ANIMAL BEHAVIOUR, 2002, **64**, 185–195
doi:10.1006/anbe.2002.3056, available online at http://www.idealibrary.com on IDEAL®

Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it 'tactical' deception?

THOMAS BUGNYAR & KURT KOTRSCHAL
Konrad Lorenz Research Station, Grünau
and
Institute of Zoology, University of Vienna

(Received 29 June 2001; initial acceptance 5 September 2001;
final acceptance 24 January 2002; MS. number: 6947R)

Group-foraging ravens scatter-hoard when they are competing for food and, to some extent, also raid the caches made by others. We investigated the effects of observational spatial memory on individual caching and raiding tactics. With captive ravens, we found visual observation was essential for locating and raiding the caches of conspecifics. Both captive and free-ranging ravens, food cachers as well as potential cache raiders, responded to each other's presence. Cachers withdrew from conspecifics and most often placed their caches behind structures, obstructing the view of potential observers. Raiders watched inconspicuously and kept at a distance to cachers close to their cache sites. In response to the presence of potential raiders or because of their initial movements towards caches, the cachers frequently interrupted caching, changed cache sites, or recovered their food items. These results suggest that ravens, regardless of whether they act as cachers or raiders, are capable of withholding information about their intentions and, hence, manipulate the other bird's attention either to prevent or to achieve social-learning opportunities. Such interactions may qualify as 'tactical' deception and may have created a considerable pressure selecting for social cognition in ravens.

Caching of food may counterbalance its ephemeral occurrence or variable availability (Vander Wall 1990). However, caches may be raided. In species that form temporary foraging groups of unrelated individuals, caching could evolve only when hoarders retrieve more of their own caches than conspecific raiders (Andersson & Krebs 1978).

Food-caching animals may use a variety of protective measures to reduce the probability of cache loss (for a review see Vander Wall & Smith 1987). Among corvids and parids, food-caching birds transport food to areas where potential raiders are scarce and scatter their caches there (Vander Wall 1990). A number of studies have shown that these birds can remember the exact locations of numerous caches (e.g. Sherry et al. 1981; Vander Wall 1982; Balda et al. 1987; Kamil & Balda 1990; Healy & Krebs 1992; Clayton & Krebs 1994). In addition, experiments have shown that the use of spatial memory benefits a cacher in retrieving caches compared with a raider searching randomly (e.g. Sherry et al. 1982; Shettleworth & Krebs 1982; Kamil & Balda 1985; Brodin 1994). Hence, the chance of conspecifics finding caches would increase markedly if they could learn through observation and remember the locations of caches they have seen others make (Hampton & Sherry 1994).

Few studies have examined whether birds watch others caching and can remember these locations (for a review see Bednekoff & Balda 1996a, b). Results suggest that the spatial memory for observed caches appears to be limited, even in species that are known for their excellent spatial memory when recovering their own caches (Vander Wall 1982; Bunch & Tomback 1986; Baker et al. 1988, 1990; Hitchcock & Sherry 1995; Clayton et al. 2001). This is particularly striking because immediate cache theft may occur in almost all of the species studied (Bednekoff & Balda 1996a).

Whether or not individuals can remember caches they see others make may determine which tactic of raiding they will successfully use. In species without observational spatial memory (Bednekoff & Balda 1996a), efficient raiding is possible only in the presence of cachers and thus demands a dominant raider (e.g. Waite 1992). In species with observational spatial memory (Bednekoff & Balda 1996a, b; Clayton et al. 2001), animals can engage in delayed raiding once the cacher has left the scene.

Correspondence and present address: T. Bugnyar, Department of Biology, University of Vermont, Burlington, VT 05405-0086, U.S.A. (email: tbugnyar@zoo.uvm.edu). K. Kotrschal is at the Konrad Lorenz Research Station, A-4645 Grünau 11, Austria.

0003–3472/02/$35.00/0

Thus, this tactic may also apply to individuals with little resource-holding potential.

Ravens are opportunistic scavengers assembling in nonkin groups (Parker et al. 1994) on ephemeral carcasses or kills, but they also use food supplies, for example, in game parks or at refuse dumps (Ratcliffe 1997). By social foraging, ravens may overcome the food defence of dominant conspecifics (Marzluff & Heinrich 1991), or may increase their safety when cofeeding with potential predators, such as wolves (Heinrich 1999; Bugnyar & Kotrschal 2001). Group formation, however, may also lead to increased competition among individuals (Heinrich & Marzluff 1991). Presumably as a consequence, ravens repeatedly carry off food and scatter-hoard at a moderate distance to the communal feeding site. Thereby, they seem to optimize their individual share (Heinrich & Pepper 1998). Ravens can remember their own caches as well as those they see others make (Heinrich & Pepper 1998) and raiding caches of conspecifics is one of the tactics ravens regularly use to scrounge food from others (Bugnyar & Kotrschal, in press).

We examined the idea that cache raiding in ravens is based on social learning and memory for observed caches. We first investigated the ravens' accuracy of finding caches of conspecifics depending on the information they could acquire through observation. We then investigated whether the threat of cache theft influences the cachers' tolerance towards being watched and whether this, in turn, affects the way potential raiders observe and raid, respectively.

