# Report

# Ravens Judge Competitors through Experience with Play Caching

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## Summary

Complex social behavior builds on the mutual judgment of individuals as cooperation partners and competitors [1]. Play can be used for assessing the others' dispositions in humans and nonhuman mammals [2], whereas little is known about birds. Recently, food-caching corvids have been found to rival primates in their ability to judge the behaviors and intentions of others in competition for hidden food [3]. Here, we show that ravens *Corvus corax* quickly learn to assess the competitive strategies of unfamiliar individuals through interactions with them over caches with inedible items and subsequently apply this knowledge when caching food. We confronted birds with two human experimenters who acted differently when birds cached plastic items: the pilferer stole the cached objects, whereas the onlooker did not. Birds responded to the actions of both experimenters with changing the location of their next object caches, either away from or toward the humans, as if they were testing their pilfering dispositions. In contrast, ravens instantly modified their caching behavior with food, preventing only the competitive human from finding the caches. Playful object caching in a social setting could thus aid ravens in evaluating others' pilfering skills.

## Results and Discussion

Predicting others' behavior is a key element of iterated social interactions and provides the basis for any form of cooperation, competition, and culture in human and nonhuman societies [4–6]. The judgment of others as being cooperative or competitive in a particular situation can rest on experience gained from previous interactions or through observation as a bystander [7–9]. This makes sense because the others' behavior often

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depends on context [10] and does not necessarily involve honest communication [11]. In some cases, the assessment of others' disposition could even involve mental simulation [12], projecting the individuals' own experience with a situation to another individual.

Food-storing corvids possess profound knowledge about the likely behavior of conspecifics that have watched them caching [13–15], and they respond adaptively by withholding information and even providing false information [16, 17]. However, in addition to these cognitively demanding skills, corvids regularly engage in seemingly "stupid" caching of inedible items (e.g., small stones, twigs, plastic objects) [18–20]. Storing such objects hardly reflects a lack of discrimination between food and nonfood items because the storers' motivation to cache appears to be uncoupled from that of feeding [19]. Moreover, some species, such as ravens *Corvus corax*, tend to prefer caching colorful objects over those that look like food [21]. In young ravens, the caching of inedible items differs from food caching mainly in the positioning of caches relative to conspecifics: Unlike food caches, object caches are often made directly in front of conspecifics [20–22], producing a high likelihood of pilfering interactions [22]. Here, we test the hypothesis that object caching might constitute a form of social play, providing birds with an opportunity to learn about others' responses [23–25] without the costs of potentially losing valuable food.

To examine whether ravens are sensitive to information about the others' behavior during object caching (phase 1), we gave hand-raised birds the opportunity to manipulate and cache small colored plastic items (see the Supplemental Data available online for details) and then experience two unknown individuals acting differently on those caches. The pilferer (P) always stole the contents of caches, whereas the onlooker (O) approached and visually inspected caches but did not remove the hidden items (Figure 1). To assure full control over the behavior of potential competitors, P and O were human experimenters. All nine ravens participating in this study had experienced (other) humans in previous studies on gaze following and social learning, but they were naive to humans pilfering their caches. Birds were subjected to three sessions with P and with O in counterbalanced order. Sessions were carried out in groups of three birds because a social setting tempers the ravens' neophobic behavior toward unknown persons and facilitates object manipulation [26]. On the basis of our observations [20–22], we expected ravens to show interest in, rather than avoidance of, interactions over object caches with human experimenters. Birds would thus respond to pilfering and onlooking (e.g., by returning to cache sites) but remain variable in where and how they cache objects.

