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# Pilfering ravens, *Corvus corax*, adjust their behaviour to social context and identity of competitors

**Thomas Bugnyar · Bernd Heinrich**

**Abstract** Like other corvids, food-storing ravens protect their caches from being pilfered by conspecifics by means of aggression and by re-caching. In the wild and in captivity, potential pilferers rarely approach caches until the storers have left the cache vicinity. When storers are experimentally prevented from leaving, pilferers first search at places other than the cache sites. These behaviours raise the possibility that ravens are capable of withholding intentions and providing false information to avoid provoking the storers' aggression for cache protection. Alternatively, birds may refrain from pilfering to avoid conflicts with dominants. Here we examined whether ravens adjust their pilfer tactics according to social context and type of competitors. We allowed birds that had witnessed a conspecific making caches to pilfer those caches either in private, together with the storer, or together with a conspecific bystander that had not created the caches (non-storer) but had seen them being made. Compared to in-private trials, ravens delayed approaching the caches only in the presence of storers. Furthermore, they quickly engaged in searching away from the caches when together with dominant storers but directly approached the caches when together with dominant non-storers. These findings demonstrate that ravens selectively alter their pilfer behaviour with those individuals that are likely to defend the caches (storers) and support the interpretation that they are deceptively manipulating the others' behaviour.

**Keywords** Raven · *Corvus corax* · Food caching · Deception

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## Introduction

Social life may enhance the foraging efficiency of individuals by allowing them to exploit the knowledge of others (social learning, using public information) and/or the resources made available by others (kleptoparasitism, scrounging; review in Giraldeau and Caraco 2000; Laland 2004). Costs associated with social exploitation may be compensated by benefits through kinship or reciprocity (e.g. Axelrod and Hamilton 1981) as well as by other benefits of group living such as facilitated predator detection (e.g. Bertram 1978; Pulliam et al. 1982). However, if costs consistently exceed the benefits, individuals should develop counter-measures against exploitation, e.g. by getting away from others (Ranta et al. 1996; Barta and Giraldeau 1998) or by withholding information and providing false information (Dawkins and Krebs 1978; Maynard Smith 1979).

Providing no or false information constitutes a form of deception since it leads to the misinterpretation of a situation by one individual as a consequence of the behaviour or signals of the other individual (Whiten and Byrne 1988a, b). Functionally, such a misinterpretation poses costs to the receiver

and benefits the deceiver (Semple and McComb 1996; see also Krebs and Dawkins 1984; Mitchell 1986). Byrne and Whiten (1985) introduced the term 'tactical' deception to emphasize a contrast between short-term tactics (in which the deception uses elements from an honest counterpart in the individuals' repertoire) and long-term strategies such as inter- and intra-specific mimicry. Such flexible deceptive tactics for social manipulation have been reported mainly for primates (review in Byrne and Whiten 1990; Tomasello and Call 1997). Since constraints imposed by social structure (e.g. risk of detection, need for cooperation; Cheney and Seyfarth 1990a) makes deceptive tactics rare and difficult to study, much of the literature on the topic consists of anecdotes (Whiten and Byrne 1988a, b; Byrne and Whiten 1992). Nevertheless, progress in evaluating the possibility of deception has been made with experimental approaches such as the 'informed forager' paradigm (Menzel 1974; Coussi-Korbel 1994; Hirata and Matsuzawa 2001; Ducoing and Thierry 2003), 'competitive experimenters' (Woodruff and Premack 1979; Kummer et al. 1996; Mitchell and Anderson 1997; Anderson et al. 2001) or 'food competition contest' (Hare et al. 2000, 2001; Fujita et al. 2002), and studies have included some non-primate species (Held et al. 2000, 2002; Bugnyar and Kotrschal 2004; Dally et al. 2005a).

From a cognitive perspective, tactical deception has been assumed to reflect intentions by the deceivers in the sense that individuals want to manipulate others (Whiten and Byrne 1988a, b). However, conclusions about the degree of intentionality, i.e. whether the deception aims to affect the other's behaviour (first-order intentionality) or the other's mental states (second-order intentionality, Dennett 1988; for a different categorization see Mitchell 1986), are speculative and therefore highly debated (e.g. open correspondence to Whiten and Byrne 1988a; Heyes 1998).

