

## Scrounging Tactics in Free-Ranging Ravens, *Corvus corax*

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### Abstract

Social foraging allows individuals to scrounge, i.e. to exploit the food others have made available. The conditions promoting scrounging as an alternative foraging tactic have yet received limited attention. We presently examine whether ravens, as opportunistic scavengers, adjust their foraging tactics according to the potential costs involved in accessing a particular food source. We observed wild ravens foraging in a game park, at the enclosures of wolves, *Canis lupus*, and wild boars, *Sus scrofa*. Wolves may aggressively defend their food and even kill ravens, whereas wild boars do not. When co-feeding with wolves, the ravens showed higher scrounging rates than with wild boars. Only at the wolves, they tended to specialize either on scrounging or on getting food directly from the site. However, scrounging techniques differed in relation to the state of food depletion. Early on, after food became available, the ravens most frequently displaced others from food, whereas towards the end, stealing, solicited sharing, and cache raiding became prevalent. These techniques differed in their profitability and their use was related to the scroungers' age, social status and affiliative relationships. This suggests that ecological conditions, such as co-feeding with potential predators, may influence the individuals' decision whether or not to scrounge in competition for food. Social conditions, on the other hand, may affect the way how to get at food possessed by others and may thus, to a large extent, determine the profitability of scrounging.

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### Introduction

Social foraging may benefit individuals either by reducing the risk of predation (e.g. Powell 1974; Bertram 1978), or by enhancing the efficiency of foraging (e.g. Krebs et al. 1972; Baker et al. 1981). Besides, social foraging allows for scrounging: instead of spending time and effort in search and capture of prey

(producer tactic), individuals may exploit the food that others have made available (Barnard and Sibly 1981; Barnard 1984; Giraldeau and Caraco 2000).

Both, theoretical models and empirical studies suggest that socially foraging individuals play either the role of producer or scrounger (producer–scrounger games, review in Giraldeau and Caraco 2000; but see information sharing models, Clark and Mangel 1984; Ranta et al. 1996). However, there is also evidence that individuals may alternate between tactics according to their payoff and the risk of starvation (e.g. Koops and Giraldeau 1996; Flynn and Giraldeau 2001). In general, members of heterogeneous groups are predicted to play the tactic in that they are competitively superior (e.g. Vickery et al. 1991; Barta and Giraldeau 1998; Broom and Ruxton 1998). Furthermore, individuals are predicted to switch between tactics in relation to their energetic reserves and the risk-sensitive properties of the foraging process (Caraco and Giraldeau 1991; Barta and Giraldeau 2000). Predation hazard, in contrast, is considered to have only marginal effects on the use of scrounging (Barta and Giraldeau 2000).

To date, there are only a few empirical studies on the conditions promoting scrounging (Giraldeau and Caraco 2000). Besides, most studies have focussed on one particular type, the exploitation of patches through scramble competition (review in Giraldeau and Beauchamp 1999). However, scrounging occurs not only during search but also the division of food (Giraldeau and Caraco 2000), and field observations indicate that individuals may use a variety of techniques to obtain food from others (often also referred to as forms of kleptoparasitism, Brockman and Barnard 1979). For instance, when patches hold a limited amount of food that requires some time for processing, scrounging is likely to occur through aggressive displacement (when a conspecific is supplanted from its food) or stealthful sequestering (when food is brought quickly out of reach of its former possessor; e.g. Diamond and Bond 1991).

Ravens are scavengers that assemble in non-kin groups (Parker et al. 1994) on ephemeral carcasses or kills, but also at regular food supplies in game parks or at garbage dumps (Haffer 1993; Ratcliffe 1997). Such food sources are often defended by either dominant conspecifics, such as territorial breeding pairs (Heinrich 1988), or by potential predators, such as wolves (Bugnyar and Kotrschal 2001). Group formation may benefit ravens in overcoming the food defence (Marzluff and Heinrich 1991), but may also lead to increased competition (Heinrich et al. 1993).

Ravens could cope with this competition in different ways. Individuals may scramble for their share of food by retrieving consecutive loads from the source and scatter-hoard at some distance to the feeding site (Heinrich 1989). In addition, individuals may exploit conspecifics that have already successfully obtained food (1) by aggressively displacing them from the food, (2) by stealthfully sequestering (bits of) the food (Bugnyar and Kotrschal 1997), (3) by soliciting others to share (Heinrich and Marzluff 1991), or (4) by raiding food caches (Heinrich and Pepper 1998). In each of these cases, individuals make use of the food others have made available and thus, per definition, engage in scrounging (Barnard and Sibly 1981; see also Giraldeau and Caraco 2000).

In this study, we examined the scrounging behaviour of ravens in relation to the potential costs involved in gaining access to a food source. We observed the foraging tactics of free-ranging ravens in a game park, at the enclosures of wolves, *Canis lupus*, and wild boars, *Sus scrofa*. Wolves may aggressively defend their food and thereby, even kill ravens, whereas the wild boars do not (Bugnyar and Kotrschal 2001). Thus, snatching food (the producer tactic) from wolves is clearly more risky for ravens than co-feeding with wild boars. At the wolves, however, scrounging may be a less hazardous alternative, as it occurs somewhat off the feeding site, e.g. in trees, bushes, at the fence of the enclosures or in the air.

We expected ravens to adjust their behaviour according to the mortality risk of producing and the profitability of scrounging. Because of the higher risk of producing at the wolves, the ravens should show a higher proportion of scrounging there than at the wild boars. The likelihood of being successful in scrounging may differ between the techniques. However, age and social status may determine which techniques the individuals can adopt. Dominant and/or older individuals should preferentially use displacing, as this technique requires being superior in interference competition. Conversely, youngsters and/or subordinates should perform stealing, as this technique relies on appropriate timing rather than a high resource holding potential. Individuals with affiliative relationships (e.g. in the course of pair formation) should make use of sharing, whereas those that fail in producing and getting food by social means should attempt cache raiding.

