



## The ontogeny of caching in ravens, *Corvus corax*

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Ravens scavenging on carcasses devote much of their time to carrying off loads of food for temporary storage in caches. Ways of reducing conspecific pilfering of these caches include camouflaging caches with debris and positioning caches at a distance from and/or out of sight of potential competitors. We examined the acquisition and improvement of these caching skills in young captive ravens. We identified a hierarchy of elements in the caching behaviour, ranging from simply pressing the caching items towards solid structures to the appropriate covering of them with surrounding material. The development of these elements was closely linked with the birds' acquisition of Piagetian Stages of object permanence. Furthermore, we distinguished between the young ravens' initial caching of edible and inedible items. We tracked the individuals' temporal development of placing their caches at a distance from and out of sight of conspecifics and their social interactions over caches. Behaviours aimed at preventing pilfering were associated with competitive interactions and were manifested only with edible items. We conclude that the skills for camouflaging caches are primarily affected by maturation of representational capacities for hidden (i.e. not visible) items, whereas the skills for the positioning of caches are strongly affected by experience gained through social interactions.

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Food caching in birds has evolved to become a complex behaviour (Lorenz 1935) comprising skills for relocating caches and remembering already emptied sites (e.g. Sherry et al. 1981; Shettleworth & Krebs 1982; Balda et al. 1987; Balda & Kamil 1992; Clayton & Krebs 1994; Healy 1995), recalling the quality and longevity of stored items (e.g. Clayton & Dickinson 1998; Clayton et al. 2003) and judging the risk of pilferage by others (e.g. Heinrich 1999; Emery & Clayton 2001). Hence, avian food caching is a useful paradigm to investigate memory and planning as well as social cognition and has greatly contributed to our understanding of cognitive capacities in birds (De Kort et al. 2006). Still, little is known about how cognitive and behavioural patterns integrate during ontogeny, for example

whether the maturation of memory for hidden items affects the camouflaging of caches and the experience of pilfering affects the positioning of caches.

In marsh tits, *Poecile palustris*, the onset of food storing depends on age but storing techniques and efficiency develop gradually and are largely affected by the individuals' experience (Clayton 1992, 1994; see Haftorn 1992 for field observations on crested tits, *Lophophanes cristatus*, and willow tits, *Poecile montanus*). Furthermore, the development of tits' caching behaviour is accompanied by increases in the hippocampal brain region (Clayton & Krebs 1995) where the neural correlate of spatial memory resides (Krebs 1990; Healy et al. 2005). In magpies, *Pica pica*, caching starts at a comparable developmental stage to that of tits (H. Prior & A. Schwarz, unpublished data) and improvement in cache retrieving appears to be linked with the maturation process of object permanence (Pollok et al. 2000) i.e. the representational capacities for items that are temporarily out of view (Piaget 1937/1954).

In humans and nonhuman animals, object permanence develops in stages (reviewed in Gomez 2005): at first, individuals show no search response to a disappearing object (Stage 1). They then begin to track the item's movement

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(Stage 2) and become able to recover a partially (Stage 3) and a fully (Stage 4) occluded item. Finally, they may retrieve an item that has been visibly (Stage 5) and invisibly (Stage 6) displaced from previous hiding locations (for details and correspondence with the measurement by Uzgi-ris & Hunt 1975 see Table 1). This Piagetian six-stage framework is useful for cross-species comparisons (Chevalier-Skolnikoff 1976; Etienne 1984) to evaluate the performance level achieved and the timing of development (Doré & Dumas 1987; Call 2001a; Pepperberg 2002). For instance, Pollok et al. (2000) suggested that memory-based hoarding behaviour creates a selection pressure in the evolution of object permanence to reach (at least) solid Stage 5 competence for keeping track of multiple hidings and updating which caches contain food and which have already been emptied; furthermore, it may be critical that this competence develops at an early age, that is, around independence.

Food-storing corvids such as magpies and European jays, *Garrulus glandarius*, indeed appear to acquire sophisticated levels of object permanence before the time of independence (Pollok et al. 2000; Zucca et al., in press). This rapid development in corvids stands in contrast to the prolonged development of object permanence in nonstoring psittacids such as kakarikis, *Cyanoramphus auriceps*, and grey parrots, *Psittacus erithacus*, which eventually also reach Stage 6 competence (Funk 1996; Pepperberg et al. 1997). The differences in developmental speed of object permanence between the two storing and the two nonstoring species could be caused by general time differences in the motor and cognitive development of corvids and psittacids rather than differences in foraging ecology (Pollok et al. 2000). Thus it would be important to show whether the time course of development of object

permanence correlates with that of how caches are made, for example that a representation of hidden items (Stage 4) corresponds with the full occlusion of items at caching, and the ability to keep track of visible displacements (Stage 5) corresponds with the multiple covering of caches with substrate and/or with recaching.

A major problem for food-storing birds is the loss of caches to pilferers (Andersson & Krebs 1978; Vander Wall & Smith 1987; Petit et al. 1989; Hampton & Sherry 1994) but little is known about the ontogeny of this social aspect of caching. In some corvids, cache pilfering appears to be a routine foraging tactic (Waite 1992; Heinrich & Pepper 1998; Emery et al. 2004) and its success depends on the possibility of learning about cache location through observation (Bednekoff & Balda 1996a, b; Emery & Clayton 2001; Bugnyar & Kotrschal 2002). Some species such as ravens, *Corvus corax*, and western scrub jays, *Aphelocoma californica*, selectively avoid conspecifics when caching and make use of obstacles that prevent others from watching (Bugnyar & Heinrich 2003; Dally et al. 2004, 2005). Although there is some evidence that experience of pilfering is necessary to develop cache protection strategies (Emery & Clayton 2001), it is unclear when and how birds acquire their manipulative social skills.