Ravens are scavengers that cache temporary surpluses of food and food that is contested by others. In the wild and in captivity, they hide themselves from others while caching (Heinrich and Pepper 1998; Bugnyar and Kotrschal 2002a) in an apparent attempt to prevent conspecifics from learning about their cache locations through observation (Bugnyar and Heinrich 2003). Ravens also protect their caches against pilfering by aggressively chasing off conspecifics that come near their caches and/or by retrieving the food for later re-caching (Heinrich 1999). Thus, pilferers that have seen the making of caches often refrain from approaching those caches as long as storers are present (Bugnyar and Kotrschal 2002a). Furthermore, pilferers that are experimentally given access to the room in which they could previously observe a storer making caches, go directly for those caches when tested in private whereas they engage in short search-bouts at places away from those caches when tested together with the storer. Searching in short bouts and at various places is a typical behaviour for ravens that are ignorant about the location of caches that they have not observed being made (Bugnyar and Heinrich 2005). These findings raise the possibility that pilferers are capable of withholding their intention and/or providing false information to avoid provoking the cache protection of storers. Alternatively, birds could delay approaching and search at places other than the caches simply to avoid conflicts with dominants.

We here discriminated between these possibilities by testing whether ravens adjust their pilfer tactics according to social context and types of competitors. We gave birds who had previously watched a dominant conspecific making caches access to that room (i) in private, (ii) together with the storer, or (iii) together with a dominant conspecific that had not created the caches (non-storer) but that had observed them being made. Thus, in both social treatments, potential pilferers were confronted with dominants that were knowledgeable about cache location. However, one was the storer that was likely to retrieve caches in defence of pilfering whereas the other one was a competitor that was likely to engage in pilfering. Subordinate potential pilferers should not approach the caches when the storer is present but wait for its distraction in order to pilfer without eliciting cache protection. By contrast, if the non-storer is present then the potential pilferer should outrace its competitor because being first at the cache would be the best tactic to get the food reward against the dominant conspecific. Hence, we expected ravens to withhold pilfering and/or provide false information by searching at other places when together with storers but not with non-storers. However, if ravens were simply avoiding conflicts with dominants, they should show those social manoeuvres with both storers and non-storers.

Since ravens are known to kleptoparasite conspecifics at monopolizable food sources as well as at caches (Bugnyar and Kotrschal 2002b, 2004), both dominant storers and non-storers could also be expected to use force to obtain the recovered cache from the focal subjects. To control for possible effects of scrounging, we used small food pieces that could be taken quickly into the beak and/or sublingual pouch (Kijne and Kotrschal 2002). Thus, in the present experiment dominants could easily use force to defend or monopolize cache sites but hardly to steal the food from others after it had been recovered.

## Methods

### Subjects and setting

Subjects were seven hand-raised ravens (five males, two females; six birds were in their first year of age, one male was in his fourth year), all of which had participated in previous studies on gaze following and food caching (Bugnyar et al. 2004; Bugnyar and Heinrich 2005). Birds were marked
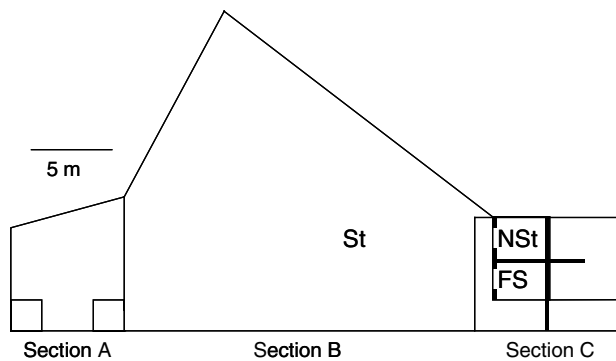
**Fig. 1** Sketch of aviary, indicating location of experimental rooms (sections B and C) and position of subjects during caching trials (St: storer; NSt: non-storer; FS: focal subject). *Bold lines* indicate opaque walls in section C; all other partitions between compartments were made of wire mesh

with coloured rings for individual identification. They were housed together in an outdoor aviary composed of three sections (section A: 30 m$^2$, section B: ca. 100 m$^2$, section C: three compartments and connecting pathways with a total area of 64 m$^2$; Fig. 1). Sections were separated by wire partition and, in case of section C, by wooden walls containing windows that could be covered with curtains. Sections A and B were equipped with natural vegetation and diverse ground cover (trees, grass; twigs, leaves, soil) whereas compartments of section C (12 m$^2$, 12 m$^2$, and 24 m$^2$) and interconnecting pathways (16 m$^2$) contained only a grass-floor and a few perches. Tests were conducted in section B, potential pilferers were enclosed in section C, and birds that did not participate in a given trial were confined to section A. When experiments were not in progress, doors between compartments were open and birds could freely roam in the entire complex. Birds were fed on their normal diet (meat, milk-products, fruits; Kabicher and Fritz 1996) after daily experiments. Water was provided ad libitum.

