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Leading a conspecific away from food in ravens (*Corvus corax*)?

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Abstract Active misleading of conspecifics has been described as a social strategy mainly for primates. Here we report a raven leading a competitor away from food in a social foraging task. Four individuals had to search and compete for hidden food at color-marked clusters of artificial food caches. At the beginning of the experiment, a subordinate male found and exploited the majority of the food. As a result, the dominant male displaced him from the already opened boxes. The subordinate male then developed a pattern, when the loss of reward to the dominant got high, of moving to unrewarded clusters and opening boxes there. This diversion often led the dominant to approach those unrewarded clusters and the subordinate then had a head start for exploiting the rewarded boxes. Subsequently, however, the dominant male learned not to follow the subordinate to unrewarded clusters and eventually started searching for the reward himself. These interactions between the two males illustrate the ravens' potential for deceptively manipulating conspecifics. We discuss under which circumstances ravens might use this capacity.

Keywords Misleading · Deception · Raven · Social foraging

Introduction

Foraging animals inevitably provide a variety of behavioral cues, such as head position or frequency of feeding bouts, that may be used by conspecifics to judge the abundance, location, or quality of a food source (review in Galef and Giraldeau 2001). Exploiting this “public information” (Valone 1989) benefits receivers as it increases foraging efficiency through social learning and/or scrounging (Giraldeau and Caraco 2000). However, if the exploitation imposes substantial costs to senders, these may develop strategies to withhold information or even provide false information (e.g. Dawkins and Krebs 1978).

At the behavioral level, deception thus constitutes the misinterpretation of situations by one individual as a consequence of the acts of the other individual (for definitions see Krebs and Dawkins 1984; Byrne and Whiten 1985; Mitchell 1986; Whiten and Byrne 1988). This operational concept refers to a variety of responses (Semple and McComb 1996) that range from species-typical patterns given in a certain context, like the feigning of injury by ground-nesting birds (e.g. Ristau 1991) or the false alarm calls of sentinel birds in mixed-species foraging flocks (Munn 1986), to a broad range of diverse behavioral patterns that are used very flexibly in different situations, as is reported for some species of primates (review in Byrne and Whiten 1990; Tomasello and Call 1997).

At the cognitive level, types of deception refer to different mental processes that are supposed to underlie the responses (Premack and Woodruff 1978). Aside from the possibility that the deception may be the result of pre-programmed responses (zero-order intentionality), the critical question here concerns the intention of the deceiver, whether to affect the other's behavior (first-order intentionality) or the other's mind (second-order intentionality, Dennett 1988; for a different taxonomy of levels see Mitchell 1986). A representation of states in the physical world, like the location of food or the fact that in a given situation some conspecifics are very likely to behave in a particular way, would be a sufficient cognitive framework

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for creating acts to alter the behavior of others (e.g. Heyes 1998). In contrast, for altering the mind of others, individuals must be aware of the perceptions of others, that is, to know what others see (e.g. Cheney and Seyfarth 1990a, 1990b). To date, there is little evidence that nonhuman animals are capable of mental perspective taking, that is, understanding that others have beliefs and desires (theory of mind, Premack and Woodruff 1978), but there are some persuasive examples of visual perspective taking (e.g. Byrne and Whiten 1990, 1992; Povinelli 1993; Tomasello et al. 1999; Hare et al. 2000). In addition, attempts have been made to specify cognitive abilities (i.e. the abilities to understand that conspecifics are manipulable and to flexibly inhibit normal behaviors) that may underlie the transition from first- to second-order intentionality (building blocks of deception, Güzeldere et al. 2002; see also Whiten 1997).

In practice, it is difficult to distinguish between different orders of intentionality, as acts carried out to affect the beliefs of others do not look any different from acts that affect merely the others' behavior (Premack 1988). As a consequence, most experiments on nonhuman animals have focused on attributional capacities (e.g. Premack and Woodruff 1978; Cheney and Seyfarth 1990a; Povinelli et al. 1991; Povinelli and Eddy 1996; Hare et al. 2000, 2001) rather than directly on intentional deception (Woodruff and Premack 1979; Kummer et al. 1996; Mitchell and Anderson 1997; Fujita et al. 2002). Few studies have examined deceptive abilities under group foraging conditions, for example, by selectively informing particular individuals about introduced goal objects (Menzel 1974; Coussi-Korbel 1994; Deaner 2000; Hirata and Matsuzawa 2001; Held et al. 2002).

To date, primates have been considered as primary candidates for intentional deception (e.g. Whiten and Byrne 1988; de Waal 1992) because their complex social life (Humphrey 1976) creates ample opportunities in which it would pay to conceal information, to distract the others' attention, or to use others as social tools. Although it is debated whether these interactions, which are subsumed under the term tactical deception (Byrne and Whiten 1985; Whiten and Byrne 1988), are based on some kind of knowledge attribution to others (e.g. Bernstein 1988; Heyes 1993, 1998), the behaviors involve cognitively demanding tactics in which one individual attempts to manipulate others (Byrne and Whiten 1992; Tomasello and Call 1997). Species other than primates who also live in a complex social environment have received comparatively limited attention (but see Held et al. 2000, 2002).

