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Will food-handling time influence agonistic behaviour in sub-adult common ravens (*Corvus corax*)?

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Abstract

Discovering a food source may invoke either competition or cooperation, depending on many factors such as divisibility and accessibility. We experimentally investigated the influence of effort to procure food on the tolerance towards others during feeding. Nine sub-adult captive ravens were tested in different foraging contexts that differed in foraging effort, namely three string-pulling conditions and two without pulling requirement. We expected that the effort to gain access to food would positively affect the tolerance towards others at feeding. As predicted, we found fewer agonistic interactions, fewer displacements of subordinates from food and prolonged feeding bouts in the three string-pulling conditions compared to the two conditions when no pulling was involved. Further, in the string pulling tasks interactions occurred mostly on the perch before pulling and only rarely was pulling interrupted by agonistic interactions. The rate of interactions did not change over trials. Our data suggests that perceived effort influences social behaviour.

Keywords

Corvids; Problem solving; Social foraging; String pulling; Food sharing

1. Introduction

Social foraging benefits individuals by reducing predation risk (e.g. Powell, 1974), by increasing the chance of finding scattered food (e.g. Krebs et al., 1972) and by overcoming resource defence by territory holders (e.g. Marzluff and Heinrich, 1991). However, social foraging may also lead to high levels of competition and ‘scrounging’ behaviours, i.e. the exploitation of food made available by others (Barnard and Sibly, 1981). The benefits versus costs of foraging in a group depend on ecological factors such as the distribution of food as well as on social factors such as group size and the type of social network (Giraldeau and

Caraco, 2000). Individual differences have been shown to affect producing and scrounging dynamics (e.g. Barta and Giraldeau, 1998; Beauchamp, 2000; Kurvers et al., 2009). Further, when and to what extent cooperation versus competition occurs may depend on the time needed to handle food (Jolles et al., 2013).

Tolerance may be beneficial because it results in a higher food intake of both individuals and in certain cases in a better defence of resources, such as in paired individuals (e.g. King et al., 2009; Jolles et al., 2013; Beauchamp, 2000). Thus, mutual tolerance affects the access to food and its distribution among individuals. It is associated with spatial proximity (Van Schaik and Carel, 2003) and attention levels towards others (Fritz and Kotrschal, 1999; Range et al., 2006; Scheid et al., 2007). More generally, tolerance has been considered to play a major role in constraining the social acquisition and transmission of information (Coussi-Korbel and Frigaszy, 1995) as well as cooperative problem solving (Chalmeau et al., 1997; Melis et al., 2006b; Mendres and De Waal, 2000). Primates and rats (*Rattus norvegicus*) are affected by others' propensity to share food in cooperation experiments (De Waal, 2000; Hauser et al., 2003; Rutte and Taborsky, 2008; Werdenich and Huber, 2002) and, when given the choice, select tolerant partners (De Waal, 2000; Melis et al., 2006b). Longtailed macaques (*Macaca fascicularis*) and vervet monkeys (*Cercopithecus aethiops*) even change their grooming pattern towards group members who have become skilled in a foraging task, suggesting that they proactively try to affect the tolerance at feeding times of these particular individuals (Seyfarth and Cheney, 1984; Stambach, 1988; Fruteau et al., 2013). In certain species, tolerance does not seem to be a fixed attribute, but is rather given or withheld, depending on the opponent as well as on the situation (Noe, 2006). Two of the situational factors are food availability and time needed to produce the food. The former has been varied by Jolles et al. (2013) in rooks. They found a higher rate of participation in the high food availability condition than in the low food availability condition. Notably, the rooks' tactical behaviour was highly consistent across the two conditions, i.e. either being a producer or a scrounger. The latter factor, handling time has not been studied in detail yet. Here, we investigated whether tolerance in ravens depends on the effort required to gain access to food.

Ravens scavenge on ephemeral food sources such as carcasses and kills of large mammals (Heinrich, 1988a; Parker et al., 1994). Immature and non-breeding ravens regularly cooperate with nonkin on a mutualistic basis (Heinrich, 1988a; Marzluff and Heinrich, 1991; Parker et al., 1994) for finding food (Marzluff and Heinrich, 1991; Marzluff et al., 1996), for overcoming the food defence by adult territory holders (Marzluff and Heinrich, 1991) and for snatching food from predators such as wolves (Bugnyar et al., 2001). However, ravens also show sophisticated manoeuvres in competition for food (reviews in Heinrich, 2011; Bugnyar, 2013), using others as a source of knowledge and profiting from others through scrounging. Scrounging tactics are context-dependent and affected by social relations (Bugnyar and Kotrschal, 2002a,b).