GENERAL METHODS

Captive Subjects

We used four zoo-bred ravens (two males, two females) who were hand-reared from 1 week after hatching to fledging in May 1995 at the Konrad Lorenz Research Station Grünau, Austria (for details see Kabicher 1996; Fritz & Kotrschal 1999). The birds had ad libitum access to water and were fed once a day. The diet consisted of various kinds of meat, milk products and fruits. In addition, the ravens fed on various kinds of invertebrates they could find in the outdoor aviary and sometimes also on mealworms, *Tenebrio molitor*, that were delivered alive. All subjects had coloured leg bands for individual identification.

Since fledging, the subjects had been in permanent contact with certain humans. They were thus undisturbed by the presence of their principal observers. All subjects appeared to cache freely during direct observation (by T.B.) and also when being videotaped. At the time of these studies, the subjects were subadult (26–40 months postfledging). They were housed in a large outdoor aviary (Fig. 1) situated in the Cumberland game park in the Austrian Alps.

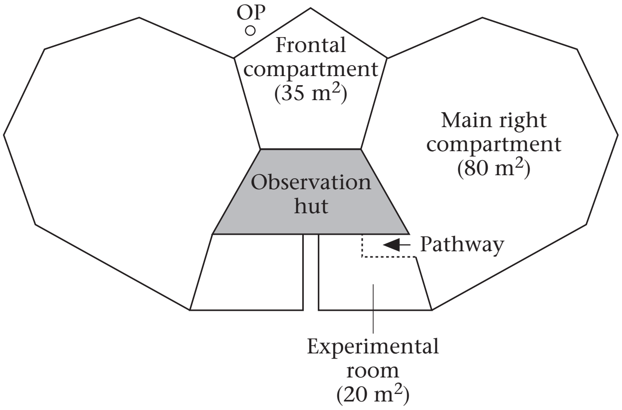

Figure 1. Map of the aviary complex. There was an opaque wall between the main compartment and experimental room. Dashed lines indicate wire mesh. OP indicates where objects were presented during distraction trials.

The aviary was divided into five compartments arranged around a wooden observation hut (Fig. 1). The two main compartments were circular tent-like buildings, 10 m in diameter and with a maximum height of 7 m. The main compartments were separated by sliding doors from a smaller compartment in the front of the complex (6.5 m in diameter, 7 m high) and two experimental rooms in the back (5 × 4 m and 3.5 m high). In contrast to the main and front compartments, which were equipped with tree trunks, rocks and natural vegetation, the experimental rooms had only fine-grained sand on the floor and a few perches. Opaque walls between the main and back compartments restricted the view into the experimental rooms from the other parts of the aviary. For the present study subjects had access to the right main compartment, the front compartment and the right experimental room (Fig. 1).

Free-ranging Subjects

The Cumberland game park in the northern part of the Austrian Alps is the year-round focus of activity of a group of 20–120 free-ranging ravens ($\bar{X} \pm SE = 35 \pm 1$). The majority are subadult nonbreeders that, together with some adult territory holders, use the park for foraging (Drack & Kotrschal 1995). Ravens snatch food at various enclosures, but are particularly active at the wolves, *Canis lupus*, brown bears, *Ursus arctos*, and wild boars, *Sus scrofa*, where food is provided either of high quality or in large quantities. Because of long-term observations, these ravens are well habituated to the presence of certain humans which makes close-distance observation (5–20 m) possible without the necessity to hide or camouflage observers or video-equipment.

At the time of our study, 25 ravens had been captured in drop-in traps baited with meat (Stiehl 1978). The trap was situated underneath trees providing shelter against hot and rainy weather. It was checked twice a day, in the morning and evening. Trapped birds were released after they were marked for individual identification. We used wing tags made of Saflag (4 × 5 cm) that were tied beside the bird's patagium and fixed with a metal rivet (for details see Kochert 1973), and a combination of two or three coloured metal leg bands (Huber 1991). We have never observed any harmful effects of the markers on ravens. Monitoring of marked individuals indicated a kind of fission–fusion organization. Ravens repeatedly joined the foraging groups at the park (median every second week), but did not stay for long periods (median 6 days; Bugnyar & Kotrschal, in press).

OBSERVATIONAL LEARNING OF CACHE LOCATION

Ravens are able to recover caches of conspecifics when present at the time of caching, but fail to retrieve artificial caches they could not see being made (Heinrich & Pepper 1998). These results suggest that finding of conspecific caches is based on social learning (local enhancement or area copying; Thorpe 1956; Galef 1988; Giraldeau 1997). However, it remains unclear which kind of spatial information is transmitted. Cache raiders may have acquired the information on the exact location through observation. Alternatively, their attention might have been focused only towards visual cues to the cache site, such as changes in the substrate's consistency. Olfactory cues might also have been used (Buitron & Nuechterlein 1985; Harriman & Berger 1986).

We aimed to determine whether ravens could find food caches more accurately after observing conspecifics during caching than when they had observed conspecifics only manipulating food and starting caching attempts in a given area, but could not see the final caching events. If cues at the cache site (either visual or olfactory) were relevant for finding the caches, we would not expect a difference in the subjects' performance depending on whether they had seen the final caching event.

Methods

We studied the four hand-reared birds from June to September 1997. Prior to the study, the subjects received individual training to cache food in the experimental room in visual and physical isolation from their cagemates. As only the two males were relaxed and continued caching during isolation, we used these two birds in alternation as demonstrators in the experiment. However, pilot studies on eight subjects revealed no sex differences in caching and recovery behaviour during daily feedings (unpublished data).

