion	(≤38–39)
4	4	8	7	3	Criterion	31 ± 0.6
				7	Correct place, no retrieval	44 ± 1.5
5	5	7	7	7	Criterion	57 ± 1.9
				7	Criterion	65 ± 1.5
6	5	7	7	7	Criterion	67 ± 0.9
				7	Criterion	66 ± 1.7
7	5	7	7	7	Criterion	97 ± 0.4
				7	Criterion	107 ± 0.8
8	5	7	7	7	Criterion	105 ± 2.5
				7	Correct place, no retrieval	120 ± 4.5
9	5	7	7	7	Criterion	135 ± 5.3
				7	Criterion	137
10	6	7	7	4	Correct place, no retrieval	165 ± 6.3
				7	Criterion	176
11	6	7	7	7	Criterion	180 ± 9.1
				7	Criterion	5.5–18 months
12	6	7	1	1	Criterion	
				1	Criterion	
13	6	7	5	5	Criterion	
				5	Criterion	
14	6	7	7	1	Place of first disappearance	
				7	Criterion	
15	6	7	7	0	Final screen	
				0	Final screen	

Note. If the number of birds that attended is smaller than the number of birds having sessions, this does not indicate that any of the birds failed but that no hiding procedure was carried out by the experimenter because the subjects did not attend when the object was shown.

^a Number of birds that were given sessions, that actually attended, and that mastered the task at a given age. ^b In addition to achievement of the criterion, this field indicates partial (e.g., correct place, no retrieval) or alternative solutions. ^c Age = means ± standard deviations for the time at which the birds achieved criterion or a partial solution; ≤ indicates that the task was mastered on its first presentation and competence may have been present earlier; therefore, these values are in parentheses.

until the birds started to lift or pull away the cover and pick up the object. The time of onset of Stage 4 (going to the correct site) and the time of completion (successful retrieval) were similar in all birds. In all birds, Stage 4 developed in two substages over a period of about 2 weeks.

Task 5

Successful retrieval of objects hidden consecutively at two sites occurred after 9 weeks. Five birds retrieved the object from the correct location (second cover) on the first session in which they took part. Two birds had two trials each in which they showed similar behavior as in the first stage of Task 4. They went to the correct location, but they did not retrieve the object. On the next session, they retrieved the object. All birds chose the correct site on all trials and did not make the A-not-B error.

Tasks 6 and 7

Tasks 6 and 7 were mastered immediately by all 7 birds.

Task 8

As on earlier tasks, competence on this task was achieved by all 7 birds at almost the same age (14 weeks). However, after the birds had mastered Task 7, it took them about 1 month before they

mastered Task 8. A critical point for the magpies was the combination of quick displacements and alternation of hiding order.

Task 9

Task 9 was mastered about 10 days after Task 8. One bird had a first incorrect trial on which only the upper cover was removed and a second incorrect trial with two covers removed before choosing correctly on the third trial; all other birds had one incorrect trial with only one cover lifted.

Controls

To control for the possibility that the subjects' choice was due to any cue emanating from the experimenter and not to the place of the object, control tests for the visible displacement tasks were carried out after the birds had mastered these tasks. During these controls, the experimenter touched all places or a wrong place with his hand before the subjects made their choice. The birds continued to perform error-free on the first and subsequent controls, thus indicating that their behavior during visible displacements was controlled by the object placement.

Task 10

As with Task 4, two steps could be observed in 4 of 7 birds. After 15 weeks, these 4 birds were choosing the correct place, but