Corvid caching behaviour is controlled not only by the feeding system (e.g. Gwinner 1965) but also by an independent caching system with the control being mediated by the incentive value of the item (Clayton & Dickinson 1999). Furthermore, corvids cache not only food but also small nonfood items (Heinroth & Heinroth 1926; Clayton 1993a; Heinrich & Smolker 1998), suggesting that the act of caching may be self-rewarding in the sense that birds 'enjoy' hiding items and, in the absence of food, become directed towards objects. Differences in value

**Table 1.** Piagetian Stages of object permanence and tasks from Scale 1 by Uzgi-ris & Hunt (1975)

Piagetian Stage	Description	Tasks from Scale 1	Criterion
2	Visual pursuit	1	Visually track moving object through arc of 180°
		2	Look at the point where moving object disappears behind screen or, after several presentations, return glance to starting point or point of reappearance
3	Partial hiding	3	Obtain partly hidden object
4	Full hiding	4	Obtain completely hidden object
5	Visible displacement	5	Immediate search in place of final disappearance (screen B), although object was previously hidden three times under screen A
		6	Search under one of two covers depending on where object was last hidden
		7	Search under one of three covers depending on where object was last hidden
		8	Immediate search in the place of final disappearance after the object was visibly passed under each of three screens
		9	Obtain object by removing three superimposed covers
		10	Corresponding to task 4, but before being hidden object is visibly placed in opaque container; after object is hidden the empty container is shown to subject
		11	Corresponding to task 5, but with object in opaque container
6	Invisible displacement	12	Corresponding to task 6, but with object in opaque container
		13	Corresponding to task 7, but with object in opaque container
		14	Corresponding to task 8, but with object placed in closed hand of experimenter; immediate search in the place of final disappearance after object is passed invisibly from screen to screen
		15	Search in reversed order: final screen, second screen, first screen when object is left under first screen but closed hand moved under each of the three screens

Originally developed for humans, tasks from Scale 1 have proved suitable for interspecies comparison. The 15 tasks correlate with the Piagetian scheme (Stages 2–6) but allow for finer subdivisions.

between stored food and object items might affect how ravens treat those caches in regard to pilfering. Accordingly, the caching of objects could be used as a kind of baseline with which the improvement in positioning and camouflaging of food caches can be compared over time.

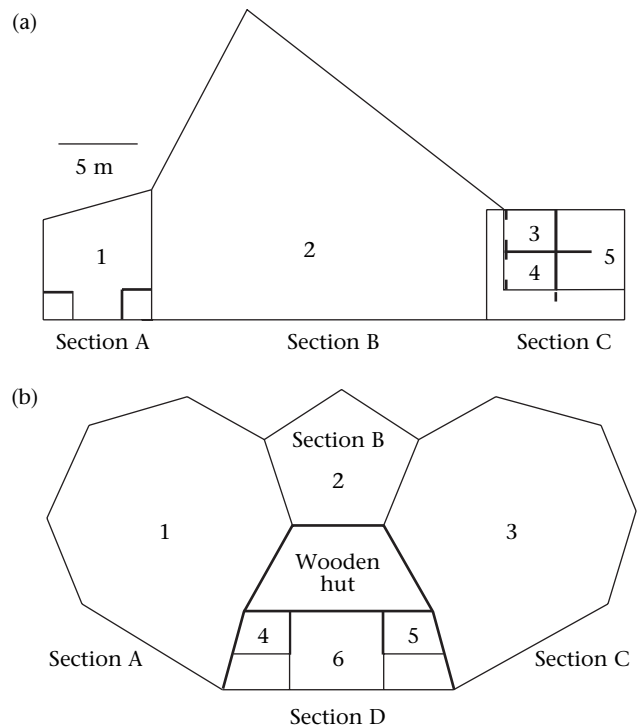
We examined the ontogeny of caching behaviour in juvenile hand-reared ravens. In contrast to other studies that aimed to control for social influences (Clayton 1992, 1994; Pollok et al. 2000), we tracked the individuals' caching skills in their social environment. Starting with fledging, we conducted standardized daily observations before and during experimentally induced feeding for a half-year period and, in parallel, tested birds individually on Scale 1 of Uzgiris & Hunt's (1975) object permanence tasks. We expected two major improvements: one in relation to the acquisition of object permanence, affecting how birds cache and one in relation to interactions with conspecifics, affecting where birds cache. In both cases, we took into account what was cached, edible or nonedible items. We predicted that the development of object permanence should have a general effect on caching so we expected no marked difference in how birds cache food and objects. In contrast, protecting caches against pilferers should depend on the value of the cached item. Thus, we expected ravens to improve in taking care where they cached food rather than where they cached objects.

## METHODS

### Subjects and Housing

We used 18 hand-reared ravens held in two social groups, one at the University of Vermont (UVM), U.S.A., and the other at the Konrad Lorenz Forschungsstelle (KLF), Austria. The main focus was on the six birds (four males, two females) of the group at UVM. They were taken from the wild at the age of 3 weeks from two separate nests, reared together in one nest, and fledged in May 2002. After fledging, the birds were held together with one adult male in an approximately 200-m<sup>2</sup> outdoor aviary complex. This arrangement simulated a typical non-breeder situation as, in the wild, young ravens regularly associate with older ones in mixed-sex groups (Heinrich et al. 1994; Parker et al. 1994). The aviary comprised three sections (A, B, C; Fig. 1a). Each section consisted of one to three compartments that allowed individuals to be isolated for experimental testing (physical isolation in sections A, B; physical and visual isolation in section C). Before and after the tests, the doors between the compartments were open and the birds could roam freely throughout the complex. Sections A and B had natural vegetation (conifer trees and bushes) and were equipped with twigs, swings and logs for perching, rain-protected platforms and shades for roosting and basins for bathing. Section C was comparatively sterile, containing only a grass floor and a few perches.

Ravens of the group at KLF were reared and kept under similar conditions as those at UVM. The 12 birds (seven males, five females) originated from five separate nests



**Figure 1.** Sketches of aviaries (a) at UVM and (b) at KLF. Numbers indicate location of compartments. Bold lines symbolize opaque wooden walls.