## Methods

### Study Site

The study was conducted in the Cumberland game park, which is located in the valley of the river Alm in the northern part of the Austrian Alps. There, 20 to 120 non-breeding ravens ( $\bar{x} \pm \text{SE} = 35 \pm 1$ ) as well as a few breeders from adjacent territories forage year-round (Drack and Kotrschal 1995).

Visitors are allowed to enter the park from 9:00 h in the morning. Prior to this, the zoo animals are fed. Ravens snatch food at various enclosures although they concentrate particularly on those of the wolves (two adult males, three adult females; area covered by enclosure = 870 m<sup>2</sup>) and the wild boars (two adult males, six adult females and their offspring of the year; area covered by enclosure = 5200 m<sup>2</sup>).

At the wolves, meat is provided exclusively ( $\bar{x} \pm \text{SE} = 5.9 \pm 0.1$  kg/daily feeding, mainly beef cut into pieces of approx. 300 g). At the wild boars, the food consists of either kitchen leftovers ( $2 \pm 0.1$  buckets/feeding) or meat ( $3.3 \pm 0.2$  kg/feeding, quality and size of pieces comparable with those at wolves), supplemented by one bucket of wild boar chow (Fixkraft Erhaltungsfutter). Differences in food quality between the wolves and wild boars were taken into account when comparing these two feeding types, and controlled for by using only the feedings in which meat alone was delivered to the boars. In contrast to wolves,

which may aggressively attack and even kill ravens at their feeding site (16 dead ravens in 3 yr), wild boars do not appear to pose a threat to foraging ravens (Bugnyar and Kotrschal 2001).

### Subjects

Ravens were captured in trap-in traps baited with meat (Stiehl 1978). They were marked with patagial wing tags made of Saflag (Kochert 1973), and with a combination of two or three coloured metal leg bands (Huber 1991). In addition, a number of body parameters were measured and age class was determined from visual markings such as the colouration of eyes, oral cavity and feathers (Heinrich 1994a,b). Accordingly, we distinguished between juveniles (birds in their first summer, with blue eyes, a pink oral cavity and brownish feathers), subadults (birds in their second to fourth summer, changing in colour to adults but still retaining parts of their juvenile features), and adults (birds older than four summers, with brown eyes, a dark oral cavity and black feathers). Sexes were estimated based on the bill length and overall body size (Gwinner 1964).

At the time of the study, 22 ravens could be individually identified (Table 1). Most of these birds repeatedly joined the foraging group at the game park during the observation period ( $\bar{x}$  = every second week) and stayed there for variable time periods ( $\bar{x}$  = 6 d; Table 1). All of these ravens participated at the feedings of wolves and wild boars (Table 1). However, juveniles were found significantly more often at the wild boars than at the wolves ( $\bar{x} \pm \text{SE} = 7 \pm 2$  observations/individual at wolves vs.  $15 \pm 6$  observations/individual at wild boars,  $\chi^2 = 11.7$ ,  $\text{df} = 5$ ,  $p < 0.05$ ).

### Data Collection

Data were collected from Jul. 1997 to Dec. 1998. Observations were carried out by eye or with binoculars (Swarowski Habicht SLC 10 × 42 WB, Absam, Austria) from the top of small hills at the enclosures of wolves ( $n = 200$  d) and wild boars ( $n = 180$  d). At most days, observations were carried out consecutively at both enclosures ( $\bar{x} \pm \text{SE} = 11 \pm 7$  d/mo at wolves;  $11 \pm 6$  d/mo at boars) to minimize the effects of weather, temperature and time of season. To control for possible differences in the ravens' hunger level, the order of feedings (wolves or wild boars occurring first) was randomly varied. As both enclosures are located within the same area of the game park (distance between enclosures = 150 m), habitat differences between the feeding sites were considered to be minimal. The absence of a canopy of leaves during the winter season facilitated observations at both sites. Because of long-term studies starting in 1993 the ravens were well habituated to the presence of certain humans who make close-distance observation (5–10 m) possible without the necessity to hide or camouflage observers and their equipment.

Observations started when food was thrown into the enclosures. At the wolves, ravens rarely fed on the ground but consumed the meat in the trees or on the fence of the enclosure (T. Bugnyar & K. Kotrschal, unpubl. data). Also, some

Table 1: The use of game park feedings by marked individuals

Individuals	Age-class	Sex	Total no. of observations		Total no. of stays at the Park	Mean duration of stays (d)	Mean duration between stays (d)
			At wolves	At boars			
A	Juv		10	15	1	43	—
G	Juv		12	43	10	2	13
H	Juv		2	4	1	5	—
I <sup>a</sup>	Juv		0	0	0	—	—
N	Juv		6	11	7	1	27
S	Juv		9	17	5	5	10
V	Juv		1	2	2	1	13
B	Subad	M	1	13	1	24	—
C	Subad	M	46	45	1	97	—
D	Subad	M	91	80	19	6	7
E	Subad	F	52	57	2	56	243
J	Subad	F	78	78	11	4	8
K	Subad	M	140	126	11	28	13
M	Subad	M	44	39	8	6	10
P	Subad	M	46	38	12	7	10
U	Subad	M	8	14	7	2	20
L	Ad	M	84	64	15	3	13
O	Ad	F	124	97	3	61	11
R	Ad	F	2	2	2	1	220
T	Ad	M	18	24	2	63	33
LL	Ad	F	8	14	4	10	15
LU	Ad	M	118	95	8	23	6

Juv, juveniles; Subad, subadults; Ad, adults; M, male; F, female. Periods of consecutive observations are labelled as stays.

<sup>a</sup>Individual 'I' was not observed during the time of data collection, although it was present for a total of 209 d before.

wolves used to retreat with food from the area where other group members were feeding. Therefore, we divided our protocols into two successive phases, (a) while the food was available on the feeding site ( $\bar{x} \pm SE = 6 \pm 0.4$  min) and (b) a 10-min phase after the feeding site was depleted and food could only be obtained by scrounging from other individuals.

