Ethology 111, 962—976 (2005)

Testing Problem Solving in Ravens: String-Pulling to Reach Food

Bernd Heinrich & Thomas Bugnyar

Department of Biology, University of Vermont, Burlington, VT, USA

Abstract

The aim of our study was to re-examine the acquisition of problem-solving behaviour in ravens: accessing meat suspended from a perch by a string. In contrast to a previous study, here we: (i) controlled for possible effects of fear of the string, competition by dominants, and social learning and (ii) devised a mechanically equivalent but non-intuitive task to test for the possibility of means–end understanding. One-year-old ravens confronted with meat on a string for the first time tried several ways to reach the food. However, five of six birds suddenly performed a coherent sequence of pulling up and stepping on loops of string, essential for solving the problem. Those five birds were also successful in the non-intuitive task where they had to pull down the string to lift the meat. A second group of birds with similar exposure to strings but without any experience in pulling up meat failed the pull-down test. These results support the idea that the ravens' behaviour in accessing meat on a string is not only a product of rapid learning but may involve some understanding of cause–effect relation between string, food and certain body parts.

Correspondence: Thomas Bugnyar, Konrad Lorenz Research Station and Department of Behaviour, Neurobiology, and Cognition, University of Vienna, 4645 Grünau 11, Austria. E-mail: thomas.bugnyar@univie.ac.at

Introduction

The use and manufacture of tools require the ability to perform a sequence of actions in order to bring about an effect (Beck 1980) and thus raises the possibility of understanding causal relationships between objects (e.g. Köhler 1925; Piaget 1954; Thorpe 1956; Griffin 1984; Povinelli 2000). Tool-use ability is correlated with enlargements of parts of the brain in primates (Reader & Laland 2002) and in birds (Lefebvre et al. 1997, 2002). However, in some species that are famous for their tool-use such as capuchin monkeys *Cebus apella* (Visalberghi & Trinca 1989; Visalberghi & Limongelli 1994), chimpanzees *Pan troglodytes* (Povinelli et al. 2000), and woodpecker finches *Cactospiza pallida* (Tebbich et al. 2001; Tebbich & Bshary 2004), the behaviour involves much learning and is not necessarily initially because of causal understanding. In some reported anecdotes (e.g. Andersson 1989) where the history of the individuals is unknown, understanding can only be a presumption (Heinrich 1989). Still other numerous well-known examples of tool use in insects (such as using stones to tamp earth in some wasps, building receptacles to hold honey, weaving thread for building traps, domiciles, etc.; review in von Frisch 1974; Beck 1980) are unrelated to large brain size or with learning and are probably more plausibly genetically hardwired.

One of the tool-use tests that has been applied to examine various levels of cognition (Povinelli 2000), is the ability to access food that is out of reach but attached to an accessible horizontal string (Köhler 1925) or placed near sticks or cane-like objects (review in Fujita et al. 2003). Pulling the food into reach could mean that animals understand the physical entities of the tool, i.e. they use the string/stick as a means to an end (Piaget 1954). However, animals could have come to pull on the tool as a result of their attempts to reach the food by manipulating its vicinity (e.g. Tolman 1936). Tests for understanding the means–end properties have involved the use of a number of strings, crossing strings and varying angle orientation (e.g. Harlow & Settlage 1934; Dücker & Rensch 1977; Osthaus et al. 2003) or choice of the tools with respect to attached food (e.g. Hauser 1997; Hauser et al. 1999, 2002a,b; Povinelli et al. 2000).

In contrast to mammals, birds have been mainly tested for their ability to access food suspended on a vertical string (reviews in Bierens de Haan 1933; Thorpe 1956; Heinrich 1995a). Pulling food up requires not only fine-tuned motor skills, such as beak–foot coordination (e.g. Altevogt 1953), but also the execution of a precise sequence of at least five different steps (reach-down, grab, pull-up, hold with foot, release with beak) repeated in the same sequence several times before the food is reached. It has been suggested that the execution of such a complex sequence shortly after first confrontation with the problem is unlikely to be acquired by rapid learning unless the animals recognize the means–end properties of the string as well as its manipulation in a precise and purposive manner (Thorpe 1956; Heinrich 1995a, 2000; but see also Altevogt 1953; Vince 1956, 1958, 1961).