(two from zoos, three from the wild). Nestlings were taken between 12 and 40 days of age, reared in four sibling groups and fledged in May 2004. After fledging, they were kept in one social group with two adult males in a spacious aviary complex (ca. 240 m<sup>2</sup>; Fig. 1b) situated in the Cumberland game park at Grünau, Austria. The aviary consisted of four sections, each made of one to three compartments, for separation of individuals during tests. When not being tested, the birds were allowed to roam throughout the complex. Apart from one section, which had only a floor of fine-grained sand and a few perches, the aviary had natural vegetation (trees and bushes), logs, rocks, water basins, rain-protected platforms and shades.

Birds of both groups had 6–10 h per day of contact with certain humans who took behavioural protocols and engaged individuals in experimental testing. Thus all birds were accustomed to video equipment and close-distance observations from inside and outside the aviary. They were marked with coloured rings for individual identification. Birds had ad libitum access to water and were fed by their human hand-rearers between five and two times per day depending on age and protocol. The diet consisted of various kinds of meat, egg, milk products and fruit (Kabicher & Fritz 1996).

Permission to take and keep wild birds was obtained from the U.S. Federal Fish and Wildlife, State of Maine Department of Inland Fisheries and Wildlife, Vermont Fish and Wildlife Department and the Ministerium für Landwirtschaft, Umweltschutz und Raumordnung des Landes Brandenburg, Austria.

## Observation of Caching Development

This part of the study is based on focal observations of item manipulation and caching behaviour of the six birds at UVM. Starting with fledging ( $\bar{X} \pm SE = 40 \pm 0.6$  days posthatch), T.B. carried out observation sessions for 10 consecutive weeks (May–July) and then in weeks 15 (August), 20 (September) and 25 (October). Each session consisted of six 5-min observations (one per bird), three of which were made before and the remaining three during an experimentally induced feeding. The order of birds varied randomly between sessions with the restriction that those subjects that were recorded before feeding in one session were recorded during feeding in the next session of that day and vice versa. Since activity bouts of ravens were relatively short in the first few days after fledging, we started with three observation sessions per day (morning, noon, afternoon), for 5 days a week. Beginning with the third week postfledging, we conducted two sessions per day (morning, afternoon), for 4 days a week. Thus the total observation time per bird per week was 75 min in the first 2 weeks and 40 min thereafter. To control for that difference, we calculated data as mean  $\pm$  SE per 5-min focal observation. Observations were made from outside the aviary (1–2 m away from the wire partition). Feedings were carried out by a second person (M.S. & B.H.). During the first 2 weeks, birds were fed by hand. Afterwards the food (0.5–1.0 kg per feeding, depending on age) was delivered at a standard location in the aviary.

Pilot studies on adult birds revealed that fully developed caching behaviour consists of three manipulative parameters (sticking an item into a crevice or loose substrate, covering an item with substrate, gently touching the substrate above and/or around the item with the beak) and two visual parameters (laterally looking at the cache by alternating between eyes, looking up and scanning the surroundings). We recorded these behavioural elements (sticking, covering, touching; checking, looking up) independently of one another and for both object and food items. Thus, we did not measure 'caching' as a single variable but operationally referred to it when at least one of the manipulative elements (sticking, covering, touching) occurred. To contrast prefunctional and functional forms of caching, we labelled sticking movements that resulted in incomplete occlusion of an item as placement (Clayton 1992) and those that resulted in complete hiding as insertion. In addition, we estimated the distance to the bird's nearest neighbour at caching (relative to a raven's body length and/or prominent structures in the aviary) and whether the cache was visible to others. In the latter case, we were extremely conservative, counting those caches as 'not visible' only when birds fully disappeared when caching, either behind the corners of wooden niches (sections A, B) or in the visually isolated compartments of section C (Fig. 1a).

The locations of caches were recorded on predrawn sketches of the aviary complex. Birds that were subsequently approaching a cache to within 1 m and visually scanning the ground and/or digging in the substrate were operationally defined as pilferers. We recorded whether

pilferers found the hidden item (successful pilfering) and whether the storer actively protected its cache, either by interrupting caching and recovering the item before a pilferer could steal it or by retrieving the cached item after the cache was aggressively defended against the pilferer. Whenever possible, we measured the elapsed time from caching to pilfering and estimated the distance of the storer to its cache at pilfering attempts.

Observations were also carried out on the birds at KLF but with the focus being on item manipulation in general (B. Kenward, C. Schloegl, A. Weir, C. Rutz, T. Bugnyar & A. Kacelnik, unpublished data). The findings on caching behaviour (measured as a subset of object manipulation) closely matched those of the study at UVM.

## Experiments on Object Permanence

The six ravens at UVM were tested on 10 of the 15 tasks of Uzgiris & Hunt's (1975) Scale 1, i.e. on tasks 3–9 (simple hiding and successive visible displacements) and tasks 13–15 (invisible displacements; Table 1). Tasks 1 and 2 were omitted because they test for visual pursuit only. Tasks 10–14 are similar to tasks 4–8, except that the item is not in the subject's view during transfer; we omitted the first three of those tasks (10–12) to examine whether ravens could solve complex invisible displacement problems without prior experience with simpler ones and stepwise training, respectively (Pepperberg et al. 1997). The performance criteria were similar to those of previous studies with Uzgiris & Hunt's (1975) tasks in nonhuman primates (e.g. Wood et al. 1980), parrots (e.g. Pepperberg & Kozak 1986; Pepperberg & Funk 1990) and jays (Zucca et al., in press). For each task, correct multiple searches had to be done consecutively, i.e. three times in a row or, if one error occurred, five times out of six. If birds erred more than once in a session, testing was terminated for that day. If birds fulfilled the criteria for a given task, they were allowed to proceed with the next task in the same test session.