We here report the deceptive behavior of a common raven (*Corvus corax*) in a social foraging task. Subadult ravens had to search for food at color-marked clusters of artificial food caches and to exploit the rewarded cluster in interaction with their siblings. The goal of the experiment was to examine the subjects' preferences for asocial learning, social learning, and scrounging. From the onset of the experiment, however, a game between two individuals became apparent: the dominant male specialized in following and exploiting the subordinate male. This article focuses on the tactics developed by the subordinate in

response to the social constraints exerted by the dominant. The precise use of these tactics and their effects on the behavior of the dominant bird during two phases of the experiment are described.

Methods

Subjects and setting

Subjects were four zoo-bred ravens (two males, Hugin and Munin; and two females, Wota and Kafunk) that 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 and Kotrschal 1999). The birds were fed on a mixed diet including insects, various kinds of meat, milk products, and fruits. They were marked with patagial wing tags and colored leg bands for individual identification. The primary subjects of this report are the two males. At the time of the study, they were subadult (15–20 months post-fledging).

Birds were housed in a large outdoor aviary situated in the Cumberland game park in the Austrian Alps. The aviary is divided into five compartments that center around a wooden observation hut. The two main compartments are circular tent-like buildings, 10 m in diameter and with a maximum height of 7 m. Main compartments are 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 (5×4×3.5 m). The main and frontal compartments are equipped with tree trunks, rocks, and natural vegetation and are aligned to the view of game park visitors. The experimental rooms are visually isolated from the exhibition part by wooden walls and contain only a floor of fine-grained sand and a few perches. For the present study, subjects had permanent free access to the right main compartment and, during tests, to the right experimental room (Fig. 1).

The study ran from July to October 1996. Typically, the birds were tested three to four times a week, with three consecutive trials per day. To familiarize the ravens with the test procedure, pre-experiments were carried out in June 1996. Experiments were divided into two phases of 18 and 17 days, respectively. Between these phases, the female Kafunk received additional training for 5 days. During both phases, behavioral protocols (i.e. approach–retreat interactions, contact sitting and preening) were taken for 20 min before and after the daily experiments to determine the social dynamics among subjects. On day 2 and day 9 of the first

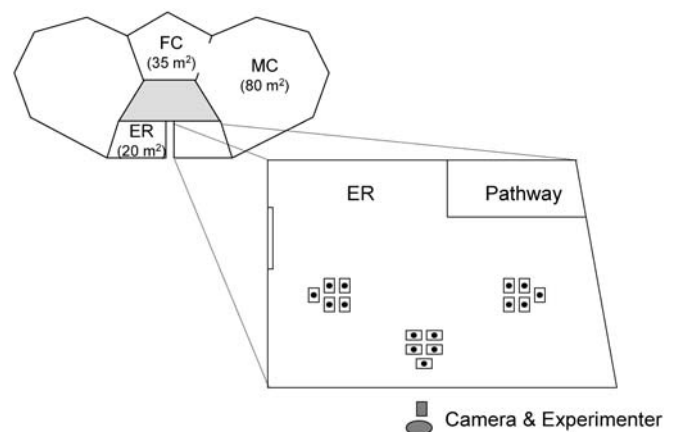


Fig. 1 Sketch of aviary (FC frontal compartment, MC main compartment, ER experimental room) and experimental set-up, showing clusters of color-marked boxes presented in a semicircle at the bottom of the experimental room

block, birds finished only two and one of the total of three consecutive trials, respectively, because of a sudden onset of work activities in the surrounding game park area.

Apparatus and procedure

Fifteen plastic boxes (Kodak film boxes, 3 cm in diameter and 5 cm high) covered with gray lids served as standardized artificial food caches. Boxes were fixed separately on wooden boards (15×12 cm) and marked on their sides in red, yellow, or blue (five boxes/color). Boxes of the same color were arranged in clusters (~10 cm distance between boxes). Clusters were presented on the ground of the experimental room in a semicircle (Fig. 1).

In the pre-experimental period, subjects were trained to open the lids of the boxes to obtain highly preferred food (three pieces of cheese/box, of about 5 g/piece). During training, none of the boxes were color-marked (i.e. they remained black) and the ravens got rewarded for all openings. During the experiment, however, only the boxes of a particular color contained food (same amount and size as in training period) and the ravens had to search for this reward. The color but not the location of the rewarded cluster remained constant over three consecutive trials per day. Between days, the rewarded color changed in random order. Thus, the ravens would do best by following the rule “look for the rewarded color in the first trial and then consistently choose this color for the rest of the trials on that day”.

Boxes were provisioned inside the observation hut in visual isolation from the ravens. For positioning the clusters in the experimental room, the birds were locked in the main aviary compartment. A trial began with opening the door to the experimental room (so that the birds could walk and/or fly into the room one after another in an order chosen by themselves; mostly the dominant birds were first) and ended after the 15 boxes had been uncovered (mean±SD: 50±36 s). If the boxes remained covered for more than 2 min after the correct cluster had been exploited, the trial was also terminated (terminated trials, $n=28$).