Corvids are, next to parrots (Pepperberg 1999), especially well known for both excellent beak–foot coordination (e.g. Gwinner 1966; Hunt 1996) and cognitive skills (e.g. Kamil & Balda 1985; Clayton & Dickinson 1998; Weir et al. 2002). Ravens *Corvus corax* are perhaps the most generalized of the corvids with flexible behaviour in respect to ecological and social challenges (Heinrich 1999). In previous tests, adult ravens successfully mastered the vertical string-pulling task several minutes and sometimes seconds after encountering the problem, suggesting means–end comprehension (Heinrich 1995a, 2000). However, the initial observations and experiments suffered from unanticipated problems of a potential confounding influence of neophobia (Heinrich 1995b), competition (Heinrich 1994; Heinrich & Pepper 1998), social learning (Fritz & Kotrschal 1999) and age (Marzluff & Heinrich 1991). We here re-examined string-pulling in new groups of naïve hand-reared ravens, taking the above-mentioned problems into account. Furthermore, we examined whether the birds' task acquisition was merely a product of trial-and-error learning (with the food coming closer to them being the rewarding stimulus for continuing with the behaviour and initiating the step-on sequence) or guided by some sort of understanding (i.e. that string is a means to obtain food) by devising a mechanically similar but non-intuitive task, requiring a string to be pulled down to get meat to come up. If the ravens' success in vertical string pulling was strictly because of trial-and-error learning, then it should be arbitrary whether they have to pull up or down and both types of pulling should be acquired with equal facility. However, if means–end understanding is involved, then solving the non-intuitive pull-down task should be more difficult for naïve birds than the pull-up problem.

General Methods

The Birds and the Aviary

We used two groups of hand-reared birds. The six ravens (two males, four females) of the first group and first part of the study were reared from three separate nests. They were reared together in one nest and fledged in June 1997. The experiments reported here were conducted in Jan. and Feb. 1998, when the birds were 9–10 mo old. They were identified by coloured leg-bands (abbreviated B, G, O, R, W, Y).

After fledging, the young birds were confined in an approx. 725 m^3 aviary complex composed of two sections separated by a wire partition and a door (Fig. 1). The birds roosted at night in a roofed and semi-enclosed 7 m high shed in section A of the aviary complex. They regularly flew back and forth between sections A and B through the interconnecting door that was usually open. Both partitions of the aviary contained trees, horizontal poles for perching, natural ground cover and shading from external trees in and at the edge of the aviary. The birds had about an hour of daily contact with humans to keep them habituated until the time of the experiment, after which they were released.

The second group of six hand-reared birds (four males, two females; abbreviated A, B, F, J, V, Z) were reared from two nests. They fledged in Jun. 2002, and the experiments were performed in Jan. to Feb. 2003 when birds were 9–10 mo of age. They were retained in the same aviary that had held the first group and they also had extensive contact with humans because they had been used in other experiments.

Pre-Training

In the previously reported string-pulling experiments, some of the birds were afraid of food suspended on a string and/or of the string itself (Heinrich 1995a). To help to reduce this problem, all birds used in the present experiments had the opportunity to see the string without being allowed to pull it up and/or to use it as a tool to access food. For both groups, 4 mo prior to the experiments, four strings were left dangling directly on the wire walls of the aviary and two other strings

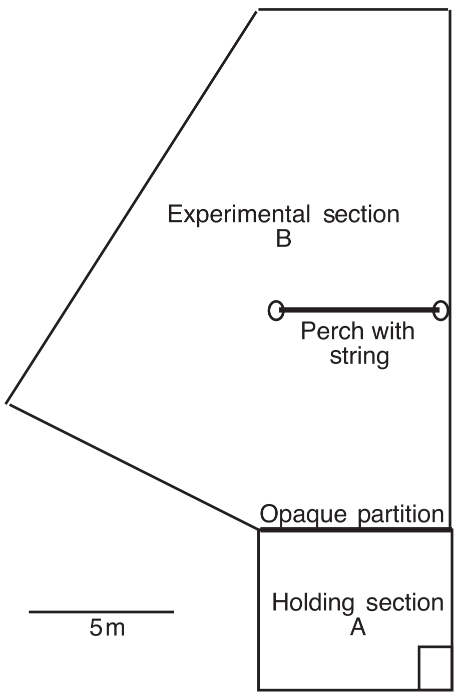

Fig. 1: The aviary complex used for the string-pulling experiments. The birds had their sleeping roost in section A, where they were also held when one of them was tested in section B. Double line indicates the horizontal perch where the string-pulling tests were conducted

were tied vertically top and bottom, between the solid branches of the trees in the aviary.

Unlike in the experiments with adult birds (Heinrich 1995a), the aviary for our experiments had partitions so that individual birds could be separated from the group (Fig. 1). A month before the experiments began, the wall and door between sections A and B were covered with opaque plastic sheeting. The birds continued to regularly use the open door between the two partitions. A day prior to the experiment, the experimental bird was lured into the section B while the other birds remained in the holding aviary A behind a closed door. The experimental bird was left without food for a day before testing.

Prior to the string-pulling experiments, the six birds of each of the two groups were fed communally on calf and road-kill carcasses and kitchen scraps. A month prior to testing, they were also fed on a first-come-first-serve basis by pieces of meat that were placed onto the horizontal pole (a 5-cm-diameter oak sapling) later used as the site for the string-pulling experiments (Fig. 1). The meat either had approx. 20–30 cm of string tied onto it (but not onto the perch) or it was without string. These feeding trials served to habituate the birds even further to string and food tied to a string before testing possible string-pulling skills.