Procedure

The general line of testing was the same as in Bugnyar and Heinrich (2005). Tests consisted of a caching trial and a retrieval trial for focal subjects ($n = 3$ trials per treatment). During caching trials, a storer received three pieces of food (meat, 10 g per piece) that it was free to cache in the entire section B. Caching trials were terminated when all food was cached (mean ± SE number of caches made per storer: $3.6 ± 0.4$) and/or consumed (mean ± SE pieces recovered and consumed per storer: $1 ± 0.2$) and, on average, lasted for $5(± 0.4)$ min; afterwards, the storer was called out of section B by offering a small treat in the pathways of section C. During every caching trial, the focal subject and its non-storing competitor were enclosed in section C. Each of them was in a compartment with a transparent window and/or in

the adjacent pathway from which they had clear view of the storer and the entire section B; the partition between compartments was made of wire mesh so that each bird had full visual access to the other's room (Fig. 1).

Retrieval trials started 5 min after caching trials and lasted for 10 min. During retrieval trials ($n = 3$ trials per treatment), focal subjects were allowed to pilfer the caches either in private or in competition with the storer and non-storer, respectively. In both social treatments, competitors were dominant to the focal subject. The order of treatments as well as the identity of competitors per treatment changed in a pseudo-randomized order. In each treatment, birds were confronted with the same competitor in the first trial and, in case the birds' position in dominance rank hierarchy allowed for more combinations, with different competitors in the second and third trial (e.g. bird with dominance status 2 was tested three times per condition with bird of dominance status 1 as storer and as non-storer; bird with dominant status 6 was tested in each condition first with bird of dominance status 5, then with birds 4 and 3). Dominance status of individuals was known before the onset of the experiments and calculated on the basis of approach-retreat interactions.

Due to the size of the test compartment (section B), video-taping was inappropriate to capture the behaviour of two competitors simultaneously. Therefore, T.B. recorded all data by direct observation, marking cache locations onto pre-drawn sketches of the test compartment and describing behaviours by speaking onto a voice recorder (Olympus Pearlcorder S701). Birds were fully habituated to T.B. taking those types of protocols from a given point outside the aviary which was a standard procedure executed since fledging for 1–3 h per day. During caching trials, he recorded the location of caches, the order in which they were made and the number of immediate recoveries by the storer (see above). During retrieval trials, he measured the number and location of searches by the focal subject (labelled as search-bouts), the time (s) spent searching and the total time elapsed until the first cache was approached <1/2 m and/or successfully pilfered. In addition, he noted all social interactions between subjects in the competitive treatments. Searching was defined as digging in the substrate with the beak and/or looking into holes and under objects that were lifted with the beak. Searches conducted <1/2 m near a cache were regarded as pilfer attempts; searches conducted >2 m away from a cache were referred to as 'non-cache sites'. (Searches conducted between 1/2 m and 2 m of a cache comprised only $4 ± 3\%$ of all search-bouts; those cases were excluded from the analysis). Videos made in the pilot phase (in which we had two ravens let out into section B and both cached and pilfered simultaneously) were used to validate the reliability of data collection. T.B. and a person familiar to the ravens but not involved in the present experiment showed a high

level of agreement (Cohen's $K = 0.87$) on their ratings of behavioural categories on that video material.

Analysis

Analysis concentrated on the period until the focal subjects' first pilfer attempt. Only this early period allowed a standardized comparison between trials and treatments because the subjects' behaviour after the first pilfer attempt was affected by the fate of the cache (i.e. whether or not it was pilfered, recovered, or still in place) and by the total number of caches available (which was due to the storer's performance in the caching trial). Pilfer success was calculated as proportion of first pilfer attempts that resulted in gaining the food. Failure of pilfering could be caused by not finding the cache despite of searching within a range of 1/2 m, not finding the food because the cache has already been emptied by the storer, or because of aggression by the storer or non-storer.