Data collection and analysis

The entire study was video-taped (Sony DCR-VX 700E) and data were coded from the tapes. At the beginning of a trial, the position of each subject was noted as <0.5 m from the entrance, >1 m away from clusters, <1 m from left, middle, or right cluster, or at a particular box of the left, middle, or right cluster. Consequently, data were coded as a stepwise change of these positions. Thus, when a subject moved to or from a cluster, between clusters, or even between the boxes of a cluster, its new position was measured together with the position of the other group members. At each position, the subjects' behavior was recorded in terms of *opening lids* (attempting to find food), *scrounging* (attempting to feed on food of boxes opened by conspecifics), and *approach-retreat* interactions. Scrounging could occur either by *displacing* others from the box or by quickly *stealing* pieces out of the box. Retreats could oc-

cur right at the encounter with a conspecific or after the subject was threatened or even punished (*forced* retreat).

The subjects' success was measured in terms of cheese pieces gained per trial. This could be the result of both the subjects' efficiency in searching for the rewarded cluster and the efficiency in exploiting conspecifics. In cases of a subject searching for the reward, its efficiency was calculated as the number of opened boxes until the first rewarded box was found per trial (for only those trials in which the subject was first at the rewarded cluster). In addition, the relative frequency of each subject being first at the rewarded cluster was calculated over all trials per experimental phase. The subjects' efficiency in exploiting others was calculated as the proportion of successful scrounging attempts relative to the total number of scrounging attempts.

To analyze the subjects' performance over the course of the experiment, we calculated the behavioral categories as means (±SD) of the daily trials. This allowed us to control for the effects of asocial learning of the rewarded color *within* the trials of a day (birds were generally faster in finding the correct cluster on the second and third trial/day). Specifically for the two males, Munin and Hugin, we used logarithmic regressions to analyze the improvement in a given behavior (i.e. searching for the reward and following a conspecific) over the course of the experiment. In addition, we used cross-correlations to analyze (a) the effects of the interactions with Munin on Hugin's use of deceptive tactics (i.e. moving to unrewarded clusters) and (b) the effects of the interactions with Hugin on Munin's use of counter-tactics (i.e. not following to unrewarded clusters) over the days in the experiment. This procedure allowed not only the correlation of the data of the same point in the time series (days in the experiment) but also the correlations with lags of 1, 2, or more days (Schlittgen and Streitberg 1995). Only correlations between lags with $P<0.05$ are mentioned in the results. For a comparison of a subject's behavior between different situations (e.g. with and without Hugin's moves) as well as between the two phases of the experiment, we used a Wilcoxon signed ranks test. For the within-subject comparisons, the significance level was set at $\alpha=0.10$. All test results are given as two-tailed.

Results

Days 1–18

Overview of the group's behavior

Although all subjects were able to open lids from the onset of the experiment, only two actually did so during this phase of the study. The subordinate male Hugin uncovered 67% of all boxes per trial (mean±SD: 4±1 rewarded boxes, 6±3 unrewarded boxes/trial; Fig. 2a). He was the first at the rewarded cluster in 82% of the trials. In searching for the rewarded boxes, Hugin quickly learned not to

Fig. 2 Opening and scrounging attempts of subjects (mean±SD number per trial) during the first (a) and second (b) phases of the study

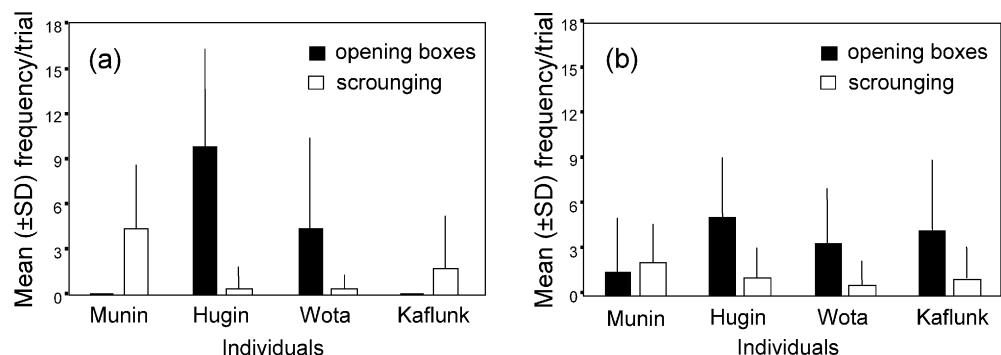
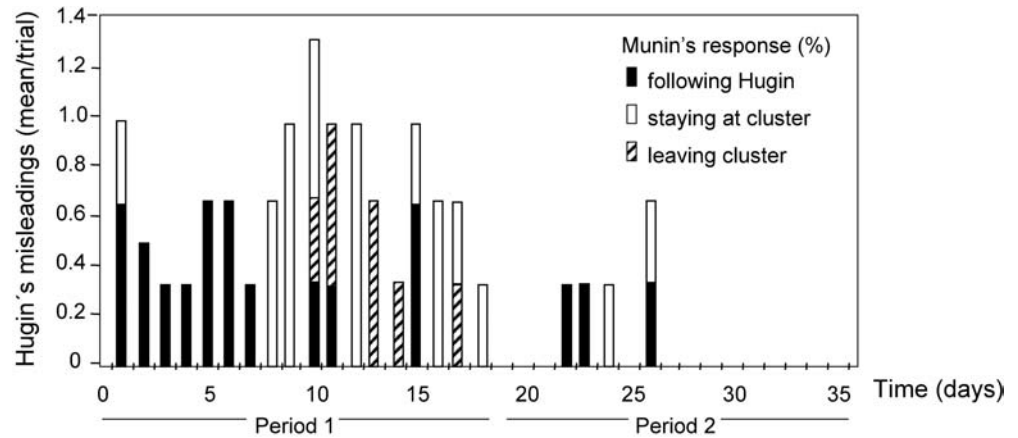