Experiment 1: Pulling up Meat on String

Meat suspended on string could potentially be reached by flying at it and ripping pieces off (provided the meat is soft and/or easily rendered), breaking, tearing or untying the string where it is attached, or pulling it up to the perch in a long series of pull, foot step, grasp, pull, foot step, etc. We prevented rewarding the birds for the first options by providing frozen untearable meat, with solid string and firmly knotted attachments. Our aim was to induce the birds to pull up the meat in order to repeat previous experiments of string-pulling (Heinrich 1995a), while controlling for interference caused by dominance, neophobia and social learning.

Methods

The six birds of group 1 were individually confronted with meat (15 g; attached to skin and bone) suspended 50 cm from the horizontal perch by a white nylon 3-mm-diameter string (Fig. 2). The first author stood nearby to directly record: (a) time to first contact string, (b) time to first reach the meat, (c) the methods used to obtain access, and (d) the number and sequence of intervening behavioural acts until the meat was reached or the effort to reach it was abandoned. Once birds had successfully pulled up meat, they were re-tested on the pull-up problem for a series of at least 50 trials (all of which occurred in the same session). To avoid reinforcing birds with food between trials, they were not allowed to consume the reward but were evicted from the perch each time they

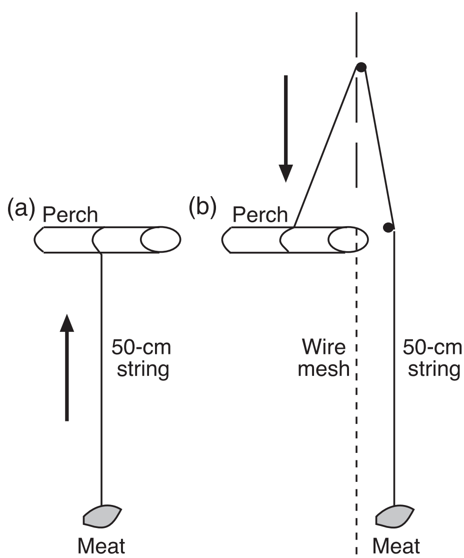

Fig. 2: Set-up for (a) vertical pull-up task, and (b) pull-down task. Arrows indicate direction of pulling

Table 1: Number and kind of behaviours of naïve ravens confronted with the pull-up task

Individuals	Flying-up at meat	Pecking at string	Twisting of string	Yanking at string	Stepping on loops	Total acts	Success
B	0	27	3	7	10	47	Yes
G	1	2	0	6	1	10	Yes
O	0	3	2	17	4	26	Yes
R	1	5	0	2	9	17	Yes
W	0	6	0	18	2	26	Yes
Y	214	8	1	30	0	253	No

All acts, including the stepping on pulled-up loops, refer to those preceding the sequential series when the meat was reached for the first time. In case of individual Y, numbers depict the total amount of acts shown in the course of five trials. Applying a G-test (for homogeneity of distribution of behaviours, corrected for the total number of occurrences per bird) revealed that each individual differed significantly from the theoretically expected value. The results held even when bird Y was excluded (G-test: B: $G = 27.1$, $df = 4$, $p < 0.001$; G: $G = 37.7$, $df = 4$, $p < 0.001$; O: $G = 16.7$, $df = 4$, $p < 0.01$; R: $G = 17.8$, $df = 4$, $p < 0.01$; W: $G = 19.3$, $df = 4$, $p < 0.01$).

had pulled up the meat by a startle response induced by the experimenter. In birds that were not successful in pulling up food after 15 min, the session was terminated and resumed the next day for a total of 5 d.

Results

During the experiment, the ravens showed no interest, and no nervousness, to a blank string attached to their perch, but when meat was attached to the string their behaviour changed markedly. The birds tried several potential options to get the suspended meat (Table 1). These included: (1) flying up from the ground directly at the food and grasping it with their bills apparently trying to rip it off the string, (2) pecking at the string, apparently trying to break it near its attachment point, (3) grabbing the string with the bill and twisting laterally, (4) grabbing the string and yanking back with a jerk, and (5) reaching down as far as possible with the head, grabbing the string, pulling up and stepping on loops of the string. The six individuals attempted most of the above methods, and five of them attained the meat by adopting the repetitive sequences of the pull-up-step-on method, i.e. they perched above the string and the meat, reached far down below the perch, grabbed the string in the bill, pulled it up, laid the loop of pulled up string onto the perch, placed a foot upon the loop, released the bill from the string while continuing to exert pressure with the foot on the string, reached down again, and if there was no slippage, repeated the process four to six times until the meat was brought up to the perch.