The string-pulling paradigm (food out of reach is accessed by pulling the string) is a versatile task, as it has been used to test for cognitive capacities, such as means-end understanding and insight learning, in various species (Heinrich and Bugnyar, 2005; Thorpe, 1943; Werdenich and Huber, 2006) as well as in a social foraging scenario (Jolles et al.,

2013). The vertical version of this task (string dangling from the perch) requires a series of coordinated movements (pulling up the string, stepping on the pulled up loop, repeating the sequence) and is thus a task which is probably unparalleled in a natural foraging scenario of ravens (Heinrich, 1995). However, the task enables a reproducible method of varying the amount of effort required to reach the food by varying the length of the string (this study) or the number of strings (Jolles et al., 2013). Moreover, it eliminates the profitability of scrounging since displacing an individual from food attached to the string usually results in the food being dropped (Heinrich, 2000). The scrounger therefore cannot take advantage of any pulling effort already invested by the original producer. As such the string pulling paradigm is a producer-scrounger game (Barnard and Sibly, 1981; Giraldeau and Caraco, 2000; Jolles et al., 2013). The vertical string pulling paradigm was used in this study to investigate how effort to gain access to food affects tolerance during feeding in sub-adult captive ravens. Previously, all birds were successfully tested individually to assess their string pulling skills in the standardized paradigm (50 cm-string; Bonechi et al., unpubl. data).

In the current study, birds were tested in dyads either with two vertical strings each of (a) 10 cm, (b) 50 cm or (c) 160 cm or, with a simpler task that required no pulling where two pieces of food were tied to (d) the perch or (e) the wire-mesh of the enclosure. In each of the five conditions, birds were tested in dyads with different partners to increase the possibility of having birds in both roles, dominant and subordinate. We were interested how the ravens' behaviour was influenced by the presence of one conspecific engaged in a similar task and whether the time it took to gain access to food mattered. We also looked at whether the birds would show any signs of co-action or cooperation (i.e. pulling together). This design of testing two birds on two strings/baits simultaneously allows us to study the role food handling has on tactic use, and the interplay of it with dominance.

Mutual tolerance might be expected to decrease with increasing food procuring effort. For instance, the more effort birds invest in stripping a carcass or snatching food from predators, the less tolerant they should become of conspecifics that try to steal the food. The reduced tolerance could result in high levels of aggression and more scrounging attempts. To our knowledge this has not been investigated in a controlled study yet. In some situations the mutual tolerance could increase with food procuring effort. Increased tolerance could be expected in the string-pulling task because firstly it requires birds to focus their attention on the problem (performing a series of coordinated beak and foot movements), and secondly because it is not a profitable set-up for scrounging. The latter is due to food being dropped and the effort of the procurer is lost as well as rarely any food pieces falling to the ground (which depends on the type of bait used, in Jolles et al. (2013) baits could fall to the ground, rarely in our case). We thus expected ravens to show fewer agonistic interactions and fewer displacements about the food and to spend more time feeding without interference in the high-effort/complex manipulation tasks compared to the low- effort/no manipulation tasks. Agonistic interactions might be about place (securing the best source of food rather than about the food item per se) because of its small size. If the birds learn to adjust their tolerance levels to the experimental conditions, we would expect to find an increase in tolerance across sessions or, if the birds learn rapidly, across the trials of the first session. To test for the possibility that the location of food presentation (perch or ground), rather than

the effort to pull the food up, explains the ravens' behaviour, we compared the two non-pulling tasks to the string pulling tasks. If the effort to produce food is the crucial variable then the two non-pulling tasks should differ from the three string pulling tasks, and the string pulling tasks differ ordered by the length of the string.