Table 1 Amount of reward subjects gained by opening boxes and scrounging and lost through scrounging during the two experimental phases

No. pieces	Phase 1				Phase 2			
	Munin	Hugin	Wota	Kaflunk	Munin	Hugin	Wota	Kaflunk
Gained: opening	0	11.3±4	3.7±3.9	0	0.9±1.6	6.1±3.7	4.1±3.7	3.9±3.1
Gained: scrounging	4.3±1.6	0.2±0.7	0.1±0.2	0.6±0.7	3.1±1.9	1.2±1.4	0.4±0.7	0.9±1.1
Lost: scrounging	0.2±0.4	3.6±2.2	1.2±1.6	0	0	2.5±2	1.7±1.8	1.3±1.8
Net gained	4.1±1.6	7.8±2.8	2.5±2.8	0.6±0.7	4±2	4.7±2.6	2.8±2.2	3.4±2
% net gained	27%	52%	17%	4%	27%	31%	19%	23%

Fig. 3 Mean number of Hugin's misleading attempts per trial (height of bars) and the proportion of Munin following Hugin to unrewarded clusters (*black bars*), staying at the rewarded cluster (*white bars*) and leaving the rewarded cluster without following Hugin to unrewarded clusters (*striped bars*) over the days in the experiment

return to clusters where he had already opened unrewarded boxes (he did this only three times during the first trial of day 1). Also, the mean number of opened unrewarded boxes per trial until he found the first rewarded box declined over days (log regression: $R^2=0.31$, $F_{1,14}=6.38$, $P=0.024$). On average, Hugin gained 52% of the total amount of 15 cheese pieces per trial (Table 1). Other than Hugin, the female Wota actively searched for the reward (Fig. 2a) but in only 39% of the trials simultaneously with Hugin. On average, she opened 1 ± 1 rewarded box and 4 ± 3 unrewarded boxes and gained 17% of the total amount of cheese pieces per trial (Table 1).

The two other group members, Munin and Kaflunk, exclusively went for scrounging opportunities (Fig. 2a). The dominant male Munin directed 79% of his scrounging attempts toward Hugin and successfully displaced him from the opened boxes in 99% of the attempts. On average, Munin gained 27% of the cheese pieces per trial (Table 1). The female Kaflunk was only successful in 28% of her scrounging attempts and gained only 4% of the total number of cheese pieces per trial (Table 1).

Munin and Hugin's interactions over food

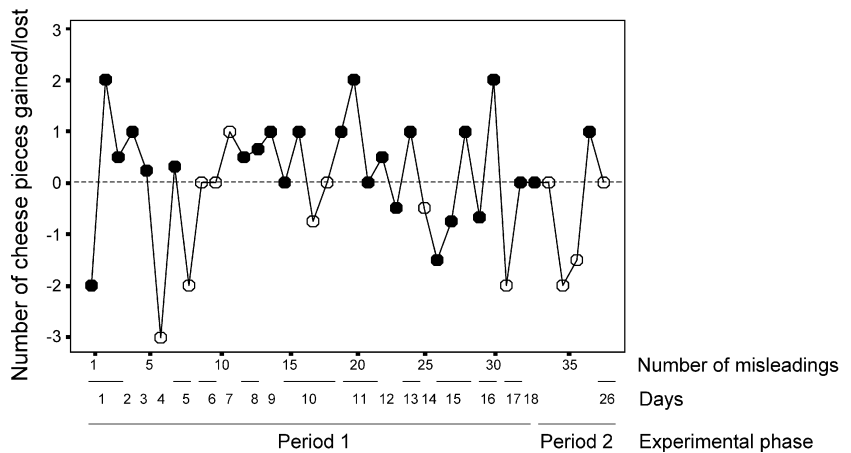
Although Munin was the first in the experimental room in 74% of the trials he always took position in the middle of the semicircle (>1 m away from the clusters) and did not approach a cluster until Hugin had started searching. When Hugin found the rewarded cluster, Munin always joined and displaced him from the already opened boxes (after

Hugin got 2 ± 1 pieces of the reward/box; range 0–3 pieces). Hugin then either opened another box at the rewarded cluster (2.1 ± 0.13 times/trial) or moved to an unrewarded cluster (0.7 ± 0.08 times/trial). Rarely, Hugin also attempted scrounging at boxes opened by Wota (0.3 ± 0.1 times/trial).

When Hugin continued to uncover boxes at the rewarded cluster in the presence of Munin, the dominant male displaced Hugin from the just-opened boxes in 83% of the cases. However, when Hugin left to open boxes at an unrewarded cluster, Munin at times also approached this cluster or, at least, left the rewarded cluster (in 21 of a total of 33 cases). In all of these cases, Hugin quickly returned to the rewarded cluster. The sequence of Hugin being displaced from his reward at the correct cluster, opening boxes at unrewarded clusters until Munin left the rewarded cluster, and subsequently returning to the rewarded cluster lasted no more than 15 s (mean±SD: 5.4 ± 0.9 s). Thus, a temporal contiguity was obvious between Hugin's responses and Munin's behavior. Hugin's leaving from the unrewarded cluster was rarely the result of agonistic interactions with Munin, as he got displaced from unrewarded boxes in only 11% of the cases.