There were great individual differences (Table 1). On first encountering meat on a string, two birds (G and R), did not hesitate to explore the string with food and to try the various options. The other four birds jumped up and down on the perch about a metre away from the food on string and then they only hesitatingly sidled up to the string and quickly jumped back after pecking it. (They did not act this way on similar meat offered separately or string without meat.) Individual Y showed great hesitation to land on the perch (that it had routinely used for several months prior to the experiments) when there was a piece of meat dangling on the string, even after the fifth day. It was the only bird of the six that did jump-ups right from the beginning. On the fifth (and last) session, Y did jump-ups exclusively, performing 138 of them consecutively. It never landed on the perch above the meat.

Excluding Y, all the birds stepped on pulled up loop of string within several minutes of perching above the bait. Most importantly, once they had stepped on a loop, they did not let the string go again but immediately continued pulling. In all but B, this coherent sequence of beak and foot use led to the acquisition of meat in the same session of the first stepping on of a loop pull-up (median of four steps on loop in two repetitive sequences until the first time of reaching the reward). Total time from first contact of string to successful pulling up meat among the five birds ranged from 4 to 8 min (median = 6 min), although most of this time the birds were not physically occupied with trying to get the meat. B almost (three-fourth way) pulled the meat up in 3 min, and then tried again eight times in succession but the string kept slipping down despite the bird's foot being on it. Eventually B gave up this approach and went back to pecking and yanking the string, before again pulling it up. B finally succeeded after 8 min, the longest time period of any bird which tried.

The five birds that solved the pull-up task were subsequently confronted with a series of pull-up trials in which they were still not allowed to consume the reward (median = 69 trials per individual; range = 50–78). In these trials, the ravens appeared to become more skilled in manipulating the string. For instance, two birds (O, W) from which records of the time needed for each of the successful pull-ups exist, became up to three times quicker in completing the task during their first 18 trials (median time to success in trials 1–9 and trials 10–18: O = 20 s vs. 11 s, Mann–Whitney test: $n = 9$, $C_L = 52$, exact $p = 0.0018$; W = 15 s vs. 4 s, Mann–Whitney test: $n = 9$, $C_L = 55.5$, exact $p = 0.0078$). A limiting factor of pull-ups was slippage of the smoothly woven nylon line on the smooth perch with gravity pulling the loaded string down. The birds may have manipulated the string in two different ways that reduced slippage. First, they appeared to become more deliberate in the placement of their feet. Secondly, they avoided slippage by stepping sideways along the branch with the pulled up string. However, all five ravens frequently changed between side-step and straight pull-up techniques (range, every second to every tenth trial; median every eighth trial). Much of the large variation in time of individual pull-ups (range = 4–50 s; median per individual: B = 12, G = 10, O = 15, R = 7, W = 9) may have been due to successive slippages vs. no slippage, although this was difficult to evaluate because of the switching and intermediate behaviour between side-step and straight pull-ups in some birds.

Discussion

These results differ from previously published experiments of older ravens pulling up of meat on a string (Heinrich 1995a). First, in the present experiments, almost all birds acquired the string-pulling behaviour within minutes, probably because their neophobia of string had been reduced through habituation. Secondly, in the previous experiments with birds not tested individually, the dominant birds typically interfered with attempts of subordinates to pull on string. The previously reported behaviours (Heinrich 1995a) were therefore less affected by social learning (Fritz & Kotrschal 1999) than by social inhibition (Marzluff & Heinrich 1991).

Our birds showed intermediate behaviour between birds a month after fledging that exhibited no string pulling but great interest in meat on string (Heinrich 2000) and adult wild-captured birds of which some pulled up meat on string in seconds after their first attempt in either the straight pull-up or the side-step pull-up apparently without trying any alternative methods (Heinrich 1995a, 2000). The 1-yr-old birds of the present study tried various options, and even after they started string pulling, they all switched back and forth between the side-step and straight pull-up techniques. The present results, like the previous, involved individual differences in exploring and manipulating the string (Table 1) yet they also showed sudden acquisition of performing a sequence of pulling up after the first and perhaps most crucial link, the step-on of pulled-up meat, had occurred. After birds could solve the pull-up problem, their performance at the task likely improved with further experience, as indicated by greater speed (two birds) and less slippage, possibly through grip-strength adjustments.

Experiment 2: Pulling Down to Have Meat Come Up

Birds could have solved the vertical string-pulling task by applying ‘innate’ feeding patterns (i.e. usage of foot and beak) towards the string (Altevogt 1953) and/or by selecting appropriate actions (i.e. stepping on pulled-up loops) through reinforcement (Vince 1958, 1961). Alternatively, acquisition of string pulling may be guided by expectations that are selected through the perception of relations (Thorpe 1956). We proposed that if the rapid proficiency of ravens in pulling up meat on string was due to understanding physical relations (i.e. means–end properties of string), then another group of string-pull naïve ravens should face difficulties in solving a mechanically similar but non-intuitive problem: pulling down to get meat to come up. However, birds that were already proficient at the pull-up task might transfer their knowledge to string-on-food provided in other ways.