During the trials, a demonstrator was separated from its group members and let into the experimental room. There, it was allowed to cache preferred food (six slices of beef, each of about 10 g, offered at the centre of the room) in a 10-min session. During this time, the other ravens, considered as potential observers, could freely move through the main and front aviary compartments. They could also enter a pathway (1.2 × 0.9 m and 2.3 m high) that connected the main aviary with the experimental room (Fig. 1). When in the pathway, the ravens were able to observe the demonstrator through a wire mesh, whereas from other parts of the main aviary, they could not see the demonstrator.

As all subjects showed strong neophobic reactions towards both the pathway and the experimental room when the wire mesh between was temporarily covered with opaque materials, we could not conduct 'non-observation' trials in this way. Instead, potential observers were prevented from staying exclusively in the pathway and, thus, from observing the demonstrator, every second trial by two assistant experimenters offering small nonedible objects to the birds in the front compartment (Fig. 1) from the second to the 10th minute of the caching sessions. Thus, the attention of potential observers was distracted only after the demonstrator had taken the food and, occasionally, had started to cache (Table 1).

Demonstrators could not see the presentation of objects to potential observers (because of the arrangement of the aviary complex, Fig. 1), nor were they offered objects themselves. They were not prevented from creating consecutive caches and from recovering their caches. At the end of the 10-min caching session, they were transferred to the main aviary compartment. Five minutes later, the potential observers were simultaneously given access to the experimental room and could search for the hidden food in a 10-min retrieval session. Both females participated for a total of 40 trials as potential observers, whereas each of the two males had 20 trials as demonstrators and 20 as potential observers. The time between trials was at least 1 day (three to five trials per week).

The entire experiment was videotaped and the data were coded from tape by T.B. During caching sessions, we measured the location of caches relative to structures in the aviary and the time of caching events. We also noted whether caching was interrupted (caching attempt), or whether the food was retrieved from the caches by the demonstrators themselves (Table 1). In addition, we scored whether potential observers were present during caching and how much time they spent in the pathway. Instead of judging whether a bird observed the caching process, we strictly defined individuals who stayed in, or directly in front of, the pathway during caching as observers, whereas individuals who were in the main or front compartments of the aviary during caching were nonobservers.

During retrieval sessions, we measured the time (s) until the caches were found by observers and nonobservers. Caches were scored as 'found' when the ravens had recovered the food item or when they had started digging with the bill in the sand where the food had been buried (± 5 cm range) but were then displaced by a conspecific. If the caches were not found during the 10-min period, we measured the time (s) each individual spent searching for the hidden food by digging in the sand and scanning the substrate with one eye. We tested several potential observers simultaneously for cache retrieval as the two females could not be tested individually. To control for possible social-learning effects within the group of potential observers, for example local enhancement of nonobservers towards observers, we analysed only the behaviour of the bird that was at the demonstrator's cache first.

We did not simply compare 'distraction' versus 'non-distraction' trials because distractions per se did not prevent the ravens from watching the demonstrator.

Table 1. Behavioural parameters recorded in the context of food caching

Caching	Individuals drop food, put food into tiny gaps (e.g. between twigs, under stones, or in substrate), cover food with various materials (e.g. grass, branches, soil), and leave the caching site
Caching attempt	Individuals drop food and eventually cover parts of the food, but then pick the food up and leave the site
Retrieving cache	Individuals return to their cache, retrieve the food from the cache and leave with the food
Defending cache	Individuals return to their cache and threaten and/or aggressively attack conspecifics approaching the cache
Raiding cache	Individuals approach cache of conspecific, retrieve food from the cache and leave with the food and/or feed on the food
Raiding attempt	Individuals move towards cache of conspecific, but then stop and leave the site without approaching the cache and digging for food

Table 2. Behaviour of four ravens as demonstrators of caching and as observers

	Munin (*N*=20)	Hugin (*N*=20)	Wota (*N*=40)	Kaflunk (*N*=40)
Demonstrators				
Caching stopped and sites changed	3.5±0.3	4.9±0.5		
Caches finished	1.5±0.2	1.9±0.3		
Caches retrieved	0.6±0.2	0.8±0.2		
Observers				
No. of times in pathway (observation bouts)*	5.3±0.6	2.4±0.4	2.9±0.4	3.6±0.5
Bout length (s)	72±16	277±76	144±34	145±35
Present during caching attempts (%)	69	63	54	57
Present during final caching events (%)	51	60	23	50

N refers to the number of trials. Data are calculated as mean±SE/trial.

*When they were observers, individuals had to stay in the pathway connecting the experimental room with the main aviary.

Distractions, however, caused potential observers to shorten their stays in the pathway (trials with versus without object presentation: pooled individuals: χ^2_8=29.3, $P<0.001$), although their number of visits to the pathway was not affected (pooled: χ^2_8=8.6, NS). Hence, potential observers were likely to miss the final caching event during distraction trials (trials with versus without object presentation: pooled individuals: χ^2_8=27.5, $P<0.01$), although their chance of seeing the demonstrator handling food was not affected (pooled: χ^2_8=4.2, NS).