We then conducted the crucial test (phase 2) of whether birds could apply their knowledge gained through object caching when caching food in the presence of P or O. In situations of food competition, ravens
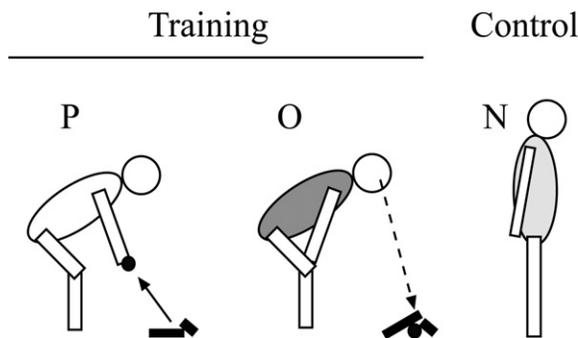
Figure 1. Sketch of the Roles of Human Experimenters

Pilferers (P) removed cached objects during training, whereas onlookers (O) did not. The solid arrow indicates the direction of removal, and the broken arrow indicates the direction of experimenter's look. As a control, nonproviders (N) visited the ravens when there were no objects to cache.

quickly start caching, scatter caches out of the sight of potential competitors, and spend some time properly camouflaging caches with loose substrate [27]. Accordingly, we predicted that birds would preferentially secure food caches from P but not from O. Furthermore, we expected them to distinguish P and/or O from another human with whom they had no previous pilfering experience (nonprovider of objects [N]). In the tests, we thus confronted birds individually with P, O, or N providing food, and we compared their behavior between these conditions. In these tests, experimenters did not respond to the birds' caching but simply took a given position in the test-compartment.

During phase 1, birds made a total of 190 object caches, of which 70 were targeted by P stealing the cached object and 88 by O looking at the cache site, respectively (median per bird with P: 8, with O: 8; Wilcoxon signed-ranks test: $T^+ = 24.5$, n = 8, tie = 1, p = 0.38; for data of individual birds, see Table 1); a further 32 caches were pilfered by conspecifics (see the Supplemental Data). All ravens were likely to inspect their cache sites if they had been subjected to either pilfering or onlooking (median with P: 68% of cases, with O: 45% of cases; $T^+ = 33$, n = 9, p = 0.25). To some extent, they also inspected caches made by others after these had been approached by an experimenter (median with P: 13% of cases, with O: 9% of cases; $T^+ = 31$, n = 8, tie = 1, p = 0.08). Thus, the birds were indeed interested in the outcome of the actions of both P and O. Interestingly, ravens showed no signs of actually modifying their cache protection strategies across sessions with P compared to sessions with O, i.e., to prevent the former from finding the objects by caching outside of the view or P or O and/or intensively camouflaging caches with the substrate (Friedman test: number of caches made outside view in sessions 1–3 with P: $\chi^2 = 3.16$, df = 2, p = 0.85; with O: $\chi^2 = 2.47$, df = 2, p = 0.29; time spent covering caches in sessions 1–3 with P: $\chi^2 = 3$, df = 2, p = 0.22; with O: $\chi^2 = 2.8$, df = 2, p = 0.25; Wilcoxon test: caches made outside view with P and O: $T^+ = 16.5$, n = 7, ties = 2, p = 0.69; time spent covering of caches with P and O: $T^+ = 22$, n = 8, tie = 1, p = 0.64; Figure 2).

In the critical food test of phase 2, ravens instantly responded differently to the presence of P and O. Not only did they start caching more quickly with P than with O (Friedman test: $\chi^2 = 6.34$, df = 2, p = 0.04), but they also placed their caches more often behind obstacles that obstructed the experimenter's view when they were with P than with O ($\chi^2 = 14.13$, df = 2, p = 0.001), and it took them a longer time to finish covering their caches with snow in the presence of P than when in the presence of O ($\chi^2 = 6.34$, df = 2, p = 0.04; Figure 2). Comparison with the control condition revealed that the ravens' behavior with N differed from that with P more than from that with O (Figure 2), indicating that our