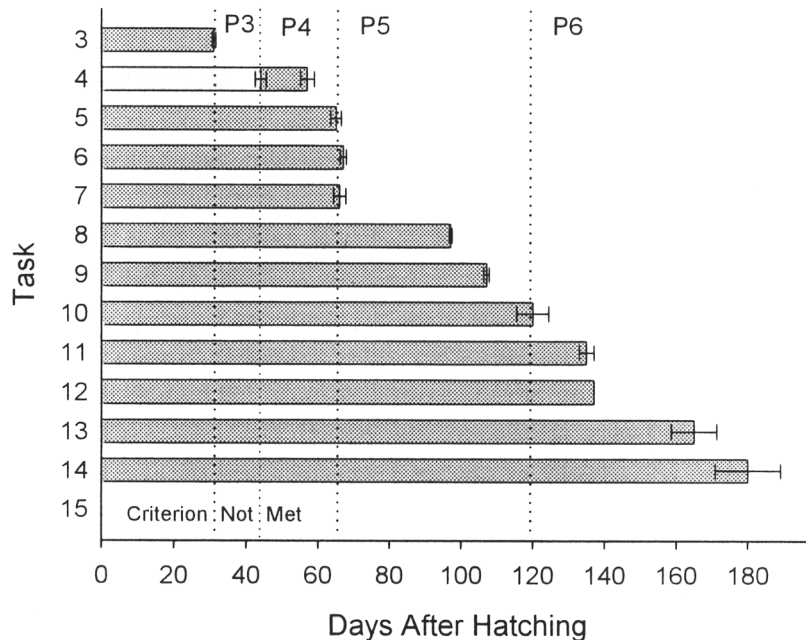


Figure 1. Mean (\pm SD) age at which the magpies mastered the hiding tasks of Scale 1 by Uzgis and Hunt (1975). The stacked bar for Task 4 indicates both onset (white bar) of Stage 4 (search at correct location, no retrieval) and its completion (successful retrieval; gray bar). The bar for Task 3 is based on 3 birds tested in 1998; all other bars are based on 7 birds tested in 1997, except for Task 12 ($n = 1$) and Task 13 ($n = 5$). Fields separated by dotted lines and labeled with P3–P6 indicate the corresponding Piagetian stages.

they did not retrieve the object; 2 weeks later, these 4 birds and the other 3 birds chose the correct location and retrieved the object. Two of the other 3 birds had incorrect trials before criterion, during which they probed with their beak for the hidden object in the container.

Tasks 11–13

Tasks 11 and 12 were mastered soon after Task 10; Task 13 was mastered a month later. The age of reaching competence on Tasks 12 and 13 should be considered with caution. On Task 12, only 1 bird took part. Before the session when the subjects mastered Task 13, two sessions of the regular schedule had to be omitted on technical grounds. Therefore, it is possible that the magpies would have mastered Task 13 sooner if they had been tested 1 or 2 weeks earlier.

Task 14

This task was mastered by most of the birds soon after mastering Task 13. The error made by 3 of 7 subjects on the first presentation was to search under the first screen of disappearance. On successful trials, the subjects went straight to the target screen.

Task 15

Initially (on Day 162), 2 subjects were searching at the screen where the “container” (the experimenter’s hand) had disappeared first. Later on, these 2 and all other subjects were searching exclusively under the screen where the container had disappeared

last. After not finding the object under the final cover, they stopped searching. To test whether the magpies would change their search behavior on Task 15, they were retested monthly up to an age of 18 months. They continued to search under the final screen. The search pattern on Task 15 provides an additional (serendipitous) control for the possibility that the magpies could have used any sensory cue (e.g., odor) to locate the object. If so, they should have been searching under the first screen (where the object—on some of the trials a food object—had been left) on at least some occasions. Table 2 shows the average number of trials on which the birds did not attend or failed before they achieved criterion on each of the 15 tasks.

Discussion

The magpies mastered all tasks of Scale 1 with two exceptions. They did not meet our criterion on Task 2, and they failed to show persistent search in the reverse order of hiding on Task 15. As predicted, object permanence up to Piagetian Stage 4 and Stage 5 competence developed before the age of nutritional independence.

Overall, the magpies showed a fairly steady progression in the mastering of subsequent tasks of Scale 1. The first 3 tasks of Stage 5 were achieved almost simultaneously at an age of about 9 weeks. This finding indicates that by the age of independence magpies easily update information on hiding places if at least a few seconds have passed between subsequent hidings regardless of whether there are two or three hiding places. The latter task was of considerable difficulty for kakarikis (Funk, 1996). A possible account for this difference is that, as a scatter hoarder, magpies are

Table 2
Trials Before Achieving Criterion

Task	Number of trials		n
	Not attended	Incorrect	
1	0.0 ± 0.0	0.0 ± 0.0	11
2			7
3	0.0 ± 0.0	3.3 ± 0.6	3
4a	0.7 ± 0.5	0.0 ± 0.0	7
4b	1.7 ± 0.5	1.9 ± 0.7	7
5	3.4 ± 1.5	0.9 ± 0.9	7
6	0.0 ± 0.0	0.0 ± 0.0	7
7	0.0 ± 0.0	0.0 ± 0.0	7
8	2.4 ± 2.0	1.4 ± 0.5	7
9	0.9 ± 0.4	1.1 ± 0.4	7
10	1.1 ± 0.4	1.3 ± 0.8	7
11	0.7 ± 0.5	1.0 ± 0.0	7
12	0	0	1
13	0.0 ± 0.0	0.0 ± 0.0	5
14	1.0 ± 0.0	0.4 ± 0.5	7
15			7

Note. Scores for Tasks 4a and 4b are cumulative.

well adapted to remember objects at different places. Magpies mastered Task 8 one month later. Thus, before the age of 13–14 weeks, magpies have difficulties in keeping track of a temporarily hidden object that changes its hiding place in quick succession, a situation not occurring in natural food-storing behavior. After 14 weeks of age, they can easily follow a quickly moving object between different hiding places, indicating that competence on visible displacements shows further maturation beyond what is required in food storing.