Methods

Frozen meat (15 g) was attached to the same perch in the same way as for the vertical pull-up test. However, the string was then looped 30 cm up and through the wire mesh of the cage to the outside, where it was clearly visible as it hung 50 cm below the perch and approx. 5 cm outside the wire mesh (Fig. 2). The birds could not reach the meat through the wire below the perch (2.5 × 5 cm mesh) but they could get to the meat by pulling down on the string attached to the perch, then stepping on it, and then repeating the sequence of behaviours similar as in the vertical string pull task (expt 1). When pulling down on the string, birds could see the meat coming closer and when it was pulled to perch level, they could easily reach it through the wire (5 × 10 cm mesh above perch).

The main focus of this study was on the six birds of group 2, all of which were naïve in regard to string-pulling. They received the pull-down task at the same age as birds of group 1 were tested on their ability to pull up meat (expt 1) and they were similarly conditioned to the presence of the string prior to testing (see General Methods). In addition, we presented the pull-down task to the six subjects of group 1 which at that time had already participated in several vertical string-pulling tasks (including patterned string problems) and of which all but one were proficient in pulling up meat on string (five subjects: median = 135 successful trials in a total of four pull-up experiments; range 97–148).

As in the pull-up task, birds of both groups were individually tested in section B in physical and visual isolation of their group members. The day before testing, individuals were deprived of food. Testing started when food was attached to the string by the experimenter. If birds were not successful in receiving the meat within 15 min, the trial was terminated and resumed the next day. Each bird was confronted with the problem for a total of 45 min, in up to three 15-min sessions.

We scored the same behavioural parameters as in the pull-up task directly during the experiment and, in case of group 2, from video-tapes (SONY CCD-TR818, Sony Corporation, Japan). For analysis, we lumped the variables 'pecking', 'twisting', 'yanking' (for description see expt 1) into a single category 'handling string' but differentiated between simply 'pulling' on string (resulting in meat coming closer) and 'stepping on' loops (Table 2). We used a Mann–Whitney test to compare the behaviour (total number of acts) of group 2 birds in the pull-down task with the total number of manipulations needed to success of group 1 birds in the pull-up task. (In case of the one unsuccessful individual in group 1, we used its responses of the first three 15-min sessions.) In addition, we applied a Wilcoxon signed ranks test for comparing the performance of group 1 birds in the pull-up task and in the pull-down task. As a result of our small sample size (n = 6 and 5 respectively), we calculated, in both tests, the exact p-values by using the tables H and J in Siegel & Castellan (1988). With such small sample sizes, tests suffer because of low statistical power which is particularly evident when comparing values between treatments of group 1 birds. p-values of the tables were multiplied times two to achieve two-tailed significance. Alpha was set at 0.05.

Results

Task acquisition of inexperienced birds: pulling-down vs. pulling-up. All birds of group 2 approached the experimental set-up several times (median = 8, range = 4–24), spending up to a total of 7 min (median = 3 min, range 0.5–

Table 2: Number and kind of behaviours in the pull-down task of (a) group 2 birds that were naive in regard to string-pulling and (b) group 1 birds that had previously experienced the pull-up task

Individuals	Flying at wire	Handling string	Pulling down	Stepping on loops	Total acts	Success
(a) Group 2						
A	5	16	7	0	28	No
B	0	0	0	0	0	No
F	1	0	0	0	1	No
J	0	0	0	0	0	No
V	0	0	0	0	0	No
Z	5	7	1	0	14	No
(b) Group 1						
B	7	7	1	3	18	Yes
G	0	8	5	5	18	Yes
O	3	5	1	4	13	Yes
R	0	6	5	5	16	Yes
W	0	15	9	2	26	Yes
Y	4	4	2	0	10	No

In case birds were successful, numbers refer to those acts preceding the first reaching of meat.

7 min) on the perch from where they had both physical access to the string and visual access to the meat. Thus, individuals confronted with the pull-down task clearly showed interest in the food and were not afraid of the string. However, they exhibited significantly fewer behavioural acts towards the string than birds of group 1 in the pulling-up task (Mann–Whitney test: group 2, $n = 6$; group 1, $n = 6$; $C_L = 26$; exact $p = 0.041$). In fact, only three birds of group 2 actually tried to get at the meat by manipulating the string and flying at the wire (Table 2a). Two of those birds also pulled loops of string down, resulting in the food coming closer to them. Although this could have been a reward stimulus for continuing the behaviour, those birds did not perform pulls subsequently. Furthermore, in sharp contrast to the pull-up group, none of the birds ever started to step on string or to perform the combination of pulling and stepping. As a consequence none of the birds in group 2 reached the meat (Table 2a). They all quickly lost interest in the string despite the food being clearly visible to them.