We used a χ^2 test to compare the number of caches that were retrieved by the demonstrators, and that were found by conspecifics, with regard to the presence or absence of potential observers during caching. In addition, we used Fisher's exact test to compare the behaviour of potential observers during distraction and nondistraction trials and Wilcoxon signed-ranks tests to compare the time each subject spent searching for the hidden food as observer and nonobserver. Because of the difficulty of controlling for both the number of caches observed and the number of caches to be found first, sample sizes varied for different individuals. We therefore performed separate statistical tests on each individual and then calculated pooled *P* values across all four individuals, using Fisher's method for combining probabilities with the formula $-2\,\Sigma \ln p$, evaluated in a χ^2 table with eight degrees of freedom (Sokal & Rohlf 1995, page 794; see Heinrich & Pepper 1998). All test results given are two tailed.

Results

During caching sessions, potential observers repeatedly entered the pathway into the experimental room and stayed there for variable lengths of time (Table 2). During each of the sessions, all potential observers were present in the pathway when the demonstrators handled food. Also, at least one, but often two (in 85% of cases) or three observers (72% of cases), were present when the demonstrators started caching. However, the demonstrators frequently stopped caching and changed cache sites ($\bar{X} \pm \mathrm{SE}=4.2 \pm 0.32$ times/session), so that in 10 out of 40 sessions, none of the ravens was present when the final caches were made.

In sum, the demonstrators finished a total of 69 caches, 56 in the presence of one to three observers, and 13 in the absence of any potential observers. Of the 56 caches made in the presence of other ravens, 27 were recovered by the demonstrators themselves during the caching session. From the remaining 29 caches, all were found during retrieval sessions by conspecifics that had been in the pathway during caching (Fig. 2). In contrast, none of the 13 caches made in the absence of other ravens was

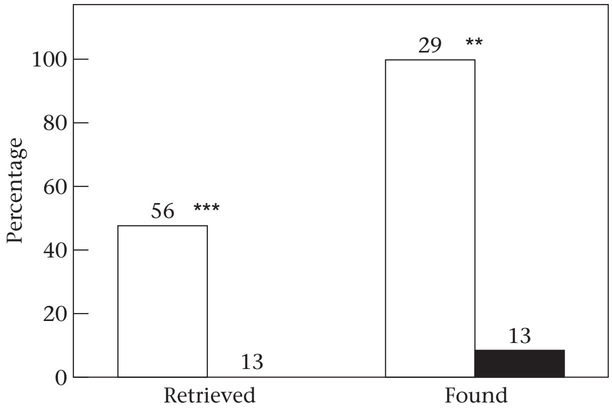

Figure 2. Percentage of caches retrieved by demonstrators and found by other ravens, dependent on the presence (□) or absence (■) of potential observers during caching. Numbers above bars indicate the total number of caches made in the presence of observers and in the absence of conspecifics. **$P<0.01$; ***$P<0.001$.

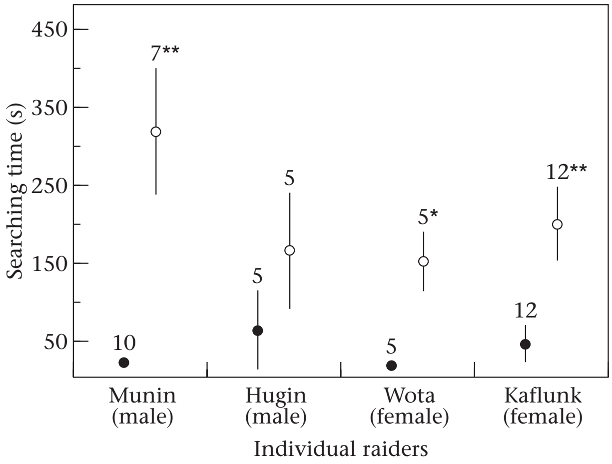

Figure 3. Effect of observation by conspecifics on time (s; $\bar{X}$±SE) ravens spent searching for caches. ●: Observers present; ○: observers absent. Numbers indicate sample sizes per individual (names along X axis). *$P<0.05$; **$P<0.01$.

recovered by the demonstrators themselves in the course of their caching sessions ($\chi^2_1=35.85$, $P<0.001$), and only one was found by a conspecific during retrieval sessions ($\chi^2_1=8.37$, $P<0.01$; Fig. 2).

All ravens moved directly to the sites where they had observed the demonstrators caching. On average, they recovered the food within the first minute of the retrieval sessions (Fig. 3). However, when the ravens had only watched the demonstrators handling food, but had not observed the final caching event, that is the location of the cache, they moved up and down the aviary, checking several locations for food by either digging with the bill in the sand or scanning the substrate by turning the head to one side. The time spent searching in these nonobserver trials was significantly longer than the time needed to find the caches in observer trials (pooled individuals: $\chi^2_8=32.2$, $P<0.001$; Fig. 3).

Discussion

Despite methodological shortcomings, such as the limited sample size and the use of distraction trials instead of an experimental manipulation of the subjects' view, our results were unambiguous. The ravens found and raided caches only when they could directly observe others caching. When they failed to observe the caching event, the ravens usually failed to find the caches, even though they were familiar with the limited general cache area (Fig. 2). This suggests that visual information on the exact location of the caches is necessary for an efficient raid and indicates that ravens primarily rely on observational spatial memory for recovering conspecific food caches, whereas visual or olfactory cues at the cache site seem to be of little importance (Heinrich & Pepper 1998).