2. Methods

2.1. Subjects and keeping

Subjects were nine sub-adult ravens (4 males, 5 females) originating from three different nests (one from the field, two from zoos). For individual identification they were marked with coloured leg bands. Birds were hand-raised at the Konrad Lorenz Research Station during 2004 (Schloegl et al., 2007) and, at the time of the study, were kept in two social groups composed of affiliated individuals at the Cumberland Wildpark Grünau. The birds will remain in captivity until the end of their natural life span. Group 1 consisted of two sibling pairs, two males and two females; Group 2 consisted of one sibling group, two males and two females, and one unrelated female. Birds were housed in a large naturalistically designed outdoor enclosures consisting of three outdoor compartments (80, 80, 30 m²; 7 m high) and five small indoor compartments (total area of 40 m²; 3 m high, picture in Bugnyar et al., 2007). The two groups were physically separated from each other in the two large outdoor compartments but had visual and acoustic contact. All outdoor parts were equipped with rocks, tree trunks, perches, vegetation cover, shelter, and natural soil. For the current study, we fixed three additional perches (each 4–5 m long) 190 cm above the ground in the outdoor compartments. These modifications occurred one month before the onset of the experiment to allow time for habituation to the new structures.

The experiments were conducted daily in the early afternoon between February and October 2006. During this period, ravens kept their standard feeding schedule (twice a day, around 7:30 and 16:00). In the morning they were given some fruits, bread and milk products while in the afternoon, after the experimental session was finished, they received their full diet supplemented with different kinds of meat. The birds were never deprived of food, and water was provided ad libitum.

2.2. Experimental set-up and procedure

Experiments were carried out in two stages. In both steps ravens were tested in dyads and confronted with two identical pieces of meat that were always 1 m apart (corresponding roughly to two times the length of a raven body). In stage 1 (February to July 2006), we manipulated the difficulty of accessing food:

‘50 cm string task’ (‘50 cm’) – the two pieces of meat were tied to the ends of two 50 cm long nylon strings attached to one of the new perches. To gain access to the food, the ravens had to pull the vertically dangling string up to the perch by repeatedly reaching down, grasping the string with the beak, pulling up a section of the string and stepping on the pulled-up loops. All birds had previous experience with this task but only in a non-social setting (Bonechi, unpubl. data).

‘Wire mesh task’ (“wire mesh”) – two pieces of meat were tied to the wire mesh of the aviary at ground level right below the perches with two short pieces of nylon strings (15 cm). The birds could reach the meat directly from the ground without any string-pulling effort.

To account for possible confounding effects of feeding on a perch (e.g. balance, possibility to move in only two directions) compared to feeding on the ground, and to vary the manipulation time (as a proxy for effort) until the ravens had access to meat, we added further tasks in stage 2 (July to October 2006):

‘Perch task’ (“perch”) – two pieces of meat were tied with two short nylon strings directly onto the perch. Food could be accessed simply by stepping onto it. The only difficulty in this task consisted of feeding while standing on the perch (i.e. keeping balance). ‘Short string task’ (“short”) – two pieces of meat were dangling from very short strings requiring only one pull to gain access. ‘Long string task’ (“long”) – two pieces of meat were dangled from strings so that they were ca. 20 cm above the ground. In this task, the string was ca. three times as long (160 cm) as in the 50 cm strong task, requiring extensive pulling. The meat was accessible from the ground, however tearing off pieces of meat was very challenging without a fixed structure (perch or wire mesh) that enabled the piece to be fixated.

Tests were carried out in one of the three outdoor compartments. Ravens that were not participating in a given test were locked into an adjacent compartment, but remained in visual and acoustic contact with the pair in the test situation. Separation was done with tempting by dog kibbles. Birds were tested in all possible dyads within each group (six dyadic combinations in group one, 10 dyadic combinations in group two). Individuals were tested four times per dyad. To avoid pseudo-replication, each testing session focused on only one bird. For example, dyad A–B was tested four times, then raven A was the focal bird twice and so was raven B. Each session consisted of three identical trials and data was averaged for individuals per trial and condition. In stage 1 condition 50 cm string and wire mesh were counterbalanced. In stage 2 conditions long, short and perch were counterbalanced. That means within each stage the order of tasks was randomized but not between stages. The order in which pairs were tested per day and which raven was the focal individual was pseudo-randomized by drawing lots.

After separation, the experimenter would attach two baited strings to the perch, move approximately 2 m away from the perch, and started videotaping. Note that the birds were rarely distracted by the non-participating ravens. In any case of distraction, as also occurred during overflying wild ravens, the trial was repeated. Each raven only participated in one testing session per day, and each trial lasted one minute. We could not reliably measure latency to the setup because the birds often immediately approached the meat after it was attached to the wire mesh or perch. Thus, a trial started with the first bird manipulating the piece of meat and/or the string (not required to pull), and ending with the interference of an experimenter (MG or GP). Inter-trial interval was set to minimum two minutes during which the meat pieces were retrieved, re-baited, and attached again. If one or both individuals failed to enter the set-up within three minutes of the two pieces being offered, we repeated the trial on another day.