Task acquisition of birds experienced with meat on string. Contrary to group 2, five of the six birds of group 1 quickly solved the pull-down task by reaching up, pulling a loop of string down, stepping onto the string and repeating the sequence until the meat could be reached (Table 2b). After the first reaching of meat, all these five birds instantly repeated those coherent behaviours four to six times. Time to access meat in the first trial of the pull-down task as well as the number of manipulations needed to succeed did not differ significantly from those of the pull-up task (Wilcoxon signed-rank test, time to success: $n = 5$; $T^+ = 8.5$; exact $p = 0.82$; total number of behaviours: $n = 5$, 1 tie; $T^+ = 8$; exact $p = 0.38$). Thus, accessing food by the new string configuration was solved approximately as rapidly as the 'normal' pull-up task by experienced ravens. Individual Y, which had never pulled up meat in previous tests, did not once pull on any loop of string in the pull-down task, although it showed interest in the meat and appeared to try to reach it by crowding up to the wire (Table 2b).

Discussion

Pulling down to have meat come up requires a similarly precise sequence of repetitive motor patterns (grab string, pull, hold with foot, release with beak) than pulling up meat on string. Moreover, in either case, pulling on string results in food coming closer to the bird so that ravens would receive the same kind of 'psychological' reward for rapid trial-and-error learning. However, instead of similar performance in both tasks, we found striking differences in the ravens' ability to solve the pull-down and pull-up problem. None of the birds confronted only with the pull-down task were able to reach the meat whereas all but one of the birds confronted with the pull-up task did. As we carefully controlled for factors such as age at testing, conditions of keeping, experience with humans and exposure to string, we suppose that differences in performance reflect the ravens' sensitivity to means–end properties of the tasks. Assuming means–ends comprehension, the direction of pulling would be essential for acquiring the skill because pulling down to get something come up is counterintuitive.

Alternatively, the ravens' failure in the pull-down task could be due to the birds' relatively low rate of manipulating the string compared with the pull-up condition, resulting in little pulling of loops and thus a reduced likelihood of incidentally stepping on string. Still, at least one bird of group 2 that pulled down loops several times would have had the chance to use a foot for holding the string but it never did. Despite their low propensity to manipulate the string, all ravens visually inspected the experimental set-up of the pull-down task intensively. Possibly, they were hampered by the wire-partitioning from trying to get to the food. However, all of the birds were known to regularly take objects such as twigs as well as pieces of food from close outside or on top of the aviary and pull it through the wire mesh whereby the direction of pulling (horizontal or down) did not seem to make any difference (B. Heinrich and T. Bugnyar, unpubl. obs.). Finally, the pull-down task might be considered as too difficult for ravens in general. However, those five birds of group 1 who were experienced with meat on string solved the problem approximately as quickly as they did in the pull-up task, suggesting that they had generalized information from previous experiments (e.g. pulling is a successful behaviour if repeated several times) and transferd skills to a novel situation.

Considering our relatively poor knowledge with respect to how ravens deal with variants of string-pull problems, further studies would be fruitful to examine the birds' abilities in pull-down tasks (e.g. how they would perform when pulling down is both effective and intuitive, or whether prior experience of horizontal string-pulling – which does not require the stepping on loops – would facilitate the task acquisition similar as having experience in pulling-up).

General Discussion

The aim of this study was to experimentally examine the basis and course of acquisition of problem-solving behaviour in ravens. Our protocol centred on string-pulling behaviour, because it is unlikely to be ecologically relevant to these animals, and therefore they are not likely to have been programmed by evolution to execute it. Furthermore, our examination involved young naïve hand-raised birds as they first encountered the problem, so that they could not have learned it during ontogeny.

Our tests corroborate that ravens are capable of quickly solving vertical string problems (Heinrich 1995a, 2000). Naïve year-old birds did not instantaneously perform string-pulling behaviour but tested several alternative ways of getting the reward. Once they came to pull on string, all but one showed sudden acquisition of performing the essential elements, i.e. a precise coordination of the behavioural patterns 'pulling' and 'stepping/holding string', in a repeated sequence and subsequently applied those sequences in slightly different ways (e.g. side-step vs. straight pull-up techniques). In sharp contrast, a coherent sequence of beak and foot-use was not shown by any bird of a second group confronted with a non-intuitive problem in which the direction of pulling countered the movement of the reward. These findings suggest that the ravens' success in string-pulling may not only be due to learning (e.g. sorting out options how to get the reward, improvement of motor skills such as placement of feet in holding string) but also involves some kind of understanding of means–end relationships, i.e. an apprehension of a cause–effect relation between string, food, and certain body parts.

Still, more studies are needed to specify what ravens know about food on strings, e.g. whether they attend to functional design features such as attachment of food (Hauser 1997; Hauser et al. 1999) or even understand abstract concepts such as connectedness (Povinelli 2000; Hauser et al. 2002a,b). Functional abilities have recently been demonstrated in New Caledonian crows *Corvus moneduloides* (Hunt 1996; Chappell & Kacelnik 2002, 2004; Weir et al. 2002) and, to a given extent, in woodpecker finches (Tebbich & Bshary 2004), both of which routinely use and manufacture tools during foraging. All other tested birds have generally failed to show signs of means–end understanding (Dücker & Rensch 1977). However, recent studies on keas *Nestor notabilis* (Werdenich and Huber, in press) and grey parrots *Psittacus erithacus* (Pepperberg 2004) may change this picture.