Tests were administered by two persons (T.B., M.S.) who alternated in taking the role of the experimenter (hiding an item according to the protocol of tasks) and of videotaping the bird's response. Items used for hiding were pieces of preferred food (dog food, cheese) and highly valued objects (coloured pencils, plastic spoons). They were placed on to the ground 1–2 m in front of the bird and covered with pieces of paper, leaves or bark. In the latter stages of the experiment, pieces of wood and small plastic boxes were used as screens. All cover materials were part of the aviary equipment before the experiment to temper neophobic responses. Furthermore, all covers were put in contact with food before testing to control for the possibility of olfactorial cueing. Videorecording was done from outside the aviary, 3–5 m from the bird being tested. While subjects made their choices, the experimenter was about 1.5 m from the set-up and looked at a given point of the aviary, away from the set-up, to prevent cueing via gaze direction or face orientation.

The birds were tested in the presence of their group-mates during the first 2 weeks (i.e. days 10–16 postfledging). However, testing individuals in the entire group

became more and more difficult because of interference by conspecifics. We thus stopped experiments for 15 days to allow the birds to become accustomed to temporary separation from other ravens in the compartments of section C. Before the break, we conducted tests on every fifth day. Thereafter (fourth week postfledge and later), we administered tests on average on every second day (range 1–6 days). Participation in tests was voluntary; if birds did not participate on a given day, they were tested on the next possible occasion. One male (indicated as F in Table 2) refused to land on the ground during individual separation for more than a month and thus had to be excluded from the rest of the study. Experiments were terminated in the 12th week postfledging (mid-July) because both experimenters attended scientific meetings abroad. At that time, none of the birds had successfully mastered task 15.

We used the 12 birds of the Austrian group at KLF to check for the problems encountered in the UVM study (i.e. interference by conspecifics during early tests, finishing of task 15) and to validate results obtained on object permanence. All birds of this group were habituated to individual testing as late nestlings (with temporary opaque barriers between individuals) and could be tested in physical and visual isolation almost from the beginning of the study. We administered only those tasks of Scale 1 that mark the acquisition of Piagetian Stages and/or needed replication (tasks 3, 4, 8, 9, 13–15). Furthermore, we randomly selected six or seven individuals to participate in a given task and tested birds only once per week to reduce the probability of learning across trials to a minimum. The set-up and procedure were the same as in the study in Vermont and followed the logic of Pepperberg et al. (1997). If a bird did not meet the criterion during a total of five test sessions, it was considered to 'fail' that task.

## Analysis

Since the use of caching elements (placement/insertion, touching, covering) as well as the Piagetian Stages of

object permanence developed quickly, we analysed these aspects on a weekly basis for the first 10 weeks postfledging. In contrast, we analysed the social parameters of caching (caching at a distance and behind obstacles, actively protecting caches) on a monthly basis for the whole observation period of half a year. In both cases, parameters were calculated for each individual as the average per 5-min observation session. Whenever possible we used parametric statistics; if data deviated from a normal distribution we performed nonparametric tests.

Following Kenward et al. (2006), we used general linear models (GLM) to analyse the birds' caching behaviour. We fitted GLMs with age (weeks or months postfledge) as a covariate, item type (food or object) as a fixed factor, individual identity as a random factor, and the interactions between age and item type and between item type and individual identity. Item type was set as a fixed factor because provisioning with food, and thus the opportunity to cache edible items, was dictated by the experimental protocol. Individual identity was included as a random factor to allow generalization of results beyond the observed subjects (note that here the procedure differs from that of Kenward et al. 2006). All models were implemented in SPSS 11.0.4 (SPSS Inc., Chicago, IL, U.S.A.). Alpha was set at 0.05.

To examine the improvement in caching in relation to the development of object permanence, we identified the exact days on which birds at UVM were observed to start caching (i.e. prefunctional step of placement) and to use new elements consistently (i.e. inserting, covering). Consistency in using a certain behaviour was defined as the element occurring in more than 75% of the cases. We then compared those days marking an improvement in caching with the exact days of acquisition of Stages of object permanence; for these comparisons we used a Wilcoxon signed-ranks test (within-subject design for UVM-birds) and Mann–Whitney *U* test (observational data of UVM-birds and object permanence data of KLF-birds), respectively. The between-subjects design was used because the

**Table 2.** Age (weeks postfledging) when ravens achieved Piagetian Stages and criterion on Scale 1 tasks of object permanence

Piagetian Stage	Scale 1 task	UVM-group							KLF-group			
		Individuals							Median	N	Median	Range
		A	B	F	J	V	Z					
3	3	1	1	1	1	1	1	1	3	1	0	
4	4	2	(4)	—	2	(4)	2	2	7	2	1	
5	5	4	5	—	5	5	7	5	—	—	—	
5	6	6	6	—	6	6	7	6	—	—	—	
5	7	6	6	—	6	6	7	6	—	—	—	
5	8	6	7	—	7	6	7	7	6	7	1	
5	9	6	7	—	7	6	7	7	6	7	1	
6	13	8	8	—	8	8	8	8	7	9	1	
6	14	9	10	—	10	9	10	10	6*	10	2	
6	15	—	—	—	—	—	—	—	5*	10	2	

For birds of the UVM-group ( $N = 6$ ), individual performance and median across subjects are given. Birds at KLF ( $N = 12$ ) were randomly assigned to given tasks; here, the number of subjects tested and the median and range across subjects are given. UVM-birds listed in parentheses were not tested on task 4 from the end of the second week until the end of the fourth week postfledging.

\*Data from two subjects that failed to achieve criterion on tasks 14 (one subject) and 15 (one subject) are excluded.

sample size of UVM-birds on the exact day of acquisition of Stage 4 was only three (Table 2) and thus inappropriate for using a Wilcoxon test. The exact age at acquisition of Stages 3, 4, and 5 did not differ between birds at UVM and KLF (Mann–Whitney  $U$  test: Stage 3:  $U = 14.5$ ,  $N_1 = 6$ ,  $N_2 = 3$ ,  $P = 1.0$ ; Stage 4:  $U = 16$ ,  $N_1 = 3$ ,  $N_2 = 7$ ,  $P = 1.0$ ; Stage 5:  $U = 32.5$ ,  $N_1 = N_2 = 5$ ,  $P = 0.31$ ). Since the sample size was small, all tests were calculated by hand according to Siegel & Castellan (1988). Results are two tailed and alpha was set at 0.05.