Beginning with the second trial of the first day, Hugin left for unrewarded clusters just to return to the rewarded, but no longer occupied, cluster at least once a day during the entire first phase of the experiment (Fig. 3). However, he did not show this sequence constantly at each of the trials, nor at a given time per trial (e.g. 12% of the moves occurred after opening the first rewarded box, 24% after opening the second, 24% after opening the third, 18% af-

Fig. 4 Number of cheese pieces Hugin gained and lost right after a misleading attempt relative to his gain before the misleading attempt over the course of the experiment. *Open circles* indicate cases of Wota's interference



ter opening the fourth and 21% after opening the fifth box). Cross-correlating the rates of Hugin's moves from and to the rewarded cluster and the encounters with Munin at the opened boxes of the rewarded cluster over the first 18 days of the experiment revealed a significant effect for the same day (lag: 0, $r_{cc}=0.52$, $P<0.05$). This indicates that Hugin showed many moves on days when Munin performed frequent displacings. However, Hugin's moves did not correlate significantly with the aggression exerted by Munin (moves–forced retreats, for lags -7 to $+7$: $P>0.05$).

Within the same day, Hugin's moves from and to the rewarded cluster also correlated significantly with the number of cheese pieces Munin gained per trial (lag: 0, $r_{cc}=0.61$, $P<0.05$). Thus, Hugin showed frequent moves on days when he lost much reward to Munin. Similarly, a post hoc comparison between trials in which Hugin performed moves and trials in which he did not revealed significantly higher amounts of reward to Munin at trials in which Hugin performed moves (Wilcoxon signed ranks test: $n=20$, $z=-3.3$, $P=0.001$). However, Munin gained fewer cheese pieces from the box opened by Hugin right after a move than from boxes opened before a move (Wilcoxon signed ranks test: $n=23$, $z=-1.94$, $P=0.053$; Fig. 4). This indicates that moving from and to the rewarded cluster could give Hugin a small advantage over Munin. Nevertheless, the total amount of cheese pieces Hugin gained per trial did not differ between trials with and without his moves to unrewarded clusters (Wilcoxon signed ranks test: $n=20$, $z=-0.85$, $P=0.4$).

When both males left to unrewarded clusters, the female Wota immediately took the chance to exploit the correct cluster in 9 of 21 cases (Fig. 4). As soon as Wota started opening boxes at the correct cluster, both males returned within seconds (mean \pm SD: Munin: 2.2 ± 1.6 s; Hugin: 3.2 ± 1.9 s). Hugin's moves from and to the rewarded cluster were less efficient in terms of reward gained when Wota interfered than when Wota kept away from the correct cluster (Wilcoxon signed ranks test: $n=9$, $z=-1.9$, $P=0.057$; Fig. 4).

Despite the chance of Wota's interference, Hugin prolonged his stays and opened more boxes at unrewarded

clusters when Munin's latency to follow him from rewarded to unrewarded clusters increased (Spearman: $r=0.54$, $n=17$, $P=0.024$). Beginning with day 8, Munin often did not respond to Hugin's move at all but stayed next to the (still closed boxes) at the rewarded cluster or took position 1–2 m beside (Fig. 3). In 75% of the 12 cases in which Munin did not leave, Hugin also returned to the rewarded cluster.

Indeed, Munin learned not to follow Hugin to unrewarded clusters, as his proportion of joining Hugin at unrewarded clusters significantly decreased over days. This was particularly true for instances when Hugin had started to exploit the rewarded cluster and then moved to unrewarded clusters (log regression: $R^2=0.58$, $F_{1,14}=19.2$, $P=0.001$), but also at the begin of a trial, when Hugin was still searching for the correct cluster ($R^2=0.31$, $F_{1,15}=6.8$, $P=0.02$) and at the end of a trial, when only unrewarded boxes were covered ($R^2=0.44$, $F_{1,13}=10.1$, $P=0.007$).

Days 19–35

Overview of the group's behavior

After having received additional training, Kafklunk joined Hugin and Wota in uncovering boxes with the beginning of the second phase of the experiment (day 19). Nine days later (day 27), Munin did so as well. Thus, all subjects were actively searching for the reward (Fig. 2b). Mostly, the birds searched simultaneously at the three clusters (in 72% of the trials) and immediately gathered at the correct cluster as soon as it was found (in 85% of the cases). As a consequence of this tactic, the mean numbers of opened unrewarded boxes until the birds found the first rewarded box were very low (Munin: 0.3 ± 0.5 , Hugin: 0.6 ± 0.1 , Wota: 0.4 ± 0.9 , Kafklunk: 0.3 ± 0.8). Munin found the rewarded cluster in 17% of the trials, Hugin in 38%, Wota in 27%, and Kafklunk in 31%. (When restricting the analysis to those trials in which Munin opened boxes, Munin was first at the rewarded cluster in 31% of the cases).