Frozen pieces of meat attached to cow skin (4 cm × 5 cm × 1 cm) were used to prevent birds from tearing off large pieces and to avoid satiation within a single session (Heinrich and Bugnyar, 2005). Ravens rarely managed to get the whole piece off the string (14 times out of 488 trials, 3%) and in those cases, the trial was repeated.

2.3. Social relations

One observer (C. Schloegl) collected data on the social interactions between birds within each of the two groups. Each raven was observed every day (January 2006–October 2006) for five minutes evenly distributed over mornings and afternoons (focal sampling, Altmann, 1974). These data were taken independently from our experiment and were used to assess the affiliate relationships (expressed in allo-preening and sitting in close contact) and the dominance rank hierarchies (approach–retreat interactions).

2.4. Analysis

All trials were video-taped (SONY DCR-TRV14E, Digital Video Camera Recorder) and the following parameters were coded from the tapes: (1) which raven was the first at the set-up, (2) the latency of the second bird, (3) the number of agonistic interactions between the two birds including who initiated it and when it occurred, (4) the time invested in pulling up the string, (5) the total duration (s) of feeding, (6) the number of feeding bouts, (7) the number of scrounging attempts, and (8) the number of occasions and total duration of food sharing (co-feeding).

Agonistic interactions included approach–retreat interactions (one bird leaves as a consequence of the other bird's approach, with or without being threatened by the latter) and fights (one bird physically attacks the other with its beak and/or feet). Scrounging was successful if the other bird snatched bits of food from the producing bird. Importantly, individuals did not feed at the same time and the scrounger usually retreated with (pieces of) food. In contrast, sharing was defined as two birds feeding from the same piece of meat without agonistic interactions.

Data were analyzed using Microsoft Excel and SPSS 20.0. For analysis of the rank order based on the daily social protocols we used MatMan1.1. The Friedman test was used to compare the ravens' behaviour within the five conditions and generalized linear modelling (GLM) for assessing the influence of task and social factors including bird, kinship and the valence of the relationship within a dyad. Follow-up pairwise comparisons were conducted using a Wilcoxon test and controlling for the Type I errors across these comparisons at the 0.05 level using the LSD procedure. Since the 50 cm string task was the first string pulling task we tested for learning by comparing the results from the first and last 50 cm string trial using Wilcoxon signed-ranks test, and the Friedman test was used for comparing the three trials within the first session of the 50 cm string task. All tests used two-tailed comparisons and results were considered significant when $P < 0.05$. We analyzed per bird the time to eat, time to pull and start time based on all trials. Both MG and GP scored the 50 cm string and perch tasks. Interrater reliability, measured on the number of agonistic behaviour, was high, $\kappa = 0.94$.

2.5. Ethical statement

Individuals participating in the experiments were all handraised and either zoo-bred or collected from the wild with permission of the ‘Ministerium für Landwirtschaft, Umweltschutz und Raumordnung des Landes Brandenburg’. The birds were kept in two social groups in the Cumberland Wildpark in Grünau, Austria, accredited by the Austrian and local government (license AT00009917). This study adheres the ASAB Guidelines for the Use of Animals in Research. After completion of the present study, all individuals remained captivity housed.

3. Results

Neither within bird, nor within dyad differences were significant for the distribution of agonistic interactions across stage 1 and 2 (per bird: $N = 45$, $U = 192$, $P = 0.234$; per dyad: $F_{1,78} = 3.36$, $P = 0.071$, $\eta^2 = 0.041$); hence, the data from each of the five conditions were pooled. Table 1 shows participation rate, pull time, number of agonistic interactions, feeding time and bouts as well as instances of scrounging and co-feeding per task. The four fights were short and at a low level of aggression. No injuries occurred, the birds could escape the aggressor, and we saw no sign of stress, i.e. both birds carried on to participate in the next trial.