## Ethical Note

A year after this study, three birds of the UVM-group died of an unknown disease. The remaining birds were returned to the wild half a year later. During captivity, birds had ample contact with wild ravens (territorial breeding pairs and vagrant nonbreeders). B.H. received records on the released individuals (in association with other ravens) for up to 3 months after the opening of the aviary. Four months after the study in Austria, two birds of the KLF-group were killed by a marten that entered the aviary. The other birds are still at KLF and are the subjects of several studies.

## RESULTS

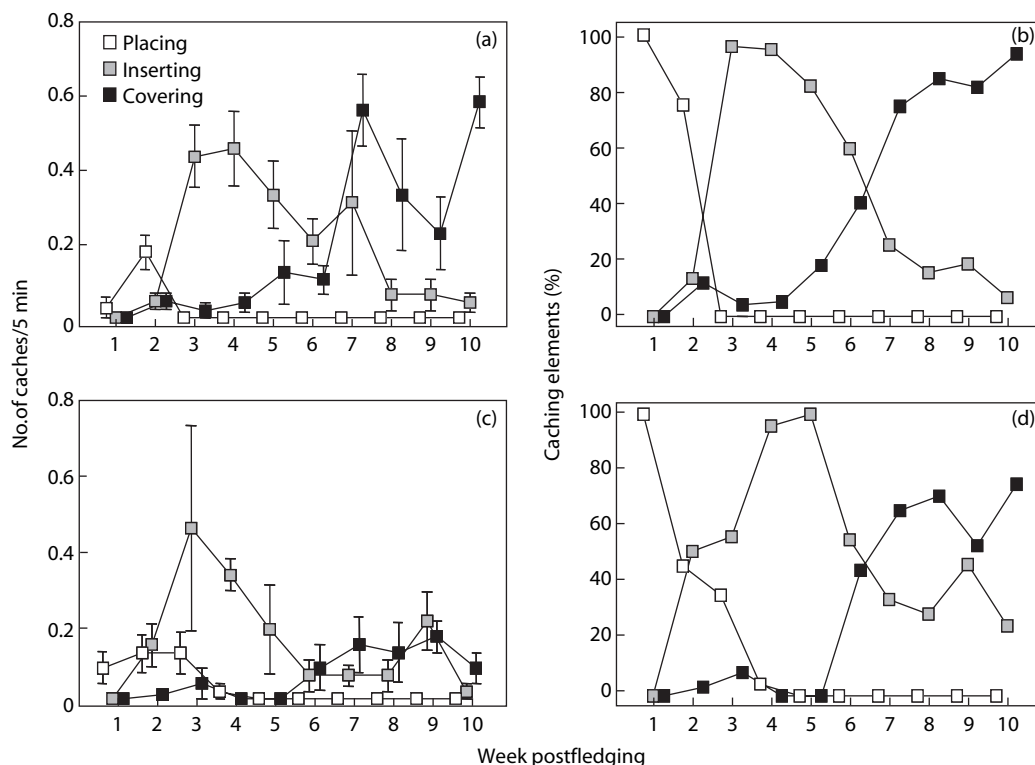
### Camouflaging Caches

The caching behaviour of juvenile ravens changed stepwise in terms of which manipulative elements were shown

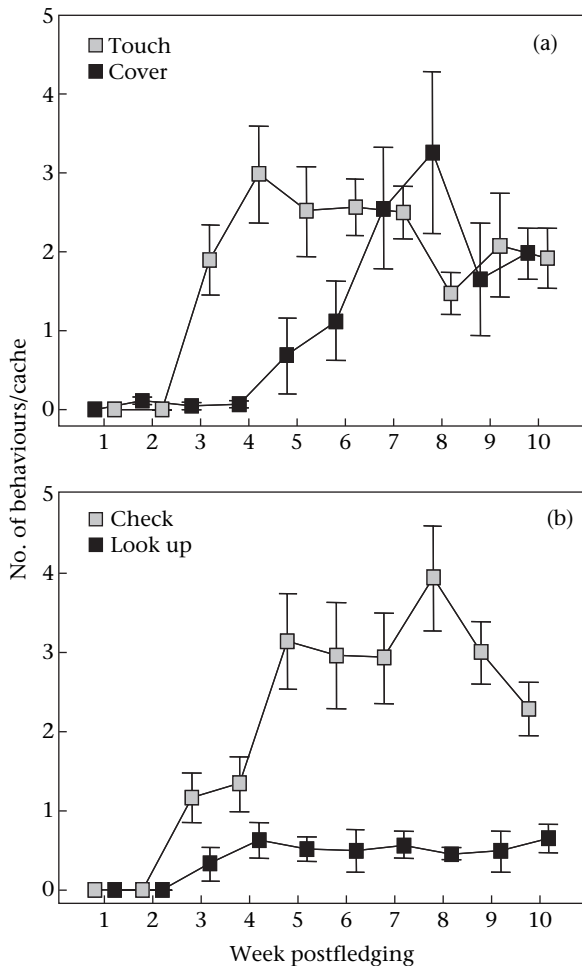
and how they were applied (Fig. 2). The relative frequency of behavioural parameters indicative of a given step was significantly affected by age (GLM: weeks postfledge: placement:  $F_{1,74} = 45.87$ ,  $P < 0.001$ ; insertion:  $F_{1,74} = 8.09$ ,  $P = 0.006$ ; covering:  $F_{1,74} = 117.55$ ,  $P < 0.001$ ) but not by item type (food or object), individual identity, and interactions age\*item type and item type\*individual identity (Fig. 2).