Hence, Hugin lost his role as the main producer. Compared to the first phase, he opened fewer boxes per trial

(Wilcoxon signed ranks test: $n=49$, $z=-5.8$, $P<0.001$; Fig. 2b) and got fewer cheese pieces per trial ($n=49$, $z=-4.1$, $P<0.001$; Table 1) but initiated more scrounging attempts per trial ($n=49$, $z=-3.33$, $P=0.001$). Munin and Kaflunk, in contrast, reduced their scrounging attempts per trial from the first to the second period (Munin: $n=49$, $z=-4.7$, $P<0.001$; Kaflunk: $n=49$, $z=-2.1$, $P=0.04$; Fig. 2b). The change from exclusively scrounging to mere producing did not affect Munin's success rates in terms of cheese pieces gained per trial ($n=47$, $z=-0.7$, $P=0.46$; Table 1). Kaflunk, however, significantly increased her payoff ($n=49$, $z=-5.8$, $P<0.001$; Table 1).

Munin and Hugin's interactions over food

Hugin was still Munin's preferred target of scrounging (65% of Munin's attempts were directed toward Hugin) and thereby always lost the box he had opened. Compared to the first phase, he responded to Munin's displacings proportionally less often with moves to an unrewarded cluster (Wilcoxon signed ranks test: $n=30$, $z=-2.09$, $P=0.04$) but more often with scrounging at boxes opened by the females ($n=30$, $z=-2.98$, $P=0.003$). Thus, Hugin now only occasionally performed moves from and to rewarded clusters (Fig. 3). Time correlations between Hugin's moves and Munin's encounters and Hugin's moves and Munin's success rates, respectively, revealed no significant relationship (both correlations, for lags -7 to $+7$: $P>0.05$).

Discussion

During the first 18 days of this experiment, Hugin found and exploited the majority of the hidden food, experiencing intense scrounging from Munin, who specialized in displacing him from the already opened boxes. Thereby, Munin gained about half of the reward disclosed by Hugin. The latter responded either by quickly exploiting further boxes of the correct cluster or by suddenly moving to unrewarded clusters and opening boxes there. He used these different behavioral patterns according to the costs exerted by Munin. At high losses of reward to Munin, Hugin was likely to move to unrewarded clusters. This often caused Munin to leave the rewarded cluster as well, which could offer Hugin a head start for exploiting the rewarded boxes at the correct cluster again. Over the days, Munin learned not to follow Hugin to unrewarded clusters, instead waiting near the rewarded boxes. Hugin nevertheless performed the moves to unrewarded clusters at low rates until Munin started opening boxes himself.

Both the repeated use and the particular conditions of its use characterize Hugin's behavior as a reliable social tactic that functioned to lead Munin away from the reward. Hugin's moves to unrewarded clusters differed from pure avoidance behavior as he never left the cluster just with the appearance of Munin, nor was his leaving due to severe aggression exerted by Munin. Instead, the close temporal contiguity between Hugin's response to Munin's

leaving suggests that Hugin had been prepared to return to the rewarded cluster as soon as Munin was off. Moreover, Hugin opened more boxes at unrewarded sites when Munin was slow to follow, which suggests that he had recognized the relationship between opening boxes and Munin's appearance. Thus, on the *behavioral* level, we may interpret Hugin's moves from and to the rewarded cluster as a case of active misleading of a conspecific (Tomasello and Call 1997). This is, to our knowledge, the first demonstration of this kind of deception in a bird species. Although a number of anecdotes suggest the potential of corvids to fool conspecifics (review in Heinrich 1999), neither of these reports quantifies behaviors nor shows flexible dyadic or group responses over time. Some ground-nesting birds feign injury to lure away potential predators (e.g. Ristau 1991; Tate 1994) but do not apply these tactics to conspecifics (Hauser 2000).

Hugin's behavior is similar to that described by Goodall (1986) for a wild chimpanzee that was socially restrained from feeding at an artificial food dispenser. The subject repeatedly induced the leaving of the whole group by walking off the site but then circled back and got more food. In addition, Hugin's behavior resembles the results of the experiments with chimpanzees (*Pan troglodytes*; Menzel 1974; Hirata and Matsuzawa 2001) and mangabeys (*Cercocebus torquatus*; Coussi-Korbel 1994) in which a particular subject was informed on the location of hidden food. The informed subjects repeatedly lost the food to a dominant conspecific and, as a consequence, began misleading the competitor. Ring-tailed lemurs (*Lemur catta*) tested with a similar procedure failed to use deceptive tactics consistently although the informed subject apparently did benefit from accidental maneuvers that distracted the competitor (Deaner 2000; Güzeldere et al. 2002). Subordinate domestic pigs (*Sus scrofa*), in contrast, showed misleading-like behaviors in response to exploitation by dominants even though these moves hardly affected their foraging success (Held et al. 2002). Hugin's misleading attempts mostly paid off (Fig. 4) but the benefit was rather small and easily affected by a third party (i.e. the female Wota).