Table 1. Behavior of Individual Birds during Training Sessions with P and O

| Individuals | Q | E | D | L | I | O | P | X | T | Sum |
|---|---|---|---|---|---|---|---|---|---|---|
| Sex | m | f | f | m | m | f | m | f | f | |
| Training group | 1 | 1 | 1 | 2 | 2 | 2 | 3 | 3 | 3 | |
| Number of Object Caches Made | | | | | | | | | | |
| with P | 9 | 10 | 4 | 18 | 16 | 3 | 10 | 8 | 6 | 84 |
| with O | 18 | 9 | 6 | 10 | 24 | 7 | 17 | 1 | 14 | 106 |
| Number of Object Caches Approached | | | | | | | | | | |
| by P | 9 | 4 | 1 | 15 | 15 | 2 | 10 | 8 | 6 | 70 |
| by O | 18 | 8 | 4 | 9 | 20 | 5 | 17 | 1 | 6 | 88 |
| Number of Caches Recovered by Storer | | | | | | | | | | |
| when P approached | 1 | 0 | 0 | 6 | 7 | 0 | 3 | 2 | 2 | 21 |
| when O approached | 10 | 3 | 1 | 1 | 7 | 1 | 6 | 0 | 2 | 31 |
| Number of Caches Inspected by Storer | | | | | | | | | | |
| after pilfering | 8 | 3 | 1 | 9 | 8 | 2 | 4 | 2 | 3 | 40 |
| after onlooking | 5 | 1 | 1 | 7 | 11 | 4 | 6 | 3 | 4 | 42 |
| Number of Caches of Others Inspected | | | | | | | | | | |
| after pilfering | 5 | 2 | 1 | 3 | 5 | 6 | 1 | 1 | 2 | 26 |
| after onlooking | 1 | 1 | 1 | 4 | 2 | 4 | 1 | 0 | 2 | 16 |

Data represent sums across sessions per condition. Individuals are ordered according to training group; "m" indicates male, and "f" indicates female.

ravens showed little effort to conceal their food caches from persons who had not been involved in interactions over object caches before.

These results support the hypothesis that object caching in a social setting aids ravens in evaluating others' likely pilfering behavior. All birds learned to discriminate between human experimenters who behaved differently toward object caches. However, this learned contingency ("P is likely to steal cached items") was only expressed during the caching of food, i.e., ravens took precautionary actions against pilfering by selectively concealing cache locations from P. This finding cannot be explained by additional reinforcement during tests with food because human experimenters never responded to the ravens' caching of food. Still, our experimental design did not control for the possibility that a relatively long-lasting acquisition of discrimination between experimenters might be confounded with the switch from objects to food. Contrary to the expectation following from this argument, the ravens' precautionary actions against human pilferers did not increase over time but rather remained constant during object caching (Figure 2). Hence, the selective cache protection instantly shown with food was probably caused by the high value of these items, and the birds' performance with food was probably the result of their previous experience with objects.

Indeed, there are two parameters indicating that ravens were capable of differentiating between P and O relatively quickly already during object caching. Both parameters feature a response to the experimenters' action: Birds tried to return to their caches and recover the objects when an experimenter was approaching (Table 1), and they changed the position of their next cache relative to the experimenter's position after they had been subjected to pilfering or onlooking. This relative change in cache position could be due to an increase or a decrease in distance to the experimenter (47% increase versus 53% decrease with P, 40% versus 60% with O). With both parameters, the response of ravens decreased significantly over the three trainings with O (Friedman test: recovery: $\chi^2 = 6.28$, df = 2, p = 0.043; distance change: $\chi^2 = 2.93$, df = 2, p = 0.009) but only marginally over the three trainings with P (recovery: $\chi^2 = 3.6$, df = 2, p = 0.17; distance change: $\chi^2 = 5.73$, df = 2, p = 0.06). In cases of distance change, the difference in response to P and O reached significance in the second session with objects (Wilcoxon test: $T^+ = 21$, n = 6, p = 0.03; Figure 3).