Observational spatial memory for conspecifc food caches has been shown in only four other species, all of them corvids: pinyon jays, *Gymnorhinus cyanocephalus* (Bednekoff & Balda 1996a), Mexican jays, *Aphelocoma ultramarina*, Clark's nutcrackers, *Nucifraga columbiana* (Bednekoff & Balda 1996b), and scrub jays, *Aphelocoma coerulescens* (Clayton et al. 2001). In some of these species, the memory for observed caches seems to be limited to a few days (Bednekoff & Balda 1996a; Heinrich & Pepper 1998) which suggests that the raiding of conspecific caches could affect the foraging success of individuals only shortly after the caches were made. In jays and nutcrackers, which store thousands of seeds for several months, the raiding of caches may thus be seen as a short-term tactic which may account for only some of the losses to cachers (Bednekoff & Balda 1996a).

Ravens, in contrast, cache limited amounts of food for short periods (Gwinner 1965). Furthermore, they store food of high quality which is heavily competed for (Heinrich 1999). Thus, compared with seed-caching corvids, cache loss to conspecifics seems to impose high costs on hoarding ravens and may be highly profitable for a raider. Therefore, ravens should show little tolerance towards others during caching but be highly attracted to others for raiding (see also recent discussion for scrub jays, Emery & Clayton 2001).

In this respect, the apparent need for raiders to observe conspecifics caching has far-reaching implications. First, potential raiders must get into viewing distance of cachers. Second, cachers could decrease the raiders' success by taking precautions against being observed, for example by increasing the distance to conspecifics or by hiding from view (Hampton & Sherry 1994). If this second assumption holds, potential raiders would do best if they could watch others caching without being seen themselves. Hence, both cachers and raiders should be sensitive to the presence and attention of conspecifics either to prevent or to achieve social-learning opportunities. This kind of manipulative skill would make ravens promising candidates for tactical deception (Whiten & Byrne 1988a) in nonprimate animals.

MANIPULATION OF OTHERS' ATTENTION

Food-caching ravens may respond to the presence of potential observers in a number of ways. They may delay caching, create 'false caches' (Heinrich & Pepper 1998), recover the food and change cache site (see above). Similar findings are reported from some other species of corvids (Bednekoff & Balda 1996a; Emery & Clayton 2001) but, to our knowledge, there are no reports on the responses of potential raiders to these actions of cachers.

We focused on the behaviour of ravens during food caching and raiding. We expected both caching and raiding ravens to attempt to manipulate the attention of other birds, either to prevent opponents from learning where the caches were located (cacher's point of view) or to gain opportunities to learn socially from the cacher (raider's point of view).

Manipulation of the other birds' attention involves one individual misinterpreting a situation because of another individual's behaviour (Whiten & Byrne 1988a, b). Ravens could manipulate the attention of other birds by withholding information or by directing their attention away from the object of interest to other objects or events. In particular, we expected cachers to conceal information about the cache location. We predicted that ravens would cache as far away from the observer as possible, preferably out of sight of the potential raiders. We also expected cache raiders to conceal their intention to observe and subsequently raid caches made by other birds. As cachers may return and retrieve the food from their caches when they were clearly observed (see above), we predicted that potential raiders would actively seek opportunities to watch others caching without attracting their attention, and to delay raiding until the cachers had left the site.

Methods

Aviary studies

T.B. observed the four hand-reared birds during daily food provisioning from autumn 1997 to summer 1998. We focused on each subject in a random order for 22 feedings. Each observation lasted 30 min. Between feedings, the size of food items (one big piece or eight smaller pieces) but not the amount (1 kg) or quality of the food (meat) was varied. Differences in divisibility affected the subjects' access to food, as one piece of meat could be monopolized by one raven, whereas a number of smaller pieces could be shared by all birds through scramble competition (unpublished data). We thus created feeding situations that, like field conditions, varied the opportunity subjects had to cache food or raid conspecific caches.

During caching, we recorded the number of attempts (for definition see Table 1) and the number of caches finally made. At the moment of caching, we recorded the cache location relative to landmarks in the aviary (e.g. trees, tree trunks, rocks, walls between compartments, observation hut) and the position of the other ravens relative to the position of the cachers (distance in m, their visibility to cachers; Fig. 4). In addition, we measured the responses of cachers when conspecifics approached their caches and calculated the success rate in preventing others from raiding (Table 1).

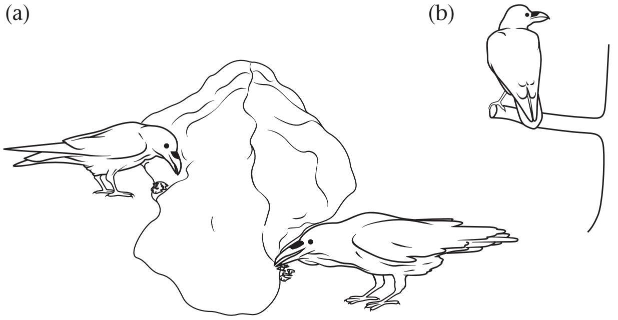

Figure 4. Sketch of ravens caching (a) out of view and (b) within sight of a potential observer (at the back).

To test whether ravens withdrew further from conspecifics during caching than during other activities, such as feeding or resting, we compared the subjects' distances to their nearest neighbours, who were not caching themselves, in these situations. To assess whether ravens used horizontal or vertical structures in the aviary (e.g. tree trunks, rocks, observation hut) to obstruct the view of potential observers, we analysed the position of the cachers relative to the structure used and the positions of other ravens relative to this structure. When the structures lay between the cachers and the other ravens, we considered the caches to be 'out of sight' because these structures then prevented potential observers from watching directly (Fig. 4). In contrast, when the caches were placed in front of the structures so that there was no visual barrier between the cachers and potential observers, we considered the caching process and the cache site to be observable by conspecifics (Fig. 4).