Mastering of 5 of 6 invisible displacement tasks raises the question as to whether magpies achieve Stage 6 competence. Although the tasks of Scale 1 are considered relevant in assessing Stage 6 competence, they might not be sufficient, and several recent studies (cf. De Blois et al., 1998) used other tasks in testing for true Stage 6 competence. Because our magpies were searching under the final screen in Task 15, the question arises as to whether they could have been using a “local rule” (cf. Gagnon & Doré, 1992) in invisible displacement tasks by always choosing the last place where the “container” was hidden. We cannot fully rule out this possibility. However, we think that the choice behavior of the magpies does not support this interpretation. The magpies made very few errors on invisible displacement tasks (Table 2), even on the first test. So they had no feedback to lead them to switch from an object-driven strategy that they clearly had used in visible displacement tests to a strategy using a local rule. One could argue that the magpies did not use a local rule during simple invisible displacements (Tasks 10–13) but did so on successive invisible displacements (Tasks 14–15). Then they would have been reinforced during the six criterion trials of Task 14 before Task 15 was administered. However, if any conditioning processes would have been at work, it is difficult to see why the magpies did not give up their search at the final screen on Task 15 during further sessions. They continued to search under the final screen for 1 year of monthly testing despite never being successful. An alternative explanation for why the magpies stopped after searching at the final screen and did not proceed by searching the whole set in

reverse order can be derived from their feeding ecology. When food-storing birds retrieve their hoards, they usually find part of their caches empty, for example, those caches that have been pilfered by conspecifics or animals from other species. Therefore, they might be predisposed to stop searching after not finding a hidden item rather than looking for it in another place. Considering this and the possible drawbacks of the invisible displacement tasks of Scale 1, we conclude that magpies achieve at least Piagetian Stage 5 competence, whereas true Stage 6 competence in this species requires further study.

Time Course of Development as Compared With Other Avian Species

Compared with a grey parrot (Pepperberg et al., 1997) and kakarikis (Funk, 1996), all stages of Piagetian object permanence (except for the difference on Task 15 and the ambiguous result on Task 2) were achieved at an earlier age by magpies. Piagetian Stage 4 object permanence was achieved about 8 weeks earlier in the magpies than in the grey parrot and 3.5 weeks earlier in the magpies than in the kakarikis. Stage 5 was reached about 9 weeks earlier in the magpies than in the grey parrot and 10 weeks earlier in the magpies than in the kakarikis (Figure 2). Thus, earlier onset was particularly pronounced with regard to those stages that correspond to cognitive abilities of high relevance to food storing and supports the hypothesis that food storing promotes early development of Stage 5 in magpies. Because phylogenetic constraints not related to food storing might also contribute to the developmental pattern in magpies, a comparison with the closely related jackdaw (*Corvus monedula*), which does not scatter hoard food, would be of interest. Preliminary data (Etienne, 1976/1977) have suggested that object permanence develops more slowly in jackdaws, which like magpies become independent at the age of 10 weeks. Further systematic studies on jackdaws and other suitable species are needed to corroborate this finding.

Interestingly, the overall time course of object-permanence development in magpies has some similarities with the time course found in cats (*Felis catus*; Dumas & Doré, 1989, 1991). This parallel underlines the importance of further comparisons of object-permanence development among and across phylogenetic groups.

Time Course With Regard to Overall Behavioral Maturation of Magpies

Spontaneous development of other sensorimotor abilities and food-storing behavior correlates well with object-permanence development (Figure 2A). The ability to follow a moving object is already established by the time young magpies start to move about the nest and its close surrounding. As reported by Pepperberg et al. (1997), we saw tracking of objects during feeding in young nestlings. For example, 2-week-old magpies in our study followed the pipette through which they received water. We were, however, cautious to take this as the beginning of Stage 2 because we did not carry out a standardized test with these very young birds.