When interpreted in cognitive terms, misleading behavior has been suggested to provide evidence for second-order intentionality (e.g. Mitchell 1986; Whiten and Byrne 1988). However, in all the described studies, including this report on ravens, the animals could, and apparently did, respond to direct cues of their companions' behavior (Byrne and Whiten 1992; Coussi-Korbel 1994). Thus, it is likely that the misleading of conspecifics is based on the manipulation of the others' behavior rather than on the others' mental state (Tomasello and Call 1997). Indirect support for this more parsimonious interpretation comes from experiments on knowledge attribution that rarely produced positive results (review in Heyes 1998; Call and Tomasello 1999; Povinelli 2001; but see Hare et al. 2000, 2001). Still, misleading may involve cognitive abilities that reach beyond those required for many types of learned behaviors, as the deceiver must be able to inhibit certain behaviors and recognize how its conspecifics, as agents, are de-

ceivable (Güzeldere et al. 2002). Hence, Hugin's actions could be considered intentional in the sense that he had an intermediate goal to modify the perceptions or experience of his competitor so that his behavior is then altered (Hauser 1997; Güzeldere et al. 2002).

Goodall (1986) proposed that the first instance of misleading may be an accident but then, on subsequent occasions, the deceiver is acting deliberately. In line with this idea, Coussi-Korbel argued that mangabeys learn how to outwit a competitor only after a few trials (Coussi-Korbel 1994). In the case of the ravens, however, Hugin began misleading Munin on the very first day of the study. Thus, we speculate that Hugin could even have some experience in deceiving Munin and that he just began to use this ability in the experimental situation. Competing for hidden food is a task ravens have to deal with during daily foraging. Because they store food for later consumption (Gwinner 1965), those birds that are socially restrained from feeding may take the chance of raiding the caches of conspecifics (Heinrich and Pepper 1998). In this context, it may pay both cachers as well as raiders to manipulate the others' attention (Heinrich 1999; Bugnyar and Kotrschal 2002) by concealing information on cache location and the intention to raid, respectively, or even by creating false caches and misleading.

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References

- Bernstein IS (1988) Metaphor, cognitive belief, and science. *Behav Brain Sci* 11:247–248
- Bugnyar T, Kotrschal K (2002) Observational learning and the raiding of food caches in ravens, *Corvus corax*: Is it "tactical" deception? *Anim Behav* 64:185–195
- Byrne RW, Whiten A (1985) Tactical deception of familiar individuals in baboons (*Papio ursinus*). *Anim Behav* 33:669–673
- Byrne RW, Whiten A (1990) Tactical deception in primates: the 1990 database. *Primate Rep* 27:1–101
- Byrne RW, Whiten A (1992) Cognitive evolution in primates: evidence from tactical deception. *Man* 27:609–627
- Call J, Tomasello M (1999) A nonverbal false belief task: the performance of children and great apes. *Child Dev* 70:381–395
- Cheney DL, Seyfarth R (1990a) Attending to behavior versus attending to knowledge: examining monkeys' attribution of mental states. *Anim Behav* 40:742–753
- Cheney DL, Seyfarth R (1990b) How monkeys see the world: inside the mind of another species. University of Chicago Press, Chicago
- Coussi-Korbel S (1994) Learning to outwit a competitor in mangabeys (*Cercocebus torquatus torquatus*). *J Comp Psychol* 108:164–171
- Dawkins R, Krebs JR (1978) Animal signals: information or manipulation? In: Krebs JR, Davies NB (eds) *Behavioral ecology: an evolutionary approach*. Blackwell, Oxford, pp 282–309
- Deaner R (2000) An experimental study of deception in ringtailed lemurs (abstract). *Am J Phys Anthropol Suppl* 30:135
- Dennett DC (1988) The intentional stance in theory and practise. In: Byrne RW, Whiten A (eds) *Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes and humans*. Oxford University Press, Oxford, pp 180–202
- de Waal FBM (1992) Intentional deception in primates. *Evol Anthropol* 1:86–92
- Fritz J, Kotrschal K (1999) Social learning in common ravens, *Corvus corax*. *Anim Behav* 57:785–793
- Fujita K, Kuroshima H, Masuda T (2002) Do tufted capuchin monkeys (*Cebus apella*) spontaneously deceive opponents? A preliminary analysis of an experimental food-competition contest between monkeys. *Anim Cogn* 5:19–25
- Galef BG Jr, Giraldeau L-A (2001) Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Anim Behav* 61:3–15
- Giraldeau L-A, Caraco T (2000) *Social foraging theory*. Princeton University Press, Princeton, N.J.
- Goodall J (1986) *The chimpanzees of Gombe. Patterns of behavior*. Harvard University Press, Cambridge, Mass.
- Güzeldere G, Nahmias E, Deaner R (2002) Darwin's continuum and the building blocks of deception. In: Bekoff M, Allen C, Burghardt GM (eds) *The cognitive animal. Empirical and theoretical perspectives on animal cognition*. MIT Press, Cambridge, Mass., pp 353–362
- Gwinner E (1965) Über den Einfluß des Hungers und andere Faktoren auf die Versteck-Aktivität des Kolkraben (*Corvus corax*). *Vogelwarte* 23:1–4
- Hare B, Call J, Agnetta B, Tomasello M (2000) Chimpanzees know what conspecifics do and do not see. *Anim Behav* 59:771–785
- Hare B, Call J, Tomasello M (2001) Do chimpanzees know what conspecifics know? *Anim Behav* 61:139–151
- Hauser MD (1997) Minding the behaviour of deception. In: Whiten A, Byrne RW (eds) *Machiavellian intelligence II: extensions and evaluations*. Cambridge University Press, Cambridge, pp 112–143
- Hauser MD (2000) *Wild minds. What animals really think*. Penguin, London
- Heinrich B (1999) *Mind of the raven*. HarperCollins, New York
- Heinrich B, Pepper J (1998) Influence of competitors on caching behavior in common ravens, *Corvus corax*. *Anim Behav* 56:1083–1090
- Held S, Mendl M, Devereux C, Byrne RW (2000) Social tactics of pigs in a competitive foraging task: the "informed forager paradigm". *Anim Behav* 59:569–576
- Held S, Mendl M, Devereux C, Byrne RW (2002) Foraging pigs alter their behavior in response to exploitation. *Anim Behav* 64:157–166
- Heyes CM (1993) Anecdotes, training, trapping and triangulating: do animals attribute mental states? *Anim Behav* 46:177–188
- Heyes CM (1998) Theory of mind in nonhuman primates. *Behav Brain Sci* 21:101–148
- Hirata S, Matsuzawa T (2001) Tactics to obtain a hidden food item in chimpanzee pairs (*Pan troglodytes*). *Anim Cogn* 4:285–295
- Humphrey NK (1976) The social function of intellect. In: Bateson P, Hinde RA (eds) *Growing points in ethology*. Cambridge University Press, Cambridge, pp 307–317
- Kabicher G (1996) *Das Versteckverhalten von handaufgezogenen juvenilen Kolkraben (Corvus corax)*. Master's thesis, KLF Grünau, University of Vienna
- Krebs JR, Dawkins R (1984) Animal signals: mind-reading and manipulation. In: Krebs JR, Davies NB (eds) *Behavioral ecology: an evolutionary approach*, 2nd edn. Blackwell, Oxford, pp 380–402
- Kummer H, Anzenberger G, Hemelrijk CK (1996) Hiding and perspective taking in long-tailed macaques (*Macaca fascicularis*). *J Comp Psychol* 110:97–102