At the wild boars, ravens were also feeding on the ground and thus, could stay at the feeding site for up to 30 min (T. Bugnyar & K. Kotrschal, unpubl. data). There, we did not divide protocols into different phases, although we took data for 15 min to match observation times between wild boars and wolves. We applied the same kind of protocols to either type of food quality (kitchen leftovers or meat) offered at the boars. However, for comparison between wolves and wild boars, we restricted the analysis to data from occasions when meat was fed to the boars.

Observations were taped on a voice recorder (Sony VR, Sony Corp., China) or on the audio-track of a video-camera (Sony DCR-VX 700 E, Sony Corp., Japan). We recorded which of the marked individuals participated (number of landings and take-offs), how often they got food directly from the feeding site (number of take-offs with food) and how often they were attacked by the wolves or wild boars (number of take-offs after being chased by one of the zoo animals). In addition, we noted various kinds of dyadic social interactions among ravens in which at least one of the marked individuals was involved, in form of the triplet complex: 'Who does what to whom' (de Waal et al. 1976).

Social interactions were classified as scrounging when one individual attempted to get food from a second individual. Techniques of scrounging were defined according to the way putative scroungers approached an individual possessing food, how they attempted to get it, and whether they were leaving or staying next to the original food owner after the food transfer had occurred (see Diamond and Bond 1991). When 'displacing', individuals directly approached conspecifics in possession of food and forced them to retreat. When 'stealing', individuals positioned themselves next to conspecifics with food, quickly took (bits of) the food and retreated. When 'sharing', individuals approached conspecifics possessing food and either participated in feeding aside with these conspecifics or solicited the passing-over of pieces using begging gestures (Gwinner 1964) and/or vocalization (i.e. 'yells'; Heinrich and Marzluff 1991). When 'cache raiding', individuals approached the caches of conspecifics, retrieved the food and left with the food and/or fed aside the emptied cache. When 'chase flying', individuals flew after conspecifics carrying food, eventually forcing them to drop it. As up to 13 birds ( $\bar{x} \pm \text{SE} = 2 \pm 0.1$ ) participated in such chases, these could result either in a bird taking the food from the target of the chase, or in a bird catching the food dropped by the chased bird. The former outcome was scored as displacement ('sensu' the above definition), whereas the latter was scored as stealing, given that the successful bird had to retreat, respectively to fly away, from others after scrounging. Some chases, however, ended outside the view of the human observer so that their outcome remained unknown. Chase flying stated as category in the text thus refers to all instances regardless of their outcome.

As ravens cache off the feeding sites (Heinrich and Pepper 1998), the possibility of observing cache raiding was limited. Thus, for estimating the profitability of raiding, we additionally recorded raiding attempts of unmarked individuals. To distinguish raiding from retrieving food out of the bird's own cache, we noticed only instances in which we simultaneously observed the cacher and the raider, or instances in which the raider approached from the opposite direction than the cacher had left.

### Analysis

We calculated behavioural categories as mean ( $\pm \text{SE}$ ) frequencies per observation day, and analysed the data separately for the feedings of wolves and wild boars. Individuals that were observed less than five times at the feedings

were excluded from the analysis (excluded at wolves:  $n = 5$ ; excluded at wild boars:  $n = 4$ ).

The individuals' attempts of getting food directly from the feeding site (producer tactic) were analysed as the number of landings on the ground per day. The success of these attempts was analysed as the number of fly-offs with food per day. This may approximate actual feeding rates when ravens were leaving the enclosure as soon as they received food, which was usually the case at the wolves. In case ravens were consuming food also on the ground of the enclosure, which mainly occurred at the wild boars, this may approach the proportion of caching trips rather than feeding rates. However, hungry ravens usually started to consume food not before having made some caching trips (Gwinner 1965; Heinrich and Pepper 1998; T. Bugnyar & K. Kotrschal, unpubl. data), so that the calculation of success rates as the number of fly-offs with food may be considered as representative also at the wild boar feedings. Still, the food eaten on the ground was not included in the analysis.

The occurrence and frequency of scrounging was analysed as the total number of scrounging attempts initiated by an individual per day, regardless of the technique used. The success of scrounging was calculated as the number of attempts per day in which a food transfer occurred. Similar to the initiated scrounging attempts, the frequency of being the target of scrounging was analysed as the total number of scrounging attempts received by an individual per day. Loosing food through scrounging was calculated as the number of received scrounging attempts per day in which a food transfer occurred.

Thus, in the course of the feedings, the ravens' behaviour could be seen as a series of decisions to play either producer or scrounger. However, the individuals' propensity to scrounge was calculated as the proportion of initiated scrounging attempts relative to the total number of attempts to get food per day (= sum of landings and scrounging attempts/d). This allowed for comparing the behaviour of individuals at the different enclosures and for comparing individuals that were present at the game park for different amounts of time.

Finally, the relative frequency of different types of scrounging was calculated as percentage of the total number of scrounging attempts made, respectively received, by individuals. The profitability of each technique was calculated as the proportion of successful attempts relative to the total number of attempts. Individuals that were involved in less than five scrounging attempts were excluded from this analysis (excluded at wolves:  $n = 7$  for initiated scrounging,  $n = 6$  for being target of scrounging; excluded at wild boars:  $n = 10$ ,  $n = 7$ ).

Dominance status of individuals was analysed on the basis of approach-retreat interactions that occurred at and around the feeding site but did not involve direct competition for food. Individuals with a low proportion of retreats in those encounters were considered to be relatively high in status, whereas individuals with a high proportion of retreats were considered to be subordinate.

Affiliative relationships between individuals were analysed in terms of preening bouts and resting in close proximity. Preening bouts were measured as the number of time periods two ravens were engaged in preening each other's

feathers. Resting in close proximity was measured as the number of time periods two ravens were sitting in less than 0.5 m distance. Both parameters were calculated as mean ( $\pm$ SE) frequencies per observation day.