We used Friedman test and Wilcoxon signed-ranks test on the individuals' mean values across trials to compare the birds' performance between treatments. When applying Friedman test ($k = 3$ treatments), we subsequently administered the multiple comparison method that is specific to this test (Siegel and Castellan 1988, pp. 180–181). Since the number of comparisons was equal to $k/[(k-1)/2]$, the value of $z$ evaluated from Table A in the appendix was 2.394 and the calculated critical value was computed to be 8.29. Differences between treatments were considered significant if the difference between the rank sums exceeded this critical value (Siegel and Castellan 1988). When applying Wilcoxon test ($k = 2$ treatments), we calculated $P$-values by hand (Sokal and Rohlf 1995, Table V) because standard software packages may give incorrect $P$-values with small sample sizes (Mundry and Fischer 1998). For all analysis, tests were two-tailed and alpha was set at 0.05.

**Results**

We found a significant difference in the focal subjects' mean latency to show the first pilfer attempt (approach a cache $<1/2$ m) between treatments (Friedman: $\chi^2 = 8.33$, df = 2, $P = 0.016$; Fig. 2). Specifically, ravens delayed pilfering when tested together with a dominant storer than when tested alone (difference between rank sums = 10, critical value = 8.29). In contrast, the birds' latency did not differ significantly from the in-private treatment when tested with a dominant non-storer (difference between rank sums = 5). However, there was also no significant difference between the storer and non-storer treatments (difference between rank sums = 5).

We also found ravens repeatedly searching at non-cache sites ($>2$ m away from caches) before they started the first
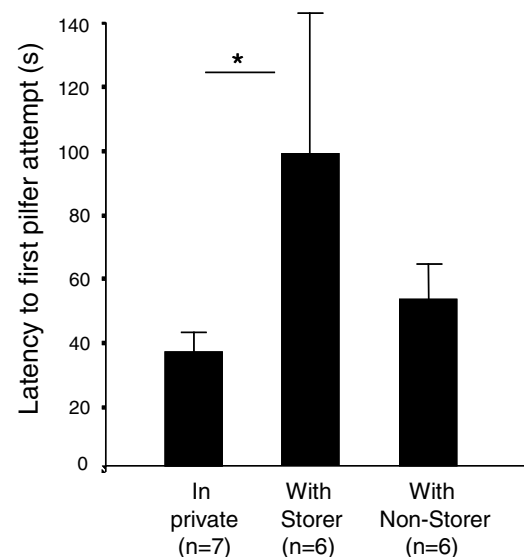


**Fig. 2** Mean ($\pm$ SE) latency until first pilfer attempt in private and when together with dominant storer and dominant non-storer. Friedman test and post-hoc multiple comparison after Siegel and Castellan (1988). *Asterisk* denotes $P < 0.05$

pilfer attempt. Both the mean time spent searching and the mean number of search-bouts differed between treatments (Friedman: search time: $\chi^2 = 11.57$, df = 2, $P = 0.003$, Fig. 3a; number of bouts: $\chi^2 = 11.57$, df = 2, $P = 0.003$, Fig. 3b). Both parameters were significantly increased in the tests with a storer compared to with a non-storer (difference between rank sums = 11.5, critical value = 8.29), whereas there was no statistical difference between the tests with a storer and in private (difference between rank sums = 6.5) and between the tests with a non-storer and in private (difference between rank sums = 5). Thus, ravens were likely to first search at places away from the actual caches when being together with a dominant storer whereas they directly attempted pilfering when being together with a dominant non-storer (Fig. 3a and b). Interestingly, the mean latency to start searching at non-cache sites in the storer treatment was shorter than the latency to start pilfering in the non-storer treatment (mean $\pm$ SE: $14 \pm 2$ s vs. $52 \pm 8$ s; Wilcoxon: $n = 6$, $T = 0$, $P = 0.031$).