When focusing on cache raiders, we recorded their position during caching relative to the position of the cachers, and relative to the position of other ravens that could be in possession of food but were not caching themselves. We also noted qualitatively whether potential raiders changed their orientation towards the cachers during observation, for instance by turning their head or by moving to the top of a perch or to the edge of a tree trunk. We measured the time (s) between the departure of cachers and the first raiding attempt, as well as the number of raiding attempts, and calculated the success rate (for definitions see Table 1). In addition, we estimated the distance (m) of the cachers from their caches at each raiding attempt, and scored various types of social interactions between potential raiders and cachers returning to their caches (Table 1).

To assess whether potential raiders approached conspecifics to observe them caching, we compared their distance to cachers with the distance to their nearest neighbour involved in activities other than food caching. We also compared for each subject the observation distance to cachers when they later attempted to raid in contrast to cases when no raiding occurred.

We used Wilcoxon signed-ranks tests to compare distances between individuals during caching and raiding. In addition, we used χ^2 tests with Yates procedure (for larger sample sizes) and Fisher's exact tests (for small sample sizes) to test for differences in the ravens' performance during caching and raiding. Sample sizes varied for different individuals because the number of caches made and the number of raiding attempts differed between birds. We therefore did separate statistical tests on each individual and then calculated pooled *P* values across all four individuals, using Fisher's method for combining probabilities ($-2\ \Sigma \ln p$), evaluated in a χ^2 table with eight degrees of freedom (Sokal & Rohlf 1995, page 794). All test results were two tailed, and were obtained by SPSS and SsS statistical software.

Field observations

Parallel to the aviary studies, we observed ravens foraging in the deciduous–conifer woodland in and around the Cumberland game park from autumn 1997 to spring 1998. T.B. made opportunistic observations on caching and raiding events of both marked and unmarked ravens that were within his sight. Rather than following the ravens by walking, T.B. used binoculars (Swarowski Habicht SLC 10 × 42 WB) to keep track of individuals leaving the feeding sites for caching. Observation positions on top of small hills around the enclosures of wolves and wild boars allowed a relatively wide view over parts of the valley, particularly during winter when trees were devoid of leaves. Maximum observation distance was ca. 300 m. When wolves were fed, ravens sometimes not only raided conspecific caches but also those made by the wolves.

We recorded the same parameters from the wild ravens as during the aviary study. However, the majority of these records were less exact. For instance, distances between cachers and potential observers were estimated at a rank level (<3, 3–10, >10 m). In addition, we often saw raiders only just before a raiding attempt and thus could not observe their previous behaviour, that is during the time they probably observed caching.

Results

Aviary studies

As predicted, caching ravens withdrew from conspecifics. Subjects were significantly further from their nearest neighbours during caching than during other activities, such as feeding or resting (pooled individuals: $\chi^2_8=50.7$, $P<0.001$). In addition, the ravens most often cached close to large objects, such as tree trunks or rocks (caching <0.5 m beside an object versus >0.5 m away from objects: pooled: $\chi^2_8=92.1$, $P<0.001$). These objects were between their caches and potential observers in ca. 80% of cases (Fig. 5). Thus, the ravens cached significantly more often outside than in the view of other ravens (pooled: $\chi^2_8=112.5$, $P<0.001$; Fig. 5). When potential observers moved towards cachers, they always interrupted the behavioural sequence of caching (see Table 1) and changed sites in all 26 observed cases (Table 3).

Food cachers still paid attention to conspecifics when they had finished caching and had left the cache site. In about two-thirds of cases, they rushed back to their caches in response to conspecifics approaching these sites (Table 3). When the cachers arrived there ahead of the potential raiders, they successfully prevented about two-thirds of raiding attempts, by aggressively chasing conspecifics, or by retrieving the food first, or because potential raiders simply stopped their attempts as soon as the cachers were at their caches again (Table 3).

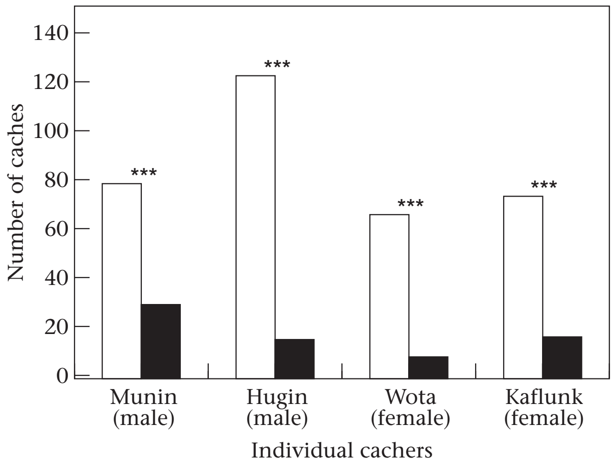

Figure 5. Total number of caches made beside objects, with the view of potential observers towards the cacher obstructed (□) or not obstructed (■). ***$P<0.001$.