Kruskal–Wallis test was used for comparing (a) the proportional use of scrounging and (b) the proportion of retreats in agonistic encounters between age classes. If a significant result was obtained, Mann–Whitney U-test was used for post hoc testing. All z statistics are from Wilcoxon matched pairs test. For comparing the relative frequency of different scrounging techniques during and after the feeding of wolves, we lumped the initiated and received scrounging attempts per individual, as some ravens were not involved in one particular direction of scrounging. For comparing the behaviour of ravens at the wolves and at the wild boars, we used only feedings in which meat were delivered to the boars. Spearman rank correlations are across individuals. All p-values are two-tailed. Unless otherwise stated, numbers provided in the text represent  $\bar{x} \pm$  SE.

## Results

### Wolf Site

Individuals present around the wolf enclosure landed at the feeding site at least once per feeding in  $93.5 \pm 2\%$  of the cases. Thus, individuals were likely to attempt getting food directly from the site ( $1.5 \pm 0.1$  times/feeding). In addition, they used scrounging ( $0.5 \pm 0.1$  times/feeding). The proportional use of scrounging did not differ significantly between age classes ( $\chi^2 = 2.8$ ,  $df = 2$ ,  $p = 0.25$ ; Fig. 1). However, age class affected the proportion of retreats in agonistic encounters ( $\chi^2 = 7$ ,  $df = 2$ ,  $p = 0.03$ ), with juveniles retreating more often than adults ( $U = 0$ ,  $n = 8$ ,  $p = 0.02$ ).

The individuals' number of landings per feeding correlated positively with their success of getting food from the site ( $0.8 \pm 0.1$  times/feeding;  $r_s = 0.59$ ,  $n = 17$ ,  $p = 0.013$ ). However, the number of landings per feeding also correlated

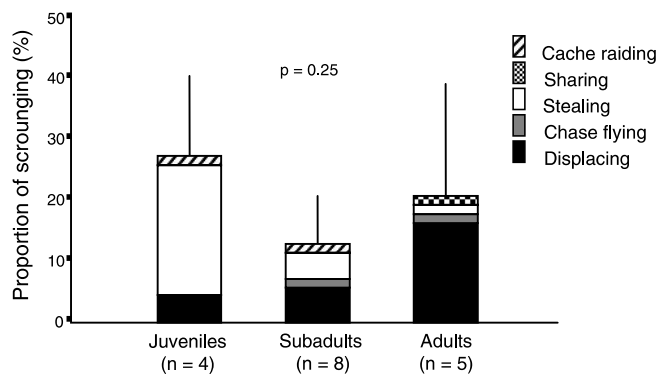


Fig. 1: Proportional use of scrounging (%) of different age classes of ravens ( $\bar{x} \pm$  SE) at the wolf feedings. Stacked bars represent proportion of techniques (%) used

positively with the number of attacks the individuals received from the wolves ( $0.4 \pm 0.04$  times/feeding;  $r_s = 0.51$ ,  $n = 17$ ,  $p = 0.036$ ). This indicates that attempting to get food directly from the feeding site increases the risk of being killed.

In line with the prediction that under high mortality risk some individuals should favour the possibility of getting food from conspecifics rather than directly from the site, we found a negative correlation between the number of scrounging attempts of individuals and the number of landings ( $r_s = -0.48$ ,  $n = 17$ ,  $p = 0.05$ ; Fig. 2a). In addition, there was a negative correlation between the individuals' success of scrounging and the success of getting food directly from the site ( $r_s = -0.53$ ,  $n = 17$ ,  $p = 0.028$ ; Fig. 2b), but a positive correlation between the individuals' scrounging attempts and their success in scrounging ( $r_s = 0.91$ ,  $n = 17$ ,  $p < 0.001$ ; Fig. 2c). This indicates that individuals may specialize on the more profitable alternative.

The proportional use of scrounging did not correlate with the proportion of retreats in aggressive encounters ( $r_s = -0.31$ ,  $n = 13$ ,  $p = 0.3$ ). Thus, individuals of high status do not generally prefer to make use of scrounging. However, when we distinguished between different types of scrounging and between the two time periods of the wolf feedings (Fig. 3), effects of social status and social relationships became apparent.

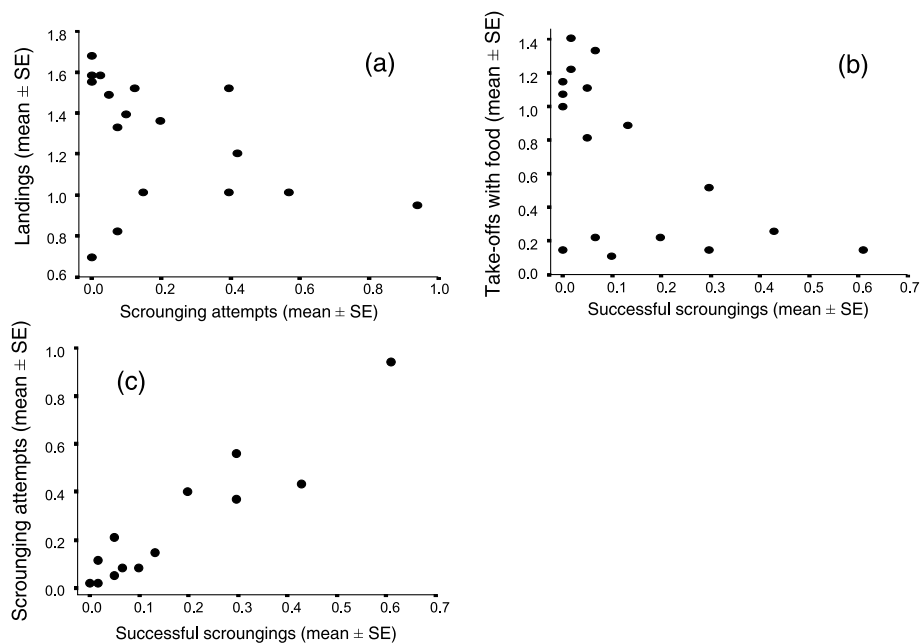


Fig. 2: Relationship between the individuals' (a) landings at the site and scrounging attempts, (b) success of getting food from the site and scrounging and (c) scrounging attempts and success of scrounging