Compared with many other birds, ravens have large brains (Heinrich 1999). Yet, corvids other than ravens exhibit impressive mental faculties. These include long-term memory of cache locations in nutcrackers *Nucifraga columbiana* (e.g. Kamil & Balda 1985), episodic-like memory and planning ability in scrub jays *Aphelocoma californica* (Clayton & Dickinson 1998; Emery & Clayton 2001) and tool manufacture and use in New Caledonian crows (Hunt 1996; Chappell & Kacelnik 2002, 2004; Weir et al. 2002). Ravens which cache primarily ephemeral meat in the wild are not likely to require mental capacities that would transfer to string-pulling behaviour, nor is ability for some kind of tool use likely a selective pressure in ravens that would result in means–end comprehension. Might their ability for causal understanding be a byproduct of social evolution (Emery & Clayton 2004; but see Iwaniuk & Arnold 2004)? Raven's life-style as crowd-foragers at carcasses pits them into constant interactions amongst themselves (Heinrich & Marzluff 1991; Bugnyar & Kotrschal 2002) and with dangerous predators such as wolves *Canis lupus* (Stahler et al. 2002; Vucetich et al. 2004). Such interactions, may have selected for the ability to predict interactions of objects/bodies in the proximate future. The ability to solve novel problems presumably requires such a representation.

Acknowledgements

We thank G. Gaydon, L. Huber, H. Nemeschkal, B. Osthaus, I. Pepperberg, J. Schall, M. Steurer, S. Tebbich, D. Werdenich and three anonymous referees for valuable comments. T.B. has been funded by an Erwin-Schrödinger Fellowship (J2064, J2225) and an Erwin-Schrödinger Follow-up Program (R31-B03) of the Austrian Science Fund. The experiments here described were approved by the Institutional Animal Care and Use Committee at the University of Vermont (on March 1, 1996, Protocol No. 96-086, and renewed on November 1, 2002, Protocol No. 01-054). Permits for ravens include US Federal Fish and Wildlife Permit Number MB689376-0, State of Maine Department of Inland Fisheries and Wildlife Permit 22077, and Vermont Fish and Wildlife Department Scientific Collecting Permit).

Literature Cited

Altevogt, R. 1953: Über das "Schöpfen" einiger Vogelarten. Behaviour **6,** 147—152.

Andersson, S. 1989: Tool use by the fan-tailed raven (*Corvus rhipidurus*). Condor **91,** 999.

Beck, B. B. 1980: Animal Tool Behavior. The Use and Manufacture of Tools by Animals. Garland STPM Press, New York.

Bierens de Haan, J. A. 1933: Der Stieglitz als Schoepfer. J. F. Ornithol **81,** 1—22.

Bugnyar, T. & Kotrschal, K. 2002: Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it "tactical deception". Anim. Behav. **64,** 185—195.

Chappell, J. & Kacelnik, A. 2002: Tool selectivity in a non-mammal, the New Caledonian crow (*Corvus moneduloides*). Anim. Cogn. **5,** 71—78.

Chappell, J. & Kacelnik, A. 2004: Selection of tool diameter by New Caledonian crows (*Corvus moneduloides*). Anim. Cogn. **7,** 121—127.

Clayton, N. S. & Dickinson, A. D. 1998: Episodic-like memory during cache recovery by scrub jays. Nature **395,** 272—278.

Dücker, G. & Rensch, B. 1977: The solution of patterned string problems by birds. Behaviour **62,** 164—173.

Emery, N. J. & Clayton, N. S. 2001: Effects of experience and social context on prospective caching strategies by scrub jays. Nature **414,** 443—446.

Emery, N. J. & Clayton, N. S. 2004: Comparing the complex cognition of birds and primates. In: Comparative Vertebrate Cognition: Are Primates Superior to Non-Primates? (Rogers, L. J. & Kaplan, G., eds). Kluwer Academic Press, New York, pp. 3—55.

von Frisch, K. 1974: Animal Architecture. Harcourt Brace Jovanovich, New York.

Fritz, J. & Kotrschal, K. 1999: Social learning in common ravens, *Corvus corax*. Anim. Behav. **57,** 785—793.

Fujita, K., Kuroshima, H. & Asai, S. 2003: How do tufted capuchin monkeys (*Cebus apella*) understand causality involved in tool use? J. Exp. Psychol. Anim. Behav. Proc. **29,** 233—242.

Griffin, D. R. 1984: Animal Thinking. Harvard Univ. Press, Cambridge, MA.

Gwinner, E. 1966: Über einige Bewegungsspiele des Kolkraben (*Corvus corax* L.). Z. Tierpsychol. **23,** 28—36.