Storers were rarely attracted to non-cache sites where focal subject were searching (Table 1) but were likely to orient in the direction of their caches when focal subjects eventually approached $<2$ m to those caches, i.e. they interrupted their activities and/or flew back to perch in the vicinity (ca. 2–3 m) of the caches (Table 1). In sharp contrast to non-storers, they never retrieved the food without experiencing another raven nearby the caches (Table 1). Once storers oriented towards caches, focal subjects could quickly dash for the cache (in 11% of the cases) or instantly stop approaching and leave the cache's vicinity for later coming back (in 89% of the cases; Table 1). In contrast, birds

**Fig. 3** **A** Mean (± SE) time spent searching at non-cache sites. **B** Mean (± SE) number of search-bouts before first pilfer attempt in private and when together with dominant storer and dominant non-storer. Friedman test and post-hoc multiple comparison after Siegel and Castellan (1988). *Asterisk* denotes $P < 0.05$
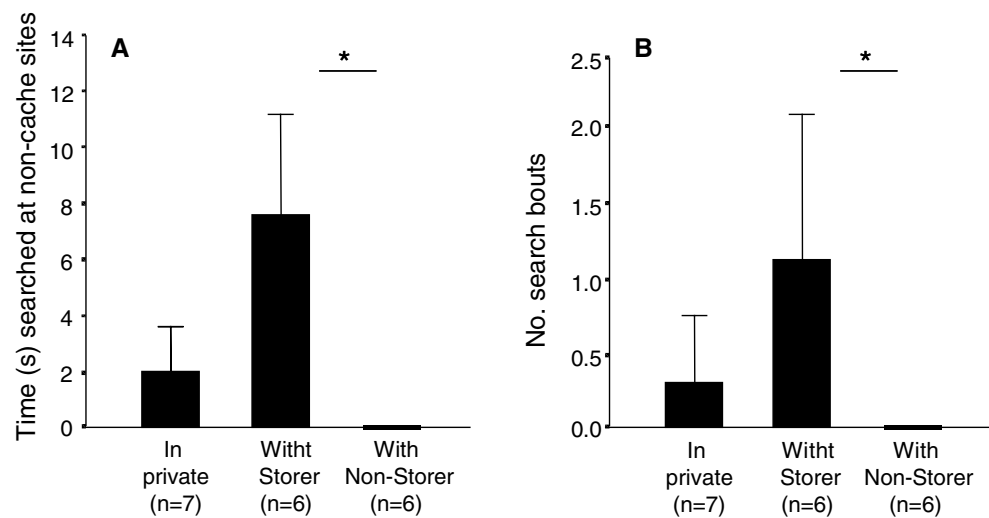


never showed any stop or delay of pilfer attempts in response to non-storers. They either tried to outrace the competitor (in 57% of the cases) or went for another cache (in 43% of the cases). The number of agonistic interactions occurring before the first pilfer attempt did not differ between storer and non-storer treatments (Wilcoxon: $n = 6$, $T = 8.5$, $P > 0.2$).

The likelihood of ravens getting the food in their first pilfer attempts differed between treatments (Friedman: $\chi^2 = 6.9$, df $= 2$, $P = 0.032$). Although none of the post hoc pairwise comparisons revealed a significant difference, there was a tendency of pilfer success being higher when in private than when with dominant storers (difference between rank sums $= 8$; critical value $= 8.29$) and when in private than when with dominant non-storers (difference between rank sums $= 7$; Fig. 4). Interestingly, failure in pilfering was mainly due to aggression when together with storers ($50 \pm 14\%$ of the cases) whereas it was due to not finding the caches despite of searching within a range of 1/2 m ($56 \pm 20\%$) and searching at caches already emptied during caching trials ($30 \pm 16\%$) when together with non-storers.

## Discussion

These results corroborate our previous observations and experimental findings that ravens delay pilfering and engage in searching at places other than the cache sites when confronted with those individuals that they have observed making the caches (Heinrich 1999; Bugnyar and Kotrschal 2002a; Bugnyar and Heinrich 2005). However, birds do not show these responses with dominants that had not created the caches but–like storers–know about their locations. This situation-dependent use of behaviours supports the idea that pilferers tactically manipulate storers by withholding intention and providing false information.
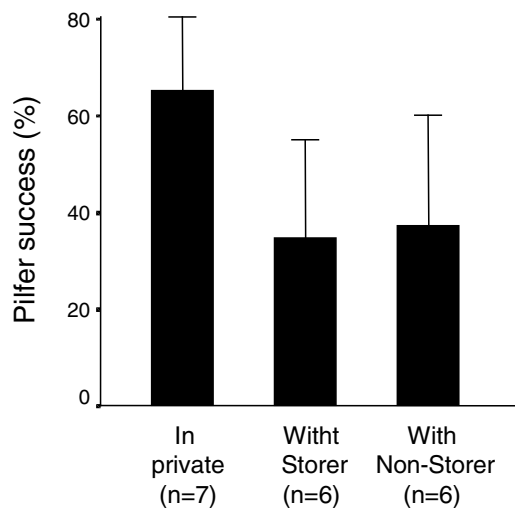
A parsimonious way of explaining the 'tactical' use of behaviours would be a combination of simple decision rules such as avoiding dominants and attending to the other's behaviour. For instance, focal subjects could inhibit pilfering with any dominant conspecific, pay attention to which cache it moves towards and then go for a cache not chosen by the competitor. When together with storers, birds might have problems in gaining local cues since storers usually stay away from their caches when conspecifics do not come close