When food could be accessed either directly at the site or from conspecifics that were already in possession of food, displacing was the most frequently used scrounging technique (about 70% of the cases; Fig. 3). The rate at which individuals were the target of displacing attempts correlated positively with their retreats in aggressive interactions ( $r_s = 0.89$ ,  $n = 11$ ,  $p < 0.001$ ). Also, younger ravens tended to be more often displaced than older ones ( $r_s = -0.47$ ,  $n = 11$ ,  $p = 0.1$ ). On average, individuals successfully obtained food at  $73 \pm 8\%$  of their displacing attempts. Hence, displacing may be a profitable tactic for high-status individuals to obtain food when the risk of predation at the feeding site is relatively high. But as there was no significant correlation between the individuals' displacing attempts and their proportional use of scrounging ( $r_s = 0.24$ ,  $n = 10$ ,  $p = 0.5$ ), ravens that used displacing as scrounging technique did not always exhibit high scrounging rates in general.

When food was no longer available at the feeding site, the relative frequency of displacing decreased and the relative frequency of stealing increased significantly compared with when food was available (displacing:  $n = 11$ ,  $z = 2.18$ ,  $p = 0.029$ ; stealing:  $n = 11$ ,  $z = 2.5$ ,  $p = 0.013$ ; Fig. 3). The rate at which individuals were the target of stealing attempts correlated negatively with their retreats in aggressive encounters ( $r_s = -0.92$ ,  $n = 11$ ,  $p < 0.001$ ). In addition, younger ravens tended to show more stealing than older ones ( $r_s = -0.59$ ,  $n = 10$ ,  $p = 0.07$ ) and stealing success was low ( $19 \pm 6\%$  of the attempts). Thus, stealing as a scrounging tactic may be used by subordinates rather than by dominants, particularly when the food at the feeding site is almost gone.

Once the feeding site was depleted, the ravens also tended to increase their attempts in getting food by sharing and cache raiding (relative frequency during vs. after feeding: sharing:  $n = 11$ ,  $z = 1.6$ ,  $p = 0.11$ ; cache raiding:  $n = 11$ ,  $z = 1.5$ ,  $p = 0.14$ ; Fig. 3). Sharing requests did not significantly correlate with retreats in aggressive encounters ( $r_s = -0.24$ ,  $n = 11$ ,  $p = 0.47$ ), but correlated



Fig. 3: Differences in the relative frequency of scrounging techniques (%) at the wolves when food was available ( $\bar{x} \pm SE$ ,  $n = 13$  individuals) and after the site has been depleted ( $\bar{x} \pm SE$ ,  $n = 11$  individuals)

positively with both parameters of affiliative relationship (food sharing–preening bouts:  $r_s = 0.62$ ,  $n = 11$ ,  $p = 0.042$ ; food sharing–resting in proximity:  $r_s = 0.64$ ,  $n = 10$ ,  $p = 0.045$ ). Both individuals that invited sharings were females whereas four of a total of five individuals that gave food were males. The success of requesting food from others was relatively low ( $17 \pm 10\%$  of the attempts).

On average, the ravens carried food off to the nearby woods at  $0.3 \pm 0.06$  times per feeding. On some of these occasions, we were able to observe individuals caching food and, even more infrequently, we could observe them during cache raiding (total number of observations made in a total of four individuals: 7). The success of the few observed raiding attempts was relatively high ( $\bar{x} = 50\%$ ,  $\bar{x} = 63\%$ ). A larger sample of observations on unmarked individuals ( $n = 43$ ) revealed similar success of raiding ( $49 \pm 0.8\%$  of the attempts). When the raiders caught the attention of cachers ( $n = 18$ ), they were chased off in 78% of the cases. This may indicate that raiders are competitively inferior to cachers.

### Wild Boar Site

Individuals that were present around the wild boar enclosure landed at least once per feeding in  $98 \pm 0.6\%$  of the cases. When meat was delivered, individuals attempted to obtain food directly from the site on  $1.7 \pm 0.1$  times/feeding, whereas they used scrounging on  $0.2 \pm 0.06$  times/feeding. Comparable with the situation at the wolves, the number of landings correlated positively with the success of obtaining food from the site ( $0.8 \pm 0.1$  times/feeding;  $r_s = 0.9$ ,  $n = 15$ ,  $p < 0.001$ ). However, foraging ravens were never aggressively attacked, or killed, by wild boars during the entire observation period.

At low mortality risk, we neither found a significant correlation between the individuals' numbers of landings and scrounging attempts ( $r_s = -0.17$ ,  $n = 15$ ,  $p = 0.6$ ), nor between their success of obtaining food from the site and the success of scrounging ( $r_s = -0.22$ ,  $n = 15$ ,  $p = 0.4$ ). Also, the proportional use of scrounging was significantly lower at the wild boars than at the wolves ( $n = 15$ ,  $z = 2$ ,  $p = 0.04$ ; Fig. 4). However, individuals that showed a high propensity of scrounging at the wolves tended to have one also at the wild boars ( $r_s = 0.47$ ,  $n = 15$ ,  $p = 0.08$ ).

As with the proportional use of scrounging, the relative frequency of some scrounging techniques differed significantly between the feeding sites. Sharing was more frequent during wild boar feedings than during wolf feedings ( $n = 11$ ,  $z = 2.38$ ,  $p = 0.017$ ), whereas individuals with food were more often the target of displacing at the wolves as compared at the wild boars ( $n = 11$ ,  $z = 2.94$ ,  $p = 0.003$ ).