At first, the birds simply pressed items under or towards large objects. These placement movements were often repeated (up to 10 times) and the 'cached' item remained partially visible. This prefunctional form of caching emerged shortly after fledging (one of the six birds showed the behaviour with an object while still in the nest), lasted for a relatively short period and totally disappeared in week 3 (with food) and week 4 (with objects) (Fig. 2). As a next step, birds stuck items into small crevices and holes in solid structures or into dense grass so that the items were no longer visible. This functional form of caching started in week 2 postfledging and was predominantly shown from week 3 on with both food and nonfood items (Fig. 2). 'Insert' caching was accompanied by touching movements at the top of the caches as well as by both visual parameters, checking laterally and looking up (Fig. 3).

As a final step, the ravens consistently picked up surrounding substrate (e.g. leaves, twigs, soil) and used it to cover caches. Manipulation of substrate next to caches started with the onset of insert caching but only occasionally proceeded to lifting pieces from the ground and selectively placing them on to the items (Fig. 3a). Such directed cover movements were not manifested before



**Figure 2.** Mean  $\pm$  SE frequencies and percentages of placing, inserting, and covering behaviour for (a, b) food caches and (c, d) object caches during the first 10 weeks postfledging (May–mid-July).



**Figure 3.** Mean  $\pm$  SE number of (a) substrate manipulations (touching, covering) and (b) visual behaviours (checking, looking up) per food-caching event during the first 10 weeks postfledging.

weeks 6 and 7 for either food or nonfood items (Fig. 2). Thus, at about 2 months postfledging (i.e. end of June), the juveniles showed all the elements of adult-like caching (manipulative actions: sticking, touching, covering; visual behaviour: checking, looking up). The usage of these elements did not differ between making food or object caches (see above) but differed slightly in respect to the number of acts performed per cache (mean  $\pm$  SE number of manipulative acts: food:  $5.2 \pm 0.3$ ; object:  $4.3 \pm 0.3$ ; paired  $t$  test:  $t_5 = 3.2$ ,  $P = 0.024$ ; mean  $\pm$  SE number of visual acts: food:  $3.3 \pm 0.1$ ; object:  $2.4 \pm 0.2$ ;  $t_5 = 3.35$ ,  $P = 0.02$ ).

The stepwise improvement in caching was paralleled by the acquisition of Piagetian Stages of object permanence with a median deviation of  $\pm 5$  days. In the first week after fledging, the ravens passed task 3 of Scale 1 (Table 2) and thus possessed the ability to uncover partly hidden items (Stage 3) necessary for placement caching (age in days when birds at UVM reached Stage 3 and when they started placement caching: Wilcoxon signed-ranks test:  $T^+ = 8$ ,  $N = 6$ ,  $P = 0.69$ ). During week 2 postfledging, all birds tested at KLF and three birds at UVM passed task 4 of Scale 1 (Table 2) and thus acquired the ability to uncover fully

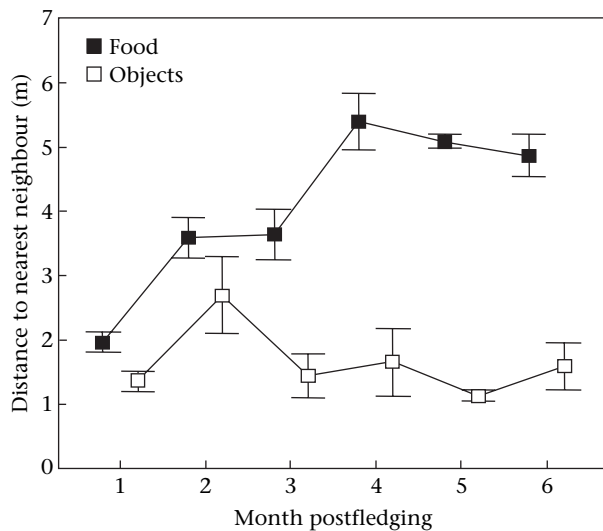
hidden items (Stage 4) exactly when insert caching emerged (age in days when birds at KLF reached Stage 4 and when birds at UVM consistently showed insert caching: Mann–Whitney  $U$  test:  $U = 49.5$ ,  $N_1 = 7$ ,  $N_2 = 6$ ,  $P = 0.29$ ). Those birds at UVM that did not pass task 4 in week 2 (which was largely due to interference by conspecifics) instantly did so after testing was resumed after a 15-day break in individual separation. However, at that time, all but one of the birds initially failed task 5 indicating that, at least until the end of week 4, ravens had problems with simple visual displacements ('a-not-b error'; Table 2).

In week 7 postfledging, birds of both groups completed the tasks of Scale 1 that indicate a fully developed understanding of visible displacements (Stage 5; Table 2). The consistent covering of caches occurred at that time and the usage of behavioural elements during caching then resembled that of adult ravens (age in days when birds at UVM reached Stage 5 and when they consistently covered caches: Wilcoxon signed-ranks test:  $T^+ = 12.5$ ,  $N = 5$ ,  $P = 0.19$ ). Within the next 3–4 weeks, most ravens also completed the tests for invisible displacement (tasks 13–15), and thus demonstrated full competence in object permanence (Stage 6; Table 2). However, in these invisible displacement tasks birds needed more errors to reach the criterion than in the tasks of visible displacements (Wilcoxon signed-ranks test on individuals' median mistakes in tasks 8, 9 and 13, 14: UVM-group: visible: 0.5; invisible: 2.5;  $T^+ = 15$ ,  $N = 5$ ,  $P = 0.06$ ; KLF-group: visible: 0; invisible: 1;  $T^+ = 21$ ,  $N = 6$ ,  $P = 0.03$ ).