- Menzel EW Jr (1974) A group of young chimpanzees in a one-acre field: leadership and communication. In: Schrier AM, Stollnitz F (eds) Behavior of nonhuman primates, vol 5. Academic Press, San Diego, Calif., pp 83–153
- Mitchell RW (1986) A framework for discussing deception. In: Mitchell RW, Thompson NS (eds) Deception: perspectives on human and non-human deceit. State University of New York Press, Albany, pp 3–10
- Mitchell RW, Anderson JR (1997) Pointing, withholding information, and deception in capuchin monkeys. *J Comp Psychol* 114: 351–361
- Munn C (1986) Birds that “cry wolf”. *Nature* 319:143–145
- Povinelli DJ (1993) Reconstructing the evolution of mind. *Am Psychol* 48:493–509
- Povinelli DJ (2001) On the possibilities of detecting intentions prior to understanding them. In: Malle B, Baldwin D, Moses L (eds) Intentionality: a key to human understanding. MIT Press, Cambridge, Mass., pp 225–248
- Povinelli DJ, Eddy TJ (1996) What young chimpanzees know about seeing. *Monogr Soc Res Child Dev* 61:3
- Povinelli DJ, Parks KA, Novak MA (1991) Do rhesus monkeys (*Macaca mulatta*) attribute knowledge or ignorance to others? *J Comp Psychol* 105:318–325
- Premack D (1988) ‘Does the chimpanzee have a theory of mind?’ revisited. In: Byrne RW, Whiten A (eds) Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes and humans. Oxford University Press, Oxford, pp 160–179
- Premack D, Woodruff G (1978) Does the chimpanzee have a theory of mind? *Behav Brain Sci* 1:515–526
- Ristau CA (1991) Aspects of the cognitive ethology of an injury-feigning bird, the piping plover. In: Ristau CA (ed) Cognitive ethology: the minds of other animals. Erlbaum, Hillsdale, N.J., pp 91–126
- Schlittgen R, Streitberg BHJ (1995) *Zeitreihenanalyse*, 6th edn. Oldenbourg, Munich
- Semple S, McComb K (1996) Behavioral deception. *Trends Ecol Evol* 11:434–437
- Tate DP (1994) Observations on the nesting behavior of the common potoo in Venezuela. *J Field Ornithol* 65:447–452
- Tomasello M, Call J (1997) *Primate cognition*. Oxford University Press, New York
- Tomasello M, Hare B, Agnetta B (1999) Chimpanzees, *Pan troglodytes*, follow gaze direction geometrically. *Anim Behav* 58:769–777
- Valone TJ (1989) Group foraging, public information, and patch estimation. *Oikos* 56:357–363
- Whiten A (1997) The Machiavellian mindreader. In: Whiten A, Byrne RW (eds) Machiavellian intelligence II: extensions and evaluations. Cambridge University Press, Cambridge, pp 144–173
- Whiten A, Byrne RW (1988) Tactical deception in primates. *Behav Brain Sci* 11:233–273
- Woodruff G, Premack D (1979) Intentional communication in the chimpanzee: the development of deception. *Cognition* 7:333–362