### Effects of Food Quality

Comparison between different food qualities (meat vs. kitchen leftovers) offered at the wild boars did not reveal significant effects on the number of landings ( $n = 15$ ,  $z = 1.08$ ,  $p = 0.28$ ) or on the success of getting food from the

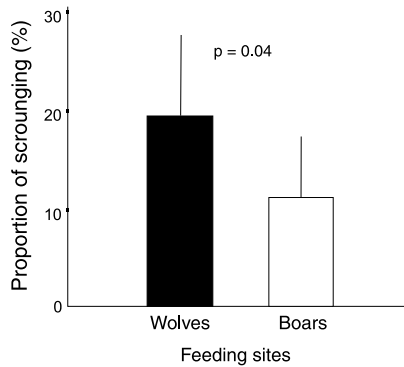


Fig. 4: Differences in the proportional use of scrounging (%) of ravens at the wolf feedings ( $\bar{x} \pm SE$ ,  $n = 17$  individuals) and wild boar feedings ( $\bar{x} \pm SE$ ,  $n = 18$  individuals)

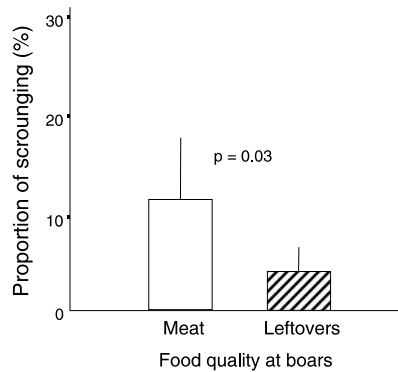


Fig. 5: Differences in the proportional use of scrounging (%) of ravens at different food qualities during wild boar feedings ( $\bar{x} \pm SE$ ,  $n = 18$  individuals)

site per feeding ( $n = 15$ ,  $z = 1.22$ ,  $p = 0.22$ ). However, the proportional use of scrounging and the success of scrounging were significantly higher when meat was provided as compared with kitchen leftovers (scrounging:  $n = 15$ ,  $z = 2.14$ ,  $p = 0.03$ ; Fig. 5; success:  $n = 15$ ,  $z = 2.23$ ,  $p = 0.026$ ). The relative frequency of scrounging techniques was not affected by food quality (displacing:  $n = 8$ ,  $z = 0.68$ ,  $p = 0.49$ ; stealing:  $n = 8$ ,  $z = 0.67$ ,  $p = 0.5$ ; sharing:  $n = 8$ ,  $z = 1.07$ ,  $p = 0.29$ ; cache raiding:  $n = 8$ ,  $z = 1$ ,  $p = 0.32$ ).

## Discussion

Our results support the assumption that the mortality risk at the feeding site affects the ravens' decision whether or not to show scrounging in competition for food. The proportional use of scrounging was higher at the wolves than at the

wild boars. In addition, the individuals concentrated either on scrounging or producing at the wolves, but not at the boars.

Hence, ravens foraging under low mortality risk appear to adopt predominantly the role of producers. Even with high-quality food such as meat, scrounging was shown only occasionally and without significant impact on the use and success of producing. Under high mortality risk, however, some individuals seem to prefer scrounging as the safer tactic to obtain food (Ranta et al. 1998). Indeed, scrounging allowed ravens to avoid being attacked by the wolves, as it usually occurred off the feeding site. This spatial separation of producing and scrounging may explain why, compared with other studies (e.g. Barta and Giraldeau 2000), our results revealed rather strong effects of predation hazard. However, this condition may be of general significance to ravens because they regularly scavenge at carcasses in the presence of potential predators (Heinrich 1999).

Still, our findings could be interpreted as a by-effect of differences in the food availability at the enclosures of wolves and wild boars. At the wolves, more meat was provided than at the boars and, at the boars, addition of meat was associated with more scrounging. Hence, a high proportion of scrounging at the wolves could be merely because of the provision of large amounts of meat rather than on high predation risk. However, according to its definition, scrounging directs on the food conspecifics have made available. For the present study, this means that scrounging may depend on the amount of food individuals obtained at the enclosures rather than on the total amount of the food source. Indeed, the take-off rates of ravens with meat were very similar at the wolves and the wild boars (at both sites:  $\bar{x} \pm SE = 0.8 \pm 0.1$  times/feeding) which indicates that there were similar amounts of food available for scrounging. Thus, differences in the food quantity provided to the zoo animals are unlikely to explain our results.

As during co-feeding with wolves, the individuals' success in scrounging was negatively related to their success in getting food directly from the site, the ravens may be forced to efficiently time either the landing at the site or the scrounging from conspecifics. Effects of divided attention on foraging efficiency have been reported mainly in the context of predator avoidance (e.g. Milinski and Heller 1978; Lima 1998; Dukas and Kamil 2000) but also for scrounging decisions (e.g. Giraldeau and Lefebvre 1987; Koops and Giraldeau 1996; Coolen et al. 2001). The fact that the negative relationship between producing and scrounging holds only for the situation with wolves, may support the idea that the degree of compatibility between both tactics varies as a function of the environmental conditions (Coolen et al. 2001). However, our data do not imply that ravens foraging under low predation pressure can go for producing and scrounging at the same time (assumption of complete compatibility, e.g. Clark and Mangel 1984), but merely demonstrate that in this condition, alternating between tactics has no detrimental effects on the efficiency of producing.

The relationship between the success of scrounging and its use at the wolves supports the assumption that individuals adopt the tactic in which they are competitively superior (e.g. Barta and Giraldeau 1998, Flynn and Giraldeau

2001). This may explain why only few individuals frequently performed scrounging, which is also consistent with the idea that the scroungers' pay-off is negatively frequency-dependent (Mottley and Giraldeau 2000). Furthermore, this may explain why, even at the wolves, producing remained the preferred tactic for many ravens. However, when the site was depleted, scrounging offered an 'additional' possibility to gain food and consequently, was shown also by individuals that performed scrounging with only limited success.

The profitability of scrounging (i.e. the proportion of successful attempts) was, to a large extent, determined by the way 'how' individuals got food from others. Displacing was about two times as profitable than stealing or sharing and it was shown particularly at the beginning when the competition for food between ravens and wolves was highest. Thus, displacing could be considered as the most important alternative to producing. Stealing and sharing were shown particularly when the feeding site was depleted. Hence, individuals that were involved predominantly in these kinds of scrounging could have failed in getting food directly from the site and/or have lost their food to other ravens. In this case, scrounging would allow ravens to 'make the best of a bad job' rather than to avoid predation risk.