The ravens' reactive treatment of object caches and proactive treatment of food caches in the experiment corresponds to our observational findings that wild and captive ravens tend to allow pilfering interactions when caching objects [22], whereas they clearly avoid interactions when caching food [27]. Indeed, during phase 1, changes in the distance of cache location after pilfering or onlooking occurred roughly at the same rate in either direction, away from and toward the experimenter. The possibility that these changes are simply a byproduct of scattering caches can be ruled out because the distance of changes relative to the experimenter decreased over trials and the decline was faster with O than with P. However, the placement of object caches sometimes near to experimenters fits the idea of
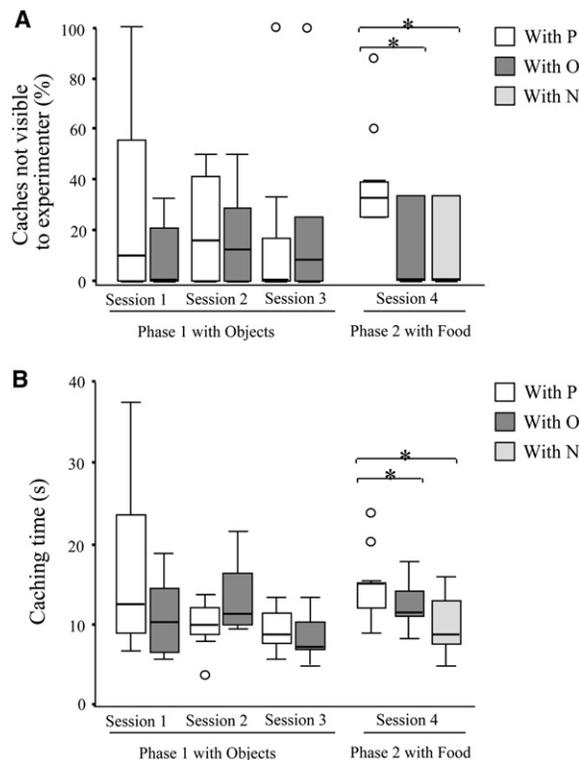


Figure 2. Effects of Experience with Experimenters on Ravens' Cache Protection Tactics with Objects and Food

The percentage of caches made outside the experimenters' view (A) and the time to cover caches with substrate (B) did not differ significantly between conditions during sessions with objects (1–3) but did differ instantly in the session with food (4): Ravens reduced the visibility of caches and prolonged the time to finish caches in the tests with the pilferer (P) compared to tests with the onlooker (O) and nonprovider (N). Box plots show the median and 25th and 75th percentiles; whiskers represent confidence intervals, and open circles indicate outliers. Significant results of post-hoc comparisons that are specific to Friedman-test are outlined above brackets ("*" indicates p < 0.05).

ravens selectively testing the response of potential competitors for their caches.

Although ravens can use object caching to involve others in interactions over caches, they do not appear to have immediate benefits from these actions. Even if they manage to keep the object, they are likely to abandon it shortly thereafter to get another one and/or engage in activities that do not include any objects at all. Playful behavior with objects in a social context has been described for several corvids [28, 29], as well as for other birds, such as babblers [30], hornbills, and parrots [31]. Similarly, the caching of objects by ravens fulfils all criteria for play [23]. It is plausible that inedible items are hidden as a function of a motivation to cache [19] rather than a motivation to play. However, when ravens cache in a social context, they clearly differentiate between food and object caches [22], indicating that they are aware of the different value of cached items and, critically, that they have different motivations to engage in interactions with others, i.e., avoid them with food versus confront them with objects. Possibly, a general motivation to cache triggers the onset of object caching that might then, in the presence of an audience,
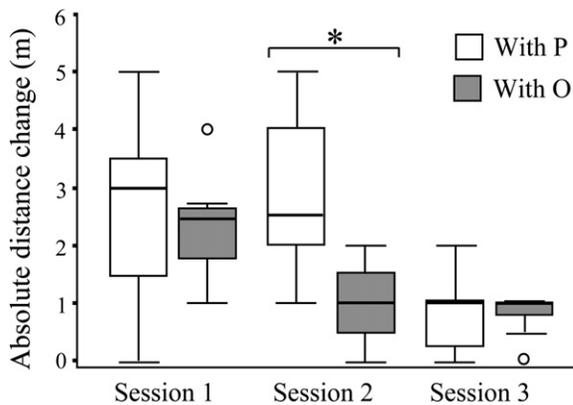
Figure 3. Distance Change in Response to Pilfering and Onlooking

After experiencing pilfering (open bars) and onlooking (full bars) of object caches, ravens placed their next object cache either away from or toward the experimenter. The absolute value of distance change decreased more rapidly across sessions with the onlooker (O) than with the pilferer (P). Box plots show the median and 25th and 75th percentiles; whiskers represent confidence intervals, and open circles indicate outliers. The asterisk above bracket indicates $p < 0.05$ (Wilcoxon signed-ranks test).

develop into social object play. From a functional point of view, learning about others via play caching would explain why rates of object caching do not decline in ravens after a short time period during development (as they do in marsh tits [32]) and why caching is not restricted to items that look like food (as in jays [18]).