When ravens observed other's caching food, they changed position relative to structures that could obstruct their view in 33% of cases, for example they went to the edge of a tree trunk, jumped on to a rock, or perched. In another 32%, potential observers did not change position, but showed distinct orientation movements of either body or head. Thus in 65% of cases, a response of a potential raider to the caching action could be observed. However, despite this interest in cachers, raiders kept their distance while these were caching (Table 3). As predicted, there was no difference in the distance to cachers between ravens that subsequently attempted to raid these caches and ravens that did not (pooled individuals: $\chi^2_8=9.46$, NS). In addition, a subject's distance to a food cacher did not differ whether it subsequently raided or not (pooled: $\chi^2_8=11.74$, NS).

As predicted, the ravens delayed their raiding attempts and did not approach as long as the cachers were close to their caching sites. On average, the first raids occurred between the first and second minute after the cachers had left (Table 3). The first attempts also occurred more often when the cachers were more than 3 m from their caches than when they were within 3 m (pooled: $\chi^2_8=96.97$, $P<0.001$). In addition, the ravens were more successful at raiding when the cachers were more than 3 m away (pooled: $\chi^2_8=24.57$, $P<0.01$; Fig. 6). This was particularly true for raiding by the two females (Fig. 6), who were subordinate to males and therefore likely to be chased away from the caches (Table 3).

Potential raiders instantly stopped orienting towards the caches when cachers interrupted caching (in all 26 cases). They also instantly stopped their raiding attempts and moved off in other directions in about half the cases when cachers had returned to their caches (Table 3).

Table 3. Behaviour of captive ravens during caching and raiding

	Munin (male)	Hugin (male)	Wota (female)	Kaflunk (female)
Caching				
Caching interrupted/stopped	0	2	13	11
Food retrieved and site changed	22	15	23	36
Caches finished	119	146	86	102
Target of raiding attempts	74	53	20	24
Return to caches	59	25	14	18
Aggressive displays towards potential raiders	23	7	2	0
Food retrieved before potential raiders arrived	0	1	2	7
Potential raiders stopped without interaction	28	10	5	3
Raiding prevented (%)	86	72	64	55
Raiding				
Time (s) to first raiding attempt ($\bar{X}$±SE)	83±20	137±17	108±11	89±13
Raiding attempts made	27	54	57	47
Returns of cachers	5	21	28	26
Raiding attempts stopped by aggression from cachers	0	5	4	7
Raiding attempts stopped by return of cachers	3	7	21	19
Raiding successful (%)	89	78	56	50

Unless otherwise stated, data refer to total numbers/observation period.

However, in 11 of 50 cases the ravens immediately returned to check these caches as soon as the cachers had left a second time.

Field observations

For consuming and manipulating food, the free-ranging ravens frequently perched close to the feeding site (at the wolf enclosure $\bar{X}\pm\text{SE}=3.1\pm0.2$ ravens/min out of 16.4 ± 0.6 ravens/min in the surrounding trees). In contrast, ravens left the feeding site for caching. Of the 112 cachings observed, only two (2%) were made within 10 m of the feeding site, 69 (62%) between 10 and 60 m, and 41 (36%) between 60 and 250 m. In addition, 86 of the caches (77%) were more than 10 m from the nearest visible neighbour. In 88 cases (78%) ravens stored food next to structures such as rocks, trees or in dense vegetation. Only 23 caches (22%) were made in highly visible places such as open meadows. Whether the ravens placed the caches away from potential observers could not be evaluated, as the objects and vegetation restricted the view of the human observer.

As in the aviary, ravens always changed site when they were approached by a potential raider (in all eight observed cases). Once the cache was finished, potential raiders in the wild kept their distance to the cachers as long as these were at the site and only attempted to raid 1 ± 0.2 min ($\bar{X}\pm$ SE) after the cachers had left. Only three of 12 raiding attempts (25%) were successful when cachers were still within 10 m of their cache, compared to 15 successful raids out of 24 attempts (63%), when the cachers were further away (χ^2_1=4.6, P=0.07). In 18 of 42 cases (43%), cachers returned to defend their cache or to retrieve their food.

Despite the danger involved (16 ravens were killed in the wolf enclosure in 1997–1999), wild ravens were observed 32 times to raid caches made by wolves. Wolves attacked ravens on nine of these occasions. As in caches made by conspecifics, ravens waited to approach the wolf caches until the owners had moved away some distance. However, in contrast to conspecific cache raiding, potential raiders perched directly above the cache locations while the wolves were still there. In contrast to ravens, wolves never interrupted caching when potentially raiding ravens were present.

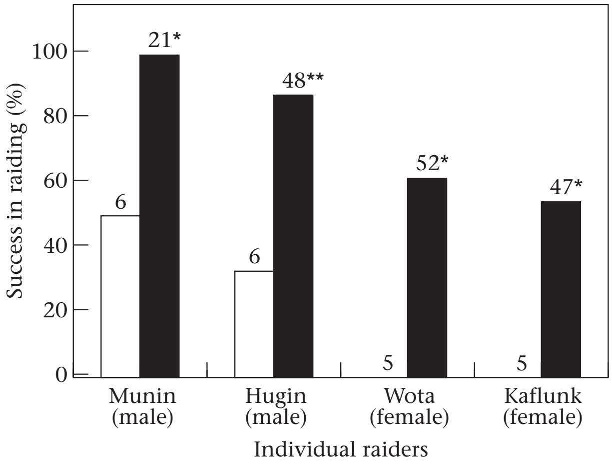

Figure 6. Raiding success (%) of individuals in relation to the distance to the cachers. ☐: <3 m away; ■: >3 m away. Numbers above bars indicate the number of raiding attempts. *$P<0.05$; **$P<0.01$.