3.1. Producing effort: effect of task on time to pull and eat

All birds were quick to approach the experimental set-up in all conditions (Fig. 1). In the two non-pulling tasks, the mean ($\pm$ SE) time to eat was 7.42 ± 0.85 s (wire mesh) and 7.32 ± 1.1 s (perch), respectively. In the short string task, start time (i.e. birds on perch) was 2.63 ± 0.56 s, time to pull 1.33 ± 0.07 s, resulting in an averaged time to eat of 3.69 ± 0.52 s. They therefore had 94% of the time (one minute) still available for feeding and ca. 3 s more as in the wire mesh and perch task, respectively. In the 50 cm string task, birds’ start time was 2.17 ± 0.41 s and pull time 7.66 ± 0.25 s, average time to eat was 9.44 ± 0.45 s. As expected, the 50 cm string task was costly in terms of time it took birds to gain access to food, however the time to eat was just 3% less than in the wire mesh and perch task. In the long string task, excluding trials where both birds attempted to access the food from the ground (12 out of 104 trials), birds landed on the perch after 5.7 ± 1.04 s. In 64 trials (of the 92) the birds would then start pulling, needing on average 34.57 ± 1.47 s to pull up the meat. The average time to eat was 35.37 ± 1.57 s on successful trials, resulting in an average of 41% of the total time available for feeding. The difference between the start times (short, 50 cm, long string) was significant, $F_{2,468} = 7.08$, $P = 0.001$, $\eta^2 = 0.029$. Post hoc Tukey showed that the birds needed more time in the long compared to the short and 50 cm string task (long-short: $P = 0.007$ and long-50 cm: $P = 0.002$), possibly to evaluate the situation. The time to pull differed between the tasks, $F_{2,383} = 776.63$, $P < 0.001$, $\eta^2 = 0.802$. As expected, the difference in time to pull significantly increased with string length, as post hoc Tukey showed (short-50 cm: $P < 0.001$, short-long: $P < 0.001$, 50 cm-long: $P < 0.001$). The difference in time to eat was significant, $F_{4,545} = 237.25$, $P < 0.001$, $\eta^2 = 0.635$. Post hoc Tukey test showed that most time to eat was available in the short string task (all 4 comparisons “short” significant, largest $P = 0.025$), followed by similar time to eat in the

wire mesh, perch and 50 cm string task, and least time available in the long string task (all $P < 0.001$).

3.2. Effects of task on amount of agonistic interactions

As predicted, agonistic interactions differed significantly between the five tasks, (Friedman test revealed $\chi^2_4=23.6$, $P < 0.00001$). The number of agonistic interactions per bird was highest in the wire mesh task, followed by the perch, short, long and 50 cm string task (Table 1). Post hoc comparisons showed that the wire mesh task differed from all but perch task and no other comparison was significant (50 cm-wire mesh: $\chi^2 = 3.11$, $P < 0.0001$, long-wire mesh: $\chi^2 = 2.5$, $P = 0.008$, short-wire mesh: $\chi^2 = 2.39$, $P = 0.014$) (Fig. 2). Note that in the long string task, 8 of the 23 agonistic interactions occurred during attempts to feed from the ground.

We found no indication of learning or decrease in agonistic interactions over trials in the 50 cm string task. The low number of agonistic interactions was found already in the first trials of the 50 cm string task. There were no agonistic interactions in the first trial, three interactions by two individuals in the second trial, and two interactions by one individual in the third trial. The mean number of agonistic interactions per bird in the first and last trial of the 50 cm string task was not significantly different ($N = 3$, ties = 6, $T^+ = 4$, $P = 0.75$).

There was a significant difference in the mean time spent feeding per trial between the tasks, (Friedman test $\chi^2_4=18.93$, $P = 0.001$). This was due to the reduced available feeding time in the long string task (all comparisons of long to the other tasks $P < 0.05$) (Fig. 1C). Due to the one-minute limit, the birds had on average less than 30 s of feeding, whereas they had over 50 s left after accessing the meat in the other tasks.

There was a different pattern for feeding bouts. Here, the tasks also differed significantly (Friedman test $\chi^2_4=30.73$, $P < 0.0001$). The number of feeding bouts per trial was significantly higher in the wire mesh compared to short and long string task (short-wire mesh: $\chi^2_1=2.44$, $P = 0.01$, long-wire mesh: $\chi^2_1=4.0$, $P < 0.0001$) and also the perch task had a higher number of bouts than the long string task (perch-long: $\chi^2_1=2.44$, $P = 0.001$) (Fig. 2), indicating that ravens were feeding longer per bout in the perch (31.5 ± 1.1 s), short (33.6 ± 2.5 s) and 50 cm string task (36.9 ± 1.09 s) in comparison to the wire mesh (21.4 ± 1.39 s) and long string task (18.3 ± 2.37 s).