The use of different techniques was related to the social relationships between the individuals (Coussi-Korbel and Fragaszy 1995). Displacing was particularly shown by dominants whereas stealing was performed by subordinates. As dominance status is a function of age in ravens (Gwinner 1964; Huber 1991), both techniques could be also linked to certain age-classes with older birds showing a tendency for displacing rather than stealing. These findings are comparable with those obtained in other birds such as keas, *Nestor notabilis* (Diamond and Bond 1991) and gulls, *Larus* sp. (Verbeek 1977; Burger and Gochfeld 1981), also in primates, such as mangabees, *Cercocebus torquatus* (Coussi-Korbel 1994) and chimpanzees, *Pan troglodytes* (Menzel 1974) and even in ungulates such as red deers, *Cervus elaphus* (Schmidt and Hoi 1999). However, our data are only partly consistent with the idea of a dominance-based producer–scrounger system where dominants show scrounging and subordinates use producing (e.g. Czikeli 1983; Barta and Giraldeau 1998). Instead, they suggest that dominance status may allow ravens to perform particular techniques of scrounging, such as displacing, more successfully than others but do not affect the individuals' propensity to scrounge in general.

In contrast to other scrounging techniques, food sharing was solicited only by birds that were probably involved in different stages of pair bonding, as indicated by mutual preening bouts and resting in close proximity before and after feeding. Food sharing as a means of scrounging between non-related social allies has been also described for chimpanzees, *P. troglodytes* (Boesch and Boesch 1989).

Although cache raiding appears to be a profitable technique, it could be observed infrequently. This may be partly because of methodological problems of data collection, e.g. a restricted view towards caches and also because of its rather rare occurrence. Cache raiding strongly depends on the ability to directly observe

others caching (Heinrich and Pepper 1998; T. Bugnyar and K. Kotrschal, in press). Therefore, potential raiders would have to leave the commonly used feeding site together with the cachers for watching them caching which, in turn, would reduce their chance to obtain food directly at the site. Indeed, cache raiding occurred not before the site was depleted of food. In addition, it was shown presumably by individuals with little resource holding potential.

In conclusion, our findings show that ravens may adopt scrounging as an alternative foraging tactic according to environmental conditions and social context.

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### Literature Cited

- Baker, M. C., Belcher, C. S., Deutsch, L. C., Sherman, G. L. & Thomson, D. B. 1981: Foraging success in junco flocks and the effects of social hierarchy. *Anim. Behav.* **29**, 137–142.
- Barnard, C. J. 1984: Producers and Scroungers: Strategies of Exploitation and Parasitism. Chapman & Hall, New York.
- Barnard, C. J. & Sibly, R. M. 1981: Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Anim. Behav.* **29**, 543–550.
- Barta, Z. & Giraldeau, L.-A. 1998: The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing-scrounging game. *Behav. Ecol. Sociobiol.* **42**, 217–223.
- Barta, Z. & Giraldeau, L.-A. 2000: Daily patterns of optimal producer and scrounger use under predation hazard: a state-dependent dynamic game analysis. *Am. Nat.* **155**, 570–582.
- Bertram, B. C. R. 1978: Living in groups: predators and prey. In: *Behavioural Ecology: An Evolutionary Approach*, 1st edn. (Krebs, J. R. & Davies, N. B., eds). Blackwell Science, Oxford, pp. 64–96.
- Boesch, C. & Boesch, H. 1989: Hunting behavior of wild chimpanzees in the Tai National Park. *Am. J. Phys. Anthropol.* **78**, 547–573.
- Brockmann, H. J. & Barnard, C. J. 1979: Kleptoparasitism in birds. *Anim. Behav.* **27**, 487–514.
- Broom, M. & Ruxton, G. D. 1998: Evolutionary stable stealing: game theory applied to kleptoparasitism. *Behav. Ecol.* **9**, 397–403.
- Bugnyar, T. & Kotrschal, K. 1997: An experimental analysis of social foraging in ravens: individual tactics, scrounging, and deception. *Adv. Ethol.* **32**, 497.
- Bugnyar, T. & Kotrschal, K. 2001: Movement coordination and signalling in ravens (*Corvus corax*): an experimental field study. *Acta Ethol.* **3**, 101–109.
- Bugnyar, T. & Kotrschal, K., in press: Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it ‘tactical’ deception? *Anim. Behav.* (in press).
- Burger, J. & Gochfeld, M. 1981: Age-related differences in piracy behaviour of four species of gulls, *Larus*. *Behaviour* **77**, 242–267.
- Caraco, T. & Giraldeau, L.-A. 1991: Social foraging: producing and scrounging in a stochastic environment. *J. Theoret. Biol.* **153**, 559–583.
- Clark, C. W. & Mangel, M. 1984: Foraging and flocking strategies: information in an uncertain environment. *Am. Nat.* **123**, 626–641.