**Table 1** Descriptive behaviour of storers and non-storers in responses to the behaviour of focal subjects (F) and (b) descriptive behaviour of focal subjects with both types of competitors (C)

Data are given as mean ± SE. We could not measure 'attraction to non-cache sites' with non-storers because F never searched away from caches in this treatment.

| (a) Behaviour | Storer (%) | Non-storer (%) |
|---|---|---|
| Starts acting before F | $0 \pm 0$ | $57 \pm 5$ |
| Gets attracted to non-cache sites by F's searching | $13 \pm 9$ | – |
| Stops own activities when F approaches cache <2 m | $34 \pm 4$ | $0 \pm 0$ |
| Perches near cache in response to F's approaching <2 m | $58 \pm 8$ | $0 \pm 0$ |
| Retrieves food without F coming <2 m to cache | $0 \pm 0$ | $63 \pm 11$ |
| Retrieves food after F coming <2 m to cache | $35 \pm 8$ | $23 \pm 10$ |
| Retrieves food after F searching <1/2 m to cache (pilfer attempt) | $65 \pm 8$ | $14 \pm 6$ |
| (B) Behaviour of F | With storer (%) | With non-storer (%) |
| Approaches caches directly | $0 \pm 0$ | $95 \pm 5$ |
| Starts pilfer attempt when C is engaged in other activities | $56 \pm 11$ | $11 \pm 7$ |
| Starts pilfer attempt when C is attentive/near cache | $11 \pm 7$ | $61 \pm 13$ |

**Fig. 4** Mean ($\pm$ SE) pilfer success in private and when together with dominant storer and dominant non-storer. Friedman test and post-hoc multiple comparison after Siegel and Castellan (1988); none of the pair-wise comparisons are significant

(Bugnyar and Heinrich 2005). Pilferers thus should have difficulties in deciding which caches are 'safe' to approach with storers rather than with non-storers. Searching at places other than the caches may result as a kind of displacement behaviour that eventually distracts storers and, as a by-product, functions as deceptive action.

Although plausible, we consider this scenario as unlikely mainly because the ravens showed a relatively quick response to storers and not, as would be predicted by the behavioural cueing model, to non-storers. Pilferers started searching at non-cache sites with storers about twice as early as they started pilfering with non-storers. Furthermore, pilferers always stayed away from cache sites when becoming active with storers but not with non-storers. This is impressive because storers never showed any object- or location-related activities that could guide the pilferers' behaviour in the beginning (Table 1). Pilferers thus appear to discriminate instantly between different types of competitors, i.e. individuals they have seen making caches and those that they have seen as bystanders at caching. These findings add to the increasing body of evidence that group foraging corvids such as ravens (Bugnyar and Heinrich 2005), scrub-jays (*Aphelocoma california*, Dally et al. 2005a, b) and magpies (*Pica pica*, Prior and Güntürkün, personal communication) take into account the identity of individuals present at caching and later use this personalized information in competition for those caches. That is, they behave logically in the social realm (Watanabe and Huber 2006).

Certainly, memory for particular individuals at particular sites at caching is only one component for successful pilfering (Heinrich 1999; Emery and Clayton 2001; Dally et al. 2005a). Attending to the other's behaviour, specifically in the vicinity of caches, seems to be a crucial factor for tim-

ing the pilfer attempts. Pilferers appear to take into account whether storers are attentive or occupied with other activities (e.g. handling objects, drinking, singing) and how they respond to others approaching their caches (i.e. whether or not they return instantly to their defence). When together with non-storers, pilferers may use the other's behaviour to judge the necessity of speeding up pilfering and/or for choosing an alternative cache they could potentially go for.