Co-feeding was observed rarely and only in the non-pulling tasks: in the wire mesh task three times out of 93 trials (5%), once between siblings (lasting 14 s) and two times between unrelated individuals dyads (lasting 42 s); in the perch task, six times out of 78 trials (8%), five times between unrelated individuals within 2 different dyads (lasting and average of 56 s) and once between siblings (lasting 4 s). Similarly, scrounging occurred mainly in the non-pulling tasks: five times in wire mesh (twice between siblings, and thrice between unrelated ravens), once between two siblings in perch, and once in 50 cm string (see below).

3.3. Effects of kinship, and valence of relationship on amount of agonistic interactions

The mean of agonistic behaviour for each dyad was tested using GLM with pair dyad as covariate. We found a significant effect of condition on the agonistic behaviour ($F_{4,11} = 10.87$, $P = 0.001$, $\eta^2 = 0.798$) as well as an interaction between condition and pair ($F_{4,11} = 3.54$, $P = 0.043$, $\eta^2 = 0.563$). There was no main effect of pair, $F < 1$. Not surprisingly some dyads had a higher number of interactions than others. To determine whether this was due to kinship or the valence of the relationship, the dyads were firstly coded as kin or non-kin. This yielded a main effect of condition ($F_{4,11} = 7.34$, $P = 0.004$, $\eta^2 = 0.727$) but no interaction ($F_{4,11} = 1.7$, $P = 0.22$, $\eta^2 = 0.382$) or effect of kinship ($F_{1,14} = 1.88$, $P = 0.19$, $\eta^2 = 0.118$). When coded into positive and negative relationships, none of the factors reached significance, condition: $F_{4,11} = 1.63$, $P = 0.24$, $\eta^2 = 0.372$, condition by relationship and relationship: both F 's < 1 . Thus, neither kinship nor the valence of the relationship explained the number of agonistic behaviours. However, the pairings did influence the number of interactions. This was also evident when we compared the agonistic behaviour with GLM by task as within factor and bird as covariate. The interaction of task and bird was significant ($F_{4,41} = 6.97$, $P = 0.043$, $\eta^2 = 0.875$).

3.4. Effect of timing

In the 50 cm and long string task we looked at when the first agonistic behaviour occurred: before string pulling started (interactions about place), during string pulling, or after the meat was pulled up (interactions about food). In the 50 cm string task, eleven interactions occurred about place, for example, the dominant bird would arrive later at the perch and choose the same string as the subordinate. In three cases the dominant intervened when the subordinate had the meat pulled up. In one of these trials the dominant bird stepped on the string and prevented the food from dropping, a successful case of scrounging. In the other two cases the meat had to be pulled up again. There was no case of interaction during pulling. At the perch in the long string task, three interactions (all by the dominant bird) occurred about place. Six interactions occurred during pulling, for example when the second bird arrived at the perch close to the first bird (five times dominant bird, once subordinate bird). In six cases the interaction happened after the meat had been pulled up (five times by dominant), which always resulted in loss of the food. We did not count it as scrounging as there was no contact with the meat or string.

There was a significantly higher proportion of interactions before any investment of string pulling was made (14 out of 29, $P = 0.029$). Notably, only in the long string task, where pulling took up to 30 s, did the other, 5 out of 6 times the dominant, bird interfere during pulling (Fig. 3). Most agonistic behaviour occurred before any effort to pull up the food had commenced or after the food was accessed with the latter occasions having a 22% success rate. During the high number of long string trials where only one bird pulled up the meat we noted that it was the subordinate in one third and the dominant bird in two thirds of trials that declined participation. Furthermore, it was mainly the dominant bird initiating agonistic behaviour (26 out of 29, $P < 0.0001$).

4. Discussion

Our results demonstrate that the manipulation time needed to reach food in experimental tasks modulates the number of agonistic interactions between dyads of affiliated sub-adult ravens with an established dominance rank hierarchy. The birds showed fewer agonistic interactions and longer feeding bouts in the tasks where birds had to pull up a string to reach the meat compared with tasks birds could feed directly from the ground or perch. Co-feeding was only seen in the non-pulling tasks.