By the time magpies start to feed partially on their own immediately after fledging and when they start to hoard food at around Day 32, Task 3 is mastered. In Piagetian terms, this might indicate that the young magpies become able to reconstruct the full object

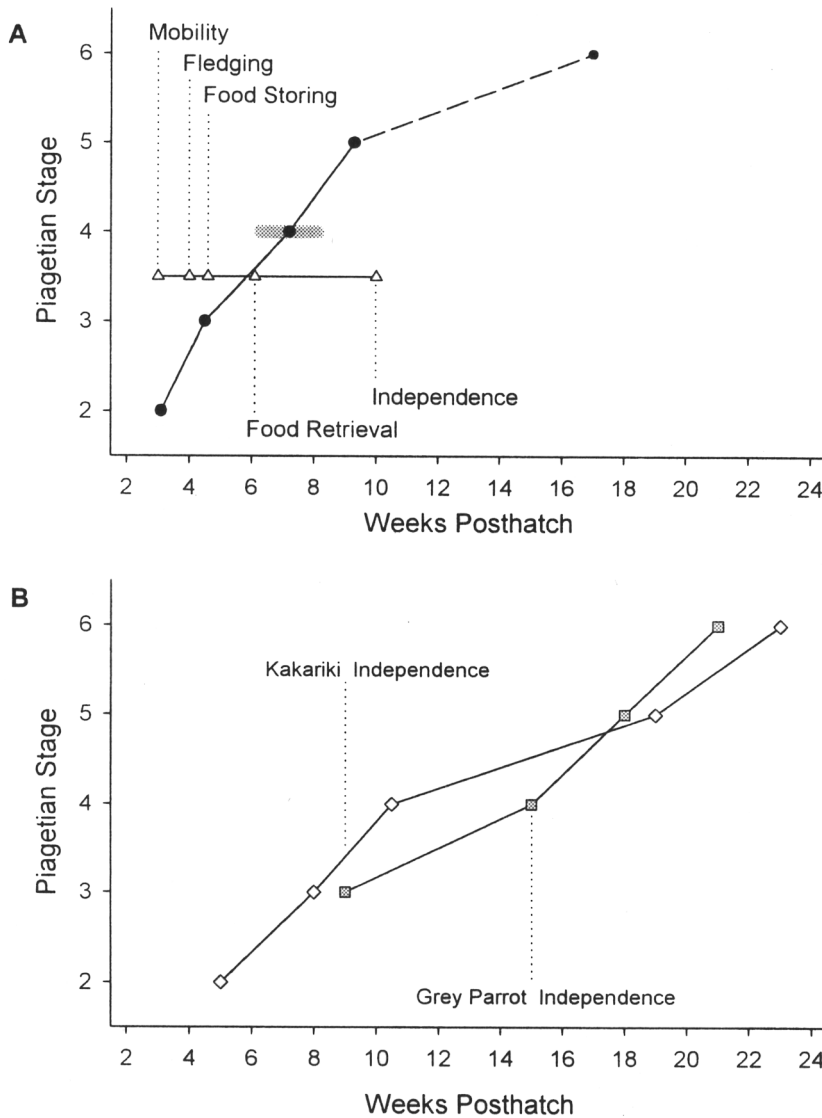


Figure 2. A: Development of object permanence in magpies as indicated by Piagetian Stages 2–6 and its relation to the general behavioral development of nestlings and youngsters on their way to independent living. Stage 2 competence is already present by the time the nestlings start to move about the nest and its close surroundings. A few days after fledging, magpies begin to hoard food. Together with the development of food storing, Piagetian Stage 3 competence is achieved, and together with the onset of cache retrieval, magpies start to demonstrate Stage 4 competence, indicating a mental representation of completely hidden objects. By the time magpies reach complete nutritional independence in the wild, Stage 5 competence is present. The gray horizontal bar on the data point for Piagetian Stage 4 in magpies indicates that this stage developed over a period of 2 weeks in all subjects. The dashed line between the data points for Stage 5 and Stage 6 and the smaller symbol for Stage 6 indicate that evidence for Stage 6 competence was less clear than for other stages (see the Discussion section in the text). Data on the general behavioral development were compiled from Birkhead (1991), and data on the development of food-storing behavior were compiled from Prior and Schwarz (1999). B: Time course of object-permanence development in kakarikis (open diamonds) and a grey parrot (filled squares). Data points for the kakarikis were averages for several birds, whereas the grey parrot data refer to 1 individual. The grey parrot data are from Pepperberg et al. (1997), and the kakariki data are from Funk (1996); the latter data refer to hand-raised kakarikis, which achieve Piagetian stages somewhat earlier than parent-raised birds; the data on independence are from Robiller (1997). Pepperberg et al. also reported data on Piagetian Stage 2, which are, however, not included because on technical grounds they represent onset of testing rather than onset of the capability.

from its parts. This might be the case, but a more parsimonious account is also possible. Young magpies are attracted by a number of different objects and also store nonfood objects of various size, color, and shape (Prior & Schwarz, 1999). In this way, they differ from the related Eurasian jay (Clayton, Griffiths, & Bennett, 1994). Jays prefer nonfood objects that closely resemble acorns and thus might have to reconstruct a complete acorn if part of it is hidden. Presumably, for young magpies, the visible part of the object per se is attractive enough to elicit retrieval behavior. Whether based on this or on reconstruction of an object, a likely account for Task 3 competence being achieved at the beginning of food storing is that by this time magpies start to pick up objects not only for immediate consumption but also to carry and handle them.