### Positioning of Caches

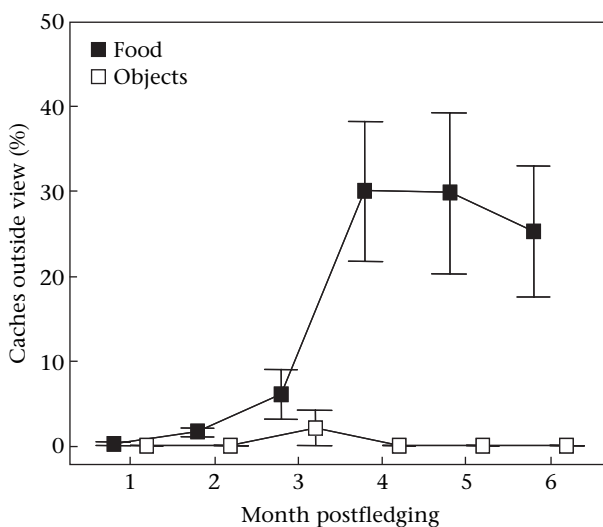
The number of both caching events and pilfering attempts increased during the first 6 months postfledging with food whereas it remained unchanged with objects (GLM: age of birds: caching:  $F_{1,58} = 15.04$ ,  $P < 0.001$ ; pilfering:  $F_{1,58} = 12.42$ ,  $P = 0.001$ ; interaction age\*item type: caching:  $F_{1,58} = 13.23$ ,  $P = 0.001$ ; pilfering:  $F_{1,58} = 7.13$ ,  $P = 0.01$ ). However, the proportion of caches that attracted pilfering attempts remained relatively stable over the whole period (with food:  $22 \pm 2\%$ ; with objects:  $35 \pm 10\%$ ) and a significant interaction effect was found only between the cache type and the birds' identity (GLM: age of birds:  $F_{1,39} = 3.94$ ,  $P = 0.06$ ; interaction age\*item type:  $F_{1,39} = 1.76$ ,  $P = 0.19$ ; interaction item type\*individual identity:  $F_{5,39} = 2.87$ ,  $P = 0.027$ ).

The storers' distance to other ravens (nearest neighbour) at caching increased with age when caching food, whereas it remained unchanged when caching objects (GLM: age:  $F_{1,58} = 13.77$ ,  $P < 0.001$ ; interaction age\*item type:  $F_{1,58} = 26.37$ ,  $P < 0.001$ ; individual identity:  $F_{5,5} = 7.56$ ,  $P = 0.02$ ; Fig. 4). Similarly, the storers' use of visual barriers against potential competitors at caching increased only when caching food (GLM: age:  $F_{1,58} = 20.91$ ,  $P < 0.001$ ; interaction age\*item type:  $F_{1,58} = 21.67$ ,  $P < 0.001$ ; Fig. 5). This increase in placing caches outside the view of others was not observed before month 4 postfledging whereas the mean distance to nearest neighbours at caching doubled in month 2 (Figs 4 and 5).



**Figure 4.** Mean  $\pm$  SE distance to nearest neighbour with food caches and object caches during the first 6 months postfledging.

Ravens also changed their responses to potential competitors approaching the caches. In the first month postfledging, storers did not attempt to hinder and/or punish pilferers. They occasionally recovered caches, but only 31% of the recoveries were a response to conspecifics showing interest in those caches. Starting with the second month postfledging, however, storers consistently protected their caches against pilfering either by aggressive defence (males: 60–80%; females: 30% of cases) or by interrupting their caching and recovering the item (males: 20–40%; females: 70% of cases). The proportion of food caches actively protected by birds per month cross-correlated negatively with the success rate of pilfering those caches in that month ( $r_{cc} = -0.54$ , lag = 0,  $P < 0.05$ ), indicating that the storers' responses to competitors coming near the caches paid off. With object caches, patterns appeared to be similar; however, we could not



**Figure 5.** Mean  $\pm$  SE percentage of food caches and object caches made behind visual barriers during the first 6 months postfledging.

carry out a statistical analysis because we did not observe the pilfering of object caches for each individual in every month.

## DISCUSSION

Based on preliminary observations on wild and captive birds (Heinrich 1999; Bugnyar & Kotrschal 2002), we predicted that skills for making caches would be primarily affected by the maturation of memory capacities for temporary not visible items (object permanence, Piaget 1937/1954), whereas the skills for the positioning of caches would be strongly affected by experience gained through social interactions. Indeed we found that the usage of behavioural elements in caching (placing and insertion of items, covering of caches) followed a linear sequence that developed in close temporal relationship to the acquisition of Piagetian Stages of object permanence. Behavioural manoeuvres to prevent pilfering (caching at a distance and outside the view of other birds, protecting caches) went along with competitive interactions over caches and were manifested only with edible items.

### Camouflaging Caches

Improvement by individuals in cache making after fledging has been reported in all of the few studies on the development of caching in birds. For marsh tits, Clayton (1992, 1994) described a short phase of 'tentative storing' (in which birds retrieve and store both food and object items several times in succession) that precedes 'true storing' (in which a food item remains in the storage site). Pollok et al. (2000) and Zucca et al. (in press) reported caching behaviour for magpies and European jays to be 'fully developed' and 'complete', respectively, about 3 weeks after the onset of its appearance. Unfortunately, neither study provided behavioural details during this transition and just defined adult-like caching, i.e. the end result of the development. Hence, our study appears to be the first to set developmental steps of caching in relation to the developmental Stages of object permanence.

Since avian food storing relies on the capacity to remember items at particular sites (Clayton & Krebs 1994; Healy 1995), a temporal link between the onset of caching and acquisition of Stage 4 competence (representation of completely hidden items) can be expected (Pepperberg & Funk 1990; Plowright et al. 1998; Pollok et al. 2000). Indeed, 'true' caching, in the sense that the cached item is no longer visible, is observed exactly at the time when ravens demonstrate Stage 4 competence. However, the basic component of caching (placement of items) is already shown 1–2 weeks earlier when birds are just capable of uncovering partially hidden items (Stage 3 competence). If one considers prefunctional sticking movements as a form of caching, then our results would fit those of Pollok et al. (2000) that 'storing' in magpies develops earlier than the competence for cache retrieval (Stage 4). Our findings suggest that the cognitive requirements for retrieving partially visible 'placement' caches would be fulfilled by Stage 3 competence or, even more

simply, by a general curiosity about half-covered items (see also Clayton 1994 for interpretation of 'tentative' storing in marsh tits).