It is assumed that in natural foraging situations tolerance decreases with the effort required to procure food. If one uses the number of co-feeding as indicator for tolerance, then our study confirms this. However, another measure is when and how many agonistic interactions occur. In the current experimental set-up, in agreement with (most of) our predictions, agonistic interactions decreased with increased task effort. Further, in the tasks with low effort interactions occurred during and after food production whereas they occurred more often before any food production started in the high effort tasks. These findings can be explained along several lines. Firstly, we found dominant birds frequently changed between food pieces that were fixed on the ground, leading to the displacement of the subordinates and a high number of relatively short feeding bouts. The challenge in the wire mesh and perch task was thus not to reach the food but to eat from a particular source. In contrast, displacing others from food was hardly profitable when accessing it was more difficult. For example, trying to steal the meat from the other raven meant to give up one's own piece, and the effort already invested by both birds, in exchange for the other's piece. In fact, the birds appeared to evaluate the situation in the beginning of the task (as indicated by the difference in start time) and hardly attempted to steal from the other even after the meat had been pulled up. Most interactions on the perch were about place or which string the (often) subordinate was allowed to pull. Ravens were less likely to approach the other bird when on a perch than when the bait was on the ground, presumably due to the costs of keeping balance. This was supported by the long string task trials split into interactions at the ground and perch. Nevertheless, the difference between perch and short/50 cm string indicates that the presentation of food on a perch could not fully explain the reduction of aggression and displacements compared to the wire mesh task. During string pulling, several steps have to be coordinated in a particular order to get to the food (Heinrich, 1995). This may have resulted in an increased attention on one's own piece of food in short, 50 cm and long string, decreasing attention towards the other raven. This notion is supported by the absence of interactions during pulling. Interruptions during pulling in the long string task came from the bird that had not pulled. In the 50 cm and long string task the birds did sometimes pause pulling but not interact, whereas in the perch and short string task the birds would pause from feeding and interact.

The number of agonistic interactions between two individuals depended to some extent on the pairing. Notably, this is not covered by dominance or affiliation in these sub-adult ravens. The dominance style in particular dyads mattered, suggesting that certain individuals did not 'get along' with each other perfectly well. Yet, the number of agonistic interactions was mainly influenced by task difficulty and timing more than by social relationships. The interactions were more about which string to pull than the food per se. Dominant birds

sometimes let the subordinate work in the two most demanding tasks with long strings (50 cm, long) and tried to get to the food after the meat had been pulled up – a strategy that was occasionally successful. Affiliation and dominance played only a minor role in our study, which is in contrast to the findings by Jolles et al. in rooks. An explanation could be that the ravens were sub-adult, and the testing done in dyads.

Because of the pulling effort involved, we expected less time to be spent on feeding in the 50 cm string than in the wire mesh task. This was not the case, most probably because dominant ravens tried to monopolize both food pieces in the wire mesh task. The resulting higher frequency of agonistic interactions (and feeding bouts) was at the expense of feeding time. Consequently, the time birds spent feeding was almost the same for all tasks except the long string task which required a very long pulling time.

In the wild, ravens scavenge on fresh carcasses and kills, with individual birds putting effort in extracting meat from bodies and scatter-hoarding the meat for later consumption (Heinrich, 1988b). Similar to our artificial set-up, such an extractive foraging scenario typically features different phases in which the effort required to access food varies. For instance, effort will depend on whether or not the carcass has already been opened up by a predator and/or whether it is defended (Heinrich, 1988a). In either case, the presence of other ravens will enhance the chances of obtaining food per individual (Marzluff and Heinrich, 1991) but also increase the risk of being kleptoparasitised (Bugnyar and Kotrschal, 2002a). In contrast to a typical scavenging situation, the ravens in our experiment could hardly scrounge but also showed hardly any food sharing (Stevens and Gibly, 2004). Aside of the task affordances, two identical pieces of food and the young age of our birds, before sexual maturity, may have contributed to the low rates of scrounging attempts and food-sharing.