By the time magpies start to retrieve food at around Day 42, "simple object permanence" (Piagetian Stage 4) has commenced. The closely related development is consistent with our prediction. How is the development of these feats interrelated? Do emerging representational abilities drive retrieval behavior, or does increased experience in retrieving lead to enhanced object representation? In the case of food storing, studies on neural development and behavior in marsh tits suggest an interplay between maturation and experience (Clayton & Krebs, 1995).

A qualitative difference from the development of object permanence in the grey parrot and kakariki is that magpies, like cats (Dumas & Doré, 1989) and dogs (Gagnon & Doré, 1994), show no A-not-B error. Because of our testing schedule, we cannot completely rule out a very transient A-not-B error. But even in the latter case, magpies are obviously less prone to the A-not-B error than are the other avian species tested so far. Several alternative explanations have been put forward in terms of the occurrence of the A-not-B error, for example, little resistance to interference, an immature allocentric spatial coding system (Bremmer, 1978), or an immature understanding of motor chaining (Baillargeon, Graber, DeVos, & Black, 1990). Like cats (Dumas & Doré, 1989), magpies that have been flying and food storing for more than 1 month by the time Stage 5 competence emerges should have a rather mature allocentric coding system, so that maturation of the spatial coding system could be a likely explanation. If so, food storing might be more important in the development of allocentric coding than movement in space, because the grey parrot and the kakariki made an A-not-B error despite having fledged several weeks before (age of fledging in the kakariki was 5 weeks and in the grey parrot was 11–13 weeks). Regarding resistance to interference, it has actually been shown that, presumably due to adaptive specializations, passerine food-storing birds have a particularly high resistance to interference (Clayton & Krebs, 1994; Hampton & Shettleworth, 1996). Therefore, we think that high resistance to interference is the most likely explanation for nonoccurrence of the A-not-B error in magpies. A well-developed allocentric spatial coding system might also contribute.

Neurobiological Considerations

A number of studies have suggested that the avian hippocampus plays a crucial role in tasks that require memorizing objects in space that are temporarily out of sight, such as cache sites in food-storing birds (Clayton & Krebs, 1995) or host nests in brood parasites (Reboreda, Clayton, & Kacelnik, 1996). One of the crucial factors might be avoidance of interference (Shapiro &

Olton, 1994). Interestingly, development of competence on Piagetian Stages 4 and 5 in magpies takes place at almost exactly the same age at which in another food-storing passerine species, the marsh tit (*Parus palustris*), a boost in the development of the hippocampus occurs (Clayton & Krebs, 1995). Though not fully covering the critical time window, comparison of hippocampal development in jackdaws and magpies (Healy & Krebs, 1993) suggests the same parallel time course in magpies. Therefore, the question arises as to whether maturation of the hippocampus could be a key process in the development of Piagetian object permanence. Seress (1998) tested this idea in humans and found support for this hypothesis. In addition to the hippocampus, the avian neostriatum caudolaterale (Hartmann & Güntürkün, 1998) as an analogue to the human prefrontal cortex (Diamond & Goldman-Rakic, 1989) might be part of a neural system supporting spatial representation in object permanence.

As in humans and several other species, Stage 4 competence of magpies developed in two steps. Piaget (1937/1954) already described a transient phase during which an infant can successfully retrieve a hidden object only if a reaching movement had been initiated before. The situation in magpies is somewhat different. They initially searched at the correct place but did not retrieve the object. However, in both cases, full Stage 4 competence appears to depend on the integration of an already established motor skill and a mental representation of something not directly visible. Maturation of hippocampal and prefrontal connectivity might be an essential step in establishing that link.

To summarize, the present findings show that several aspects of object-permanence development in magpies can be reasonably accounted for in ecological terms. Because the developmental pattern also fits well with what is known from neurobiological studies, the magpies and related food-storing birds appear to be an interesting model for an integrative study on the cognitive, ecological, and neural aspects of the development of Piagetian skills.

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