Discussion

These observations indicate that wild and aviary-kept ravens are sensitive to audiences during both food caching and cache raiding and that they adjust their behaviour accordingly. Thereby, ravens are seemingly able to manipulate the attention of conspecifcs, mainly by withholding information (Whiten & Byrne 1988a, b; Semple & McComb 1996).

Ravens appear to conceal information on cache location by caching behind large objects. Obstructing the view of potential observers may be particularly useful when escape from competitors is not entirely possible, as is usually the case in aviaries. However, situations similar to the aviary may also occur in the field. For instance, when individuals hurry to get their share of the limited supply of high-quality food at the game park, they may cache close to the feeding sites rather than make long caching trips because this would constrain the number of consecutive loads they could carry off. By caching near the food source, however, ravens are likely to encounter others, but by using natural objects as obstacles they may reduce the risk of being observed. None the less, our limited data do not allow us to exclude the possibility that the observed caching pattern is a side-effect of the birds' preference for caching beside landmarks (Vander Wall 1982).

Cache raiders, in contrast, appeared to conceal their intentions by acting cautiously during observation and by using the information gained on cache location only after the cachers had left. As ravens cannot guard their stores for long, because this would again constrain the number of consecutive caching trips, potential raiders normally had to wait just a few minutes for the cachers to leave. Nevertheless, raiders sometimes approached the caches too early. This suggests that the ability to judge the most efficient time lag for a successful raid may be shaped by individual experience. This may be particularly true for subordinate individuals, who face the risk of being punished by the cacher. Nevertheless, it may also apply to dominants, as they will lose their chance of raiding if the cacher retrieves the food first.

In contrast to the raiding of conspecific food caches, ravens did not appear to conceal their intentions when going to raid caches made by wolves. In the game park, the wolves did not alter their caching behaviour when ravens were present. Nevertheless, they attacked ravens stealing food from their caches. Thus, by raiding caches of wolves, the challenge for ravens may be to avoid being attacked, rather than not to be seen at all.

GENERAL DISCUSSION

Even though individuals of a number of food-storing species may alter their caching behaviour in the presence of conspecifics (e.g. Stone & Baker 1989; Waite 1992; Brodin 1994) to avoid having their caches raided (e.g. James & Verbeek 1983; Petit et al. 1989; Hitchcock & Sherry 1995; Lahti et al. 1998; Clayton et al. 2001), this is, to our knowledge, the first study to demonstrate countertactics on either side, cachers and raiders. Having the capacity to remember the caches of other individuals allows ravens to delay raiding and thus applies not only to dominants but also to birds that are temporarily excluded from feeding by social means (Heinrich & Pepper 1998). The raiders' need to observe other individuals caching, however, may force cachers to take care where (and possibly also when) they cache and to respond adequately to the other individual's behaviour (Heinrich 1999; see also Clayton et al. 2001; Emery & Clayton 2001). This, in turn, may put pressure on raiders to take precautions against being noticed by cachers. Hence, this competitive game for food may fuel an intraspecific evolutionary arms race for deceptive and cognitive abilities (see also Whiten 1996).

With regard to the cognitive mechanisms involved, our findings still allow for different interpretations (Premack & Woodruff 1978; Cheney & Seyfarth 1990). The behavioural adjustments of caching and raiding ravens may be strongly genetically determined (zero-order intentionality; Dennet 1987). This, however, seems unlikely because it does not permit the flexibility observed in their interactions. Individuals responded slightly differently to opponents (Table 3, unpublished data) and to use different tactics depending whether they raided caches of other ravens or wolves. Individuals also made mistakes, which strongly points to the importance of learning. A possible explanation would be that ravens acquire an 'understanding' of their behaviour (first-order intentionality, Dennett 1987; see also Heyes 1998). Scrub jays relate information about their previous experience as a raider to the possibility of their own caches being raided, and modify their caching tactic accordingly (Emery & Clayton 2001).

In addition to learning, ravens may fine-tune their specific interactions by knowing what others see or intend (second-order intentionality, Dennett 1987; theory of mind, Premack & Woodruff 1978). Cacher–raider dyads, except in the aviary, hardly ever consist of the same individuals in consecutive events and behaviour varies individually (unpublished data). This would punish ravens that play this interactive cacher–raider game by the rules and would benefit individuals who were better than their opponents at attending to the other's mental state (Whiten & Byrne 1988a; Tomasello & Call 1997). Chimpanzees competing for food, for example, attribute knowledge to others (Hare et al. 2000, 2001). Testing for the cognitive mechanisms involved in raven cacher–raider interactions will be our next step.

Acknowledgments

The study was financially supported by FWF-project P12472-BIO, by the 'Cumberland-Stiftung', and the 'Verein der Förderer'. T.B. is supported by a postdoctoral fellowship of the K. L. I. Altenberg. We thank H. Pechlaner and D. Schratter from the Vienna Zoological Garden for the donation of ravens, the Cumberland game park Grünau for permanent support, and H. Lindner, P. Winkler, G. Steinmaurer and A. Buchegger for their cooperation. We are grateful to N. Clayton, J. Daisly, J. Dittami, J. Fritz, G. Gajdon, L. Huber, M. Kijne, M. Stöwe, A. Tschudin and B. Zisser for comments and J. Engels, A. Jüte and A. Tschudin for statistical help. E. Buchner, E. Ellis and C. Ilk provided assistance during distraction trials.

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