- Coolen, I., Giraldeau, L.-A. & Lavoie, M. 2001: Head position as an indicator of producer and scrounger tactics in a ground-feeding bird. *Anim. Behav.* **61**, 895–903.
- Coussi-Korbel, S. 1994: Learning to outwit a competitor in mangabeys (*Cercocebus t. torquatus*). *J. Comp. Psychol.* **108**, 164–171.
- Coussi-Korbel, S. & Frigaszy, D. M. 1995: On the relation between social dynamics and social learning. *Anim. Behav.* **50**, 1441–1453.
- Czikeli, H. 1983: Agonistic interactions within a winter flock of slate-coloured juncos (*Junco hyemalis*): evidence for the dominants' strategy. *Z. Tierpsychol.* **61**, 61–66.
- Diamond, J. & Bond, A. B. 1991: Social behavior and the ontogeny of foraging in the Kea (*Nestor notabilis*). *Ethology* **88**, 128–144.
- Drack, G. & Kotrschal, K. 1995: Aktivitätsmuster und Spiel freilebender Kolkrahen *Corvus corax* im inneren Almtal/Oberösterreich. *Monticula* **7**, 159–174.
- Dukas, R. & Kamil, A. C. 2000: The cost of limited attention in blue jays. *Behav. Ecol.* **11**, 502–506.
- Flynn, R. E. & Giraldeau, L.-A. 2001: Producer–scrounger games in a spatially explicit world: tactic use influences flock geometry of spice finches. *Ethology* **107**, 249–257.
- Giraldeau, L.-A. & Lefebvre, L. 1987: Scrounging prevents cultural transmission of food finding behaviour in pigeons. *Anim. Behav.* **35**, 387–394.
- Giraldeau, L.-A. & Beauchamp, G. 1999: Food exploitation: searching for the optimal joining policy. *TREE* **14**, 102–106.
- Giraldeau, L.-A. & Caraco, T. 2000: *Social Foraging Theory*. Princeton Univ. Press, Princeton, New Jersey.
- Gwinner, E. 1964: Untersuchungen über das Ausdrucks und Sozialverhalten des Kolkrahen (*Corvus corax corax* L.). *Z. Tierpsychol.* **21**, 657–748.
- Gwinner, E. 1965: Über den Einfluß des Hungers und andere Faktoren auf die Versteck-Aktivität des Kolkrahen (*Corvus corax*). *Vogelwarte* **23**, 1–4.
- Haffer, J. 1993: Der Kolkrahe. In: *Handbuch der Vögel Mitteleuropas*, Vol. 13 (Glutz von Blotzheim, U. ed.). Aula Verlag, Wiesbaden, pp. 1947–2022.
- Heinrich, B. 1988: Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven, *Corvus corax*. *Behav. Ecol. Sociobiol.* **23**, 141–156.
- Heinrich, B. 1989: Ravens in Winter. Simon & Schuster, New York.
- Heinrich, B. 1994a: Age and mouth color in common ravens. *Condor* **94**, 549–550.
- Heinrich, B. 1994b: When is the common raven black? *Wilson Bull.* **106**, 571–572.
- Heinrich, B. 1999: *Mind of the Raven*. Harper-Collins, New York.
- Heinrich, B. & Marzluff, J. M. 1991: Do common ravens yell because they want to attract others? *Behav. Ecol. Sociobiol.* **28**, 13–21.
- Heinrich, B. & Pepper, J. 1998: Influence of competitors on caching behaviour in common ravens, *Corvus corax*. *Anim. Behav.* **56**, 1083–1090.
- Heinrich, B., Marzluff, J. M. & Marzluff, C. S. 1993: Common ravens are attracted by appeasement calls of food discoverers when attacked. *Auk* **110**, 247–254.
- Huber, B. 1991: Bildung, Alterszusammensetzung und Sozialstruktur von Gruppen nichtbrütender Kolkrahen. *Met. Schriftenr. Naturschutz* **2**, 45–92.
- Kochert, M. N. 1973: Evaluation of a vinyl wing marker for raptors. *Raptor Res.* **7**, 117–118.
- Koops, M. A. & Giraldeau, L.-A. 1996: Producer–scrounger foraging games in starlings: a test of rate-maximizing and risk-sensitive models. *Anim. Behav.* **51**, 773–783.
- Krebs, J. R., MacRoberts, M. H. & Cullen, J. M. 1972: Flocking and feeding in the great tit *Parus major*: an experimental study. *Anim. Behav.* **114**, 507–530.
- Lima, S. L. 1998: Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Adv. Study Behav.* **27**, 215–291.
- Marzluff, J. M. & Heinrich, B. 1991: Foraging by common ravens in the presence and absence of territory holders: an experimental analysis of social foraging. *Anim. Behav.* **42**, 755–770.
- Menzel, E. W. 1974: A group of young chimpanzees in a one-acre field. In: *Behavior of Nonhuman Primates* (Schrier, A.M. & Stollnitz, F. eds). Academic Press, New York, pp. 83–153.
- Milinski, M. & Heller, R. 1978: Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). *Nature* **275**, 642–644.
- Mottley, K. & Giraldeau, L.-A. 2000: Experimental evidence that group foragers can converge on predicted producer–scrounger equilibria. *Anim. Behav.* **60**, 341–350.

- Parker, P. G., Waite, T. A., Heinrich, B. & Marzluff, J. M. 1994: Do common ravens share food bonanzas with kin? DNA finger printing evidence. *Anim. Behav.* **48**, 1085—1093.
- Powell, G. V. N. 1974: Experimental analysis of the social value of flocking in starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Anim. Behav.* **22**, 501—505.
- Ranta, E., Peuhkuri, N., Laurila, A., Rita, H. & Metcalfe, N. B. 1996: Producers, scroungers and foraging group structure. *Anim. Behav.* **51**, 171—175.
- Ranta, E., Peuhkuri, N., Hirvonen, H. & Barnard, C. J. 1998: Producers, scroungers and the price of a free meal. *Anim. Behav.* **55**, 737—744.
- Ratcliffe, D. 1997: *The Raven. A Natural in History Britain and Ireland.* T. & A.D. Poyser, London.
- Schmidt, K. T. & Hoi, H. 1999: Feeding tactics of low-ranking red deer stags at supplementary feeding sites. *Ethology* **105**, 349—360.
- Stiehl, R. B. 1978: Aspects of the ecology of the common raven in Harney Basin, Oregon. PhD Thesis, Portland State University, USA.
- Verbeek, N. A. M. 1977: Age differences in the digging frequency of herring gulls on a dump. *Condor* **79**, 123—125.
- Vickery, W. L., Giraldeau, L.-A., Templeton, J. J., Kramer, D. L. & Chapman, C. A. 1991: Producers, scroungers, and group foraging. *Am. Nat.* **137**, 847—864.
- de Waal, F. B. M., van Hooff, J. A. R. A. M. & Netto, W. J. 1976: An ethological analysis of agonistic interaction in a captive group of Java-monkeys (*Macaca fascicularis*). *Primates* **17**, 257—290.

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