Taken together, our study provides support for the idea that ravens utilize both individual and social information to quickly discriminate between human competitors who act differently toward caches. Furthermore, the study supports the idea that the item type used for caching (food or object) is of limited importance for learning the behavioral contingencies: Once the association is formed, it can be applied in the food and object context. Notably, the ravens proactively used the acquired information about the others' pilfering behavior to modify their caching behavior in the food context only. With objects, the birds did not come to adjust their caching to the competitiveness of the situation and they even appeared to stage interactions by caching close by and in full view of either of the experimenters, supporting the idea that they were playfully testing the others' pilfering behavior. Modifications of the setup (e.g., reversing conditions: training with food, testing with objects; substituting objects with nonpreferred food; including in-private trials) will be our next step in the investigation of the effects of item value and competitor assessment in detail.

Recently, corvids have been suggested to possess cognitive abilities similar to primates, including elements of a theory of mind such as mental simulation [3]. Although the current study puts the emphasis on the importance of learning about others during caching, this does not exclude the possibility that individuals might also be capable of assessing others' dispositions by projecting their own experience [3, 13] and/or that their associatively learned contingencies become represented as intervening variables coding for (some of) the others' mental states [12]. However, we argue that, in

a social setting, playful object caching sets the stage for learning about the consequences of own and others' behavior, which could, in part, explain how ravens acquire their sophisticated knowledge about competitors.

## Experimental Procedures

### Study Animals and Housing
Nine hand-reared ravens (four males, five females; all in their second year of life) served as subjects. Birds were marked with colored rings for individual identification. At the time of the study, all birds were kept together with two adult ravens in one social group in a 240 m² aviary complex situated in the Cumberland game park, Grünau, Austria. The aviary consisted of four sections arranged around a wooden observation hut. When not being tested, birds were allowed to roam throughout the complex. They had ad libitum access to water and were fed twice a day with meat, milk products, and fruit.

### Procedure
The experiment was conducted on a daily basis (about 9:00–11:00) in a 80 m² compartment of the aviary. Birds that did not participate in a given trial were temporarily refined to sections from which visual access to that compartment was blocked by the observation hut. Details of the training and test procedures (phases 1 and 2) are given in the Supplemental Data.

### Analysis
Behavioral parameters were measured from video tapes by T.B., who was blind to the experimental condition. He recorded the number of object caches made by ravens during phase 1, how many of those caches were targeted by P and O, and how many were pilfered by other ravens. For caches that were approached by P and O, he recorded whether storers came back and recovered the items before the experimenter could reach the caches and whether birds inspected caches ≤ 1 min after the experimenter had left. Inspections were defined by ravens approaching a cache targeted by P or O < ½ m and repeatedly turning the head (switching between eyes) and/or digging in the substrate with the beak; they could be directed toward the ravens' own caches and the caches made by others. During tests with food, he recorded the latency (s) to start caching, the time (s) needed to camouflage caches (cover items with substrate), and whether the caches had been reported to be visible to the experimenter. Interobserver reliability, based on coding of 20 caching events (10% of total number of caches made), was 98%, and Cohen's Kappa was 0.83.

We used Wilcoxon signed-ranks test on the sums across the sessions with P and across the sessions with O to compare the birds' behavior between conditions of phase 1. In addition, we used Friedman test to compare the behavior between the three sessions with P and O, respectively. In the tests with food, we employed Friedman test to compare between sessions with P, O, and N, and calculated by hand the multiple-comparison method that is specific to this test. For all analyses, results are given two tailed, and alpha was set at 0.05.

### Supplemental Data
Experimental Procedures, one figure, and three movies are available at http://www.current-biology.com/cgi/content/full/17/20/■■■/DC1/.

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