The quick adjustment of pilfer behaviour to different types of competitors suggests that ravens understand that storers are likely to defend caches against pilfering whereas non-storers are likely to show pilfering. It is conceivable that such contingencies as well as the appropriate responses are learned during social interactions in everyday life (own unpublished data; see also Emery and Clayton 2001). In this respect it is noteworthy that ravens are capable of adjusting their pilfer behaviour according to context which sometimes affords them showing similar responses to different types of competitors and different responses to the same type of competitor, respectively. For instance, delaying could be an appropriate response not only to storers but also to dominant non-storers when those have not seen the caching and thus are ignorant about the cache locations. Those dominants are unlikely to find the caches but may pose a threat of stealing the food at pilfering. Indeed ravens have been shown to delay pilfering with ignorant non-storers similarly as they do with storers; still, they hardly engage in searching away from caches with any type of non-storer (Bugnyar and Heinrich 2005).

The tactical use of delaying and searching away from the caches may provide an indirect hint for a certain degree of intentionality on side of the pilferers, in the sense that they want storers not to go back and recover their caches. Hence, birds would likely aim at manipulating the others' behaviour (first-order intentionality; Dennett 1988). Searching at places other than the caches could be interpreted as an attempt of distracting the storer's attention and/or leading the storer away from the caches (Whiten and Byrne 1988b; Bugnyar and Kotrschal 2004). However, this does not necessarily indicate that pilferers want storers to believe that there is something of interest at other places and thus aim at affecting their mental states (second-order intentionality, theory of mind; Premack and Woodruff 1978). Those manoeuvres could be learned and/or could be responses to subtle behavioural cues given by the competitor (Cheney and Seyfarth 1990b; Tomasello and Call 1997; Povinelli 2001). A representation of states in the physical world (Heyes 1998) would thus be a sufficient cognitive framework for explaining the manipulative behaviours of pilfering ravens, as it is the case for most reports on tactical deception in non-human animals (e.g. Coussi-Korbel 1994; Kummer et al. 1996; Mitchell and Anderson 1997; Held et al. 2002; Ducoing and Thierry 2003).

Nevertheless, there is evidence that ravens, like some other corvids (review in Emery and Clayton 2004a, b), show a sophisticated understanding of the others' visual perception (Bugnyar et al. 2004; Bugnyar and Heinrich 2005) raising the possibility that they could be capable of representing (some of) the others' mental states (Emery et al. 2004; Emery and Clayton 2004a, b). Given the complex interactions over food caches with individual ravens mutually playing the roles of storers and pilferers and the strong effects of observational spatial memory on finding the others' caches, we propose that those skills could have evolved primarily for judging competitors, i.e. whether those intend to defend or pilfer caches, whether those can or cannot see the caching, and whether those are likely knowledgeable or ignorant about cache locations. Although deceptive manoeuvres do not require higher-order intentionality, they could potentially be affected by those complex socio-cognitive skills (see also the concepts of intermediate goals and building blocks of deception; Hauser 1997; Güzeldere et al. 2002).

A requisite of tactical deception is that the behaviour results in benefits to the deceiver and costs to the deceived (Byrne and Whiten 1985; Semple and McComb 1996). In contrast to our findings in previous studies (Bugnyar and Kotrschal 2004; Bugnyar and Heinrich 2005), we could not find any advantage of social manipulation in this study. Pilfer success with dominant storers was low and comparable to that with dominant non-storers. Possibly the pilfer tactics did not pay off in this particular setup because storers could concentrate on defending their caches. Under more naturalistic situations, storers would have the choice of getting new loads of food for making further caches or staying and defending already made caches (Heinrich and Pepper 1998). Withholding pilfer-intention and/or providing misleading information about cache location should then affect the storers' decision to the advantage of the pilferers.

Taken together, we found that ravens alter their pilfer behaviour with dominants that have made the caches (storers) compared to with dominants that have only seen the caches being made (non-storers), rendering the 'avoidance of conflict' hypothesis unlikely. Birds applied different tactics (initially not approach caches but search at non-cache sites with storers vs. directly go for caches with non-storers) already before their competitors started acting, suggesting that their differentiation was not simply the outcome of different behaviours shown by the competitors. Still, behavioural cueing appears to be important for judging the appropriate timing for pilfering and to respond to the protective tactics of storers. We thus interpret the withholding of pilfering and the searching at non-cache sites as an attempt to manipulate the storers' behaviour.

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