To our knowledge, experimental studies on factors modulating tolerance between individuals are relatively rare (Fruteau et al., 2013; Noe, 2006; Van Schaik and Carel, 2003). This is surprising given the importance of tolerance for advanced social behaviours such as social learning, cultural information, transmission and cooperation (Coussi-Korbel and Fragazy, 1995; Noe, 2006; Bergmueller and Taborsky, 2010). Experiments on cooperative problem-solving have used variants of string pulling (Crawford, 1937; Hirata and Celli, 2003). Recently, effects of tolerance during feeding was shown to depend on the likelihood of solving the task (Melis et al., 2006b; Seed et al., 2008). Our set-up manipulated the effort per se but was apart from the two approaches in the long string task similar for both birds. What remains to be done is manipulating an individuals' effort during cooperation.

The context of testing is known to have substantial effects. In different situations, dominants have been reported to force subordinates to cooperate (Chalmeau, 1994; Tebbich et al., 1996), scrounge from others (Bugnyar and Kotrschal, 2002b; Fritz and Kotrschal, 1999) or be recruited by others (Marzluff and Heinrich, 1991; Melis et al., 2006a).

Subordinates can also force dominants to learn tolerance as Fruteau et al. (2013) have shown in vervet monkeys (*Chlorocebus sabeus*) playing a 'hidden circle' game. A subordinate would only open a treasure box when the dominants kept distance, which facilitated the

subordinate grabbing some treasures before the higher ranking members of the group could have access to the box. The requested distance resulted in a few important seconds head-start for the subordinate. Notably, the restraint had to be learned by each monkey separately. Interestingly, we did not find evidence of learning in our experiment, neither across sessions nor between the trials during the very first session. Possibly, the ravens have recalled their experiences gained with meat on string during individual training trials (Bonechi, unpubl. data) and were able to transfer the information to the social context of this experiment. Elaborate generalization abilities have recently been demonstrated in ravens (Bugnyar et al., 2007; Pfuhl, 2012) and other corvids such as Western scrub jays (Emery and Clayton, 2001) and rooks (Bird and Emery, 2009).

Our results indicate that the ravens are sensitive to the effort required to procure food (in terms of handling time). The ravens rarely interrupted pulling but rather interacted before pulling, i.e. interactions were about place. Dominant birds participated more and sparked off most interactions. The rate of interaction, though, depended mainly on the handling time and only secondary on the specific dyad tested.

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Fig. 1.

Time to start (left), time to pull (middle) and time to eat (right), all in seconds. WMT = wire mesh task, PT = perch task i.e. meat tied on perch, SST = short string task i.e. one-pull condition, 50ST = 50 cm string task, LST = long string task. By definition the time to start was zero in WMT and PT (begin of the trial) whereas time to manipulate the string could differ from time at perch. Time to pull is only applicable in SST, 50ST and LST. Time to eat is the time spent on acquiring the meat. The difference to 60 s is the available time for feeding. Box-plots indicate median, 25th and 75th percentile, whiskers indicate 10th and 90th percentile and dots indicate outliers, diamonds extreme outliers.

Fig. 2.

Agonistic interactions in the five tasks, Box-plots indicate median, 25th and 75th percentile, whiskers indicate 10th and 90th percentile and dots indicate outliers. WMT = meat on wire mesh, PT = meat on perch, SST = one-pull string task, 50ST = 50 cm pull condition, LST = long string task. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

Fig. 3. Temporal occurrence of agonistic interactions in the 50ST (50 cm string task) and LST (long string task, perch only) trials.

Table 1

Participation rate, time to eat, pull time, number of agonistic interactions (IA), feeding bouts and time, number of co-feeding, fights and scrounging per task.

Task	# of trials	Trials both took part	Time to eat mean (SD)	Pull time mean (SD)	Agonistic IA per bird mean (SD)	Agonistic IA per dyadic trial	Feeding bouts	Feeding time mean (SD)	Feed per bout	Co-feeding	Fights	Scrounging
WMT	96	93	7.42 (0.85)		9.67 (1.39)	0.94	2.05	45.27 (1.9)	22.08	3	1	5
PT	96	71	7.32 (1.1)		5.0 (0.94)	0.63	1.52	47.81 (1.6)	31.45	6	2	1
SST	96	66	3.69 (0.52)	1.33 (0.07)	3.1 (0.45)	0.42	1.35	49.83 (2.9)	36.91	0	1	0
50ST	96	85	9.44 (0.45)	7.66 (0.25)	1.89 (0.48)	0.20	1.25	41.41 (1.5)	33.13	0	0	1
LST	104	63	35.37 (1.57)	34.6 (1.47)	2.58 (0.38)	0.38	0.86	15.73 (2.4)	18.29	0	0	0