With acquisition of Stage 4 competence, ravens also engaged in repeated lateral head movements ('visual checking' by switching between left and right eye) and, more infrequently, in taking upright positions ('looking up') during caching. Looking at the cache with either eye is known to be crucial for orientation and spatial memory in food-storing birds (Clayton 1993b), whereas looking up during foraging has been interpreted as scanning the surroundings for predators and/or conspecific competitors (Coolen et al. 2001). Thus, as soon as ravens are capable of completely hiding cached items, they perform the visual behaviours necessary for relocating the caches and appear prepared to watch out for individuals that may pose a threat to them and/or their caches.

Finally, acquisition of Stage 4 competence went together with the onset of manipulating the surroundings of caches. However, those first manipulations did not result in covering caches with material. The birds simply kept touching the top and/or immediate vicinity of caches with the beak. Directed cover movements to camouflage caches with surrounding substrate were not seen before ravens possessed full Stage 5 competence and thus were cognitively capable of handling the problems of successive visible displacements and multiple covers. Similar to magpies and jays (Pollok et al. 2000; Zucca et al., in press), ravens reached this stage before independence (which is around late July/August, Boarman & Heinrich 1999).

Like some noncaching birds such as parrots (Pepperberg & Funk 1990), ravens were capable of acquiring full Stage 6 competence in object permanence. However, the ability to follow successive invisible displacements did not develop before 10 weeks postfledging, at a time when the birds' caching behaviour had already been fully established. Possibly, these skills come as a by-product of advanced object permanence capacities (Pollok et al. 2000). Alternatively, full Stage 6 competence could be advantageous for keeping track of multiple caches made by others, and thus would be required for effective pilfering rather than for caching. Corvids are famous for their observational spatial memory allowing them quickly to find caches made by others (Bednekoff & Balda 1996a, b; Heinrich & Pepper 1998; Emery & Clayton 2001). Furthermore, multiple caching and frequent recaching have been described as countertactics against pilfering for scrub jays (Dally et al. 2005) and ravens (Heinrich 1999). Both tactics are characterized by stors moving items from cache to cache while carrying them in their beak and/or gular pouch. We hypothesize that this scenario could be functionally analogous to the implemented covering of items in Uzgiris & Hunt's (1975) object permanent tasks 14 and 15.

### Avoiding Pilfering with Food Caches Only

While skills for making caches were constantly applied to both food and object caches, the number of caching events and the positioning of caches in respect to other

ravens soon began to differ between edible and nonedible items. Rates of food caching increased during the first half-year period postfledging, whereas rates of object caching remained constant. Furthermore, food caches were increasingly placed away from conspecifics and/or behind obstacles that could obstruct the other's view; such an increase in distance and decrease in visibility to others were not found with object caches. These findings support the idea that young ravens become experienced in positioning their caches. They may use these protective skills only with valuable food items whereas the caching of objects appears to remain 'playful'.

According to Burghardt's (2005) criteria, object caching by young ravens could be interpreted as play: it has limited immediate function, differs in performance from serious (food) caching, and occurs repeatedly and voluntarily when individuals are in a relaxed or low-stress setting (i.e. outside foraging). Functionally, playing at caching with objects may allow birds to practise motor skills (Clayton 1992). In ravens, it may also serve to practise social skills (Kabicher 1996), since object caching has the potential to elicit pilfer interactions without incurring the cost of losing high-valued resources. Learning about others via play caching would explain why rates of object caching do not decline in ravens after a short period of 'tentative' storing (as they do in marsh tits, Clayton 1992) and why caching is not restricted to items that look like food (as in jays, Clayton 1993a).

Studies on the formation of dominance rank hierarchy (M. Stöwe, unpublished data) revealed that young ravens started to monopolize food and to compete over caches in June (second month postfledging). In the same month, the distance of food caches to the nearest neighbour doubled and these caches were physically protected. Apparently, young ravens quickly learned to distance themselves from others while caching and to pay attention to the others' behaviour after caching (Lorenz 1935). In contrast, it was not until late August that they used visual barriers to avoid the other individuals seeing them caching (Fig. 5). These differences in time of development could reflect limited opportunities for practising caching behind obstacles relative to caching away from other individuals. In this respect, it is noteworthy that using barriers for caching did not show any improvement over the months of study but appeared almost all of a sudden in late summer for all of the birds. Thus, we suspect that the observed differences in the development of behavioural tactics may reflect different cognitive mechanisms. Leaving the vicinity of other individuals when caching and protecting caches could be based on associative learning only, whereas avoiding being watched might require additional cognitive capacities such as an understanding of others as agents with certain qualities (e.g. acting as observer) or even as intentional beings (Whiten 1996; Tomasello & Call 1997; Call 2001b). At the age of 6 months postfledging, caching ravens demonstrated competence in using barriers to go outside the view of potential competitors in a series of experiments (Bugnyar & Heinrich 2003) and are seemingly able to take into account another individual's perspective (Bugnyar & Heinrich 2005). Around that age, ravens also become capable of tracking

the gaze direction of human experimenters behind visual barriers (Bugnyar et al. 2004; Schloegl et al. 2007).

In conclusion, our study shows that differentiating between how, where and what to cache is a useful approach for investigating the ontogeny of storing behaviour in birds. Furthermore, exact definitions of 'caching' (i.e. prestep of placement caching, functional step of insert caching or final, adult-like step of inserting and covering) appear crucial for cross-species comparison, as different developmental steps of caching may relate to different Piagetian Stages of object permanence (i.e. Stages 3, 4, 5). Further investigation of the ontogeny of tactics to prevent pilfering seems promising in respect to nonhuman complex social cognition.

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