Harlow, H. F. & Settlage, P. H. 1934: Comparative behavior of primates: VII Capacity to solve patterned string tests. J. Comp. Psychol. **18,** 423—435.

Hauser, M. D. 1997: Artifactual kinds and functional design features: what a primate understands without language. Cognition **64,** 285—308.

Hauser, M. D., Kralik, J. & Bottomahan, C. 1999: Problem solving and functional design features: experiments on cotton-top tamarins, *Saguinus oedipus*. Anim. Behav. **57,** 565—582.

Hauser, M. D., Pearson, H. & Seelig, D. 2002a: Ontogeny of tool use in cottontop tamarins, *Saguinus oedipus*: innate recognition of functionally relevant features. Anim. Behav. **64,** 299—311.

Hauser, M. D., Santos, L. R., Spaepen, G. M. & Pearson, H. E. 2002b: Problem solving, inhibition and domain-specific experience: experiments on cottontop tamarins, *Saguinus oedipus*. Anim. Behav. **64,** 387—396.

Heinrich, B. 1989: Raven tool use? Condor **90,** 270—271.

Heinrich, B. 1994: Dominance and weight-changes in the common raven, *Corvus corax*. Anim. Behav. **48,** 1463—1465.

Heinrich, B. 1995a: An experimental investigation of insight in common ravens (*Corvus corax*). Auk **112,** 994—1003.

Heinrich, B. 1995b: Neophilia and exploration in juvenile common ravens, *Corvus corax*. Anim. Behav. **50,** 695—704.

Heinrich, B. 1999: Mind of the Raven: Investigating and Adventures with Wolf-Birds. Harper Collins, New York.

Heinrich, B. 2000: Testing insight in ravens. In: Evolution of Cognition (Heyes, C. & Huber, L., eds). MIT Press, Cambridge, MA, pp. 289—305.

Heinrich, B. & Marzluff, J. B. 1991: Do common ravens yell because they want to attract others? Behav. Ecol. Sociobiol. **28,** 13—21.

Heinrich, B. & Pepper, J. W. 1998: Influence of competitors on caching behaviour in the common raven, *Corvus corax*. Anim. Behav. **56,** 1083—1090.

Hunt, G. R. 1996: Manufacture and use of hook-tools by New Caledonian crows. Nature **379,** 249—251.

Iwaniuk, A. N. & Arnold, K. E. 2004: Is cooperatively breeding associated with bigger brains? A comparative test in Corvida (Passeriformes). Ethology **110,** 203—220.

Kamil, A. C. & Balda, R. P. 1985: Cache recovery and spatial memory in Clark's nutcracker (*Nucifraga columbiana*). J. Experim. Psychol. Anim. Behav. Proc. **11,** 95—111.

Köhler, W. 1925. The Mentality of Apes. Routledge and Kegan, London.

Lefebvre, L., Whittle, P., Lascaris, E. & Finkenstein, A. 1997: Feeding innovations and forebrain size in birds. Anim. Behav. **53,** 549—560.

Lefebvre, L., Nicolakakis, N. & Boire, D. 2002: Tools and brains in birds. Behaviour **139,** 939—973.

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.

Osthaus, B., Lea, S. E. G. & Slater, A. M. 2003: Dogs do not understand means–end connections via a string. Paper presented at the 10th Annual International Conference on Comparative Cognition, Melbourne, FL, USA.

Pepperberg, I. M. 1999: The Alex Studies. Cognitive and Communicative Abilities of Grey Parrots. Harvard Univ. Press, Cambridge, MA.

Pepperberg, I. M. 2004: "Insightful" string-pulling in Grey parrots (*Psittacus erithacus*) is affected by vocal competence. Anim. Cogn. **7,** 263—266.

Piaget, J. 1954: The Construction of Reality in the Child. Norton, New York.

Povinelli, D. J. 2000: Causality, tool use, and folk physics: a comparative approach. In: Folk Physics for Apes (Povinelli, D. J., ed.). Oxford Univ. Press, New York, pp. 73—107.

Povinelli, D. J., Reaux, J. E., Theall, L. A. & Giambrone, S. 2000: The rope, hook, touching-stick, and related problems: the question of physical connection. In: Folk Physics for Apes (Povinelli, D. J., ed.). Oxford Univ. Press, New York, pp. 206.

Reader, S. M. & Laland, K. N. 2002: Social intelligence, innovation, and enhanced brain size in primates. Proc. Natl Acad. Sci. USA **99,** 4436—4441.

Siegel, S. & Castellan, N. J. 1988: Nonparametric Statistics for the Behavioral Sciences, 2nd edn. McGraw Hill, New York.

Stahler, D., Heinrich, B. & Smith, D. W. 2002: Common ravens, *Corvus corax*, preferentially associate with grey wolves, *Canis lupus*, as a foraging strategy in winter. Anim. Behav. **64,** 283—290.

Tebbich, S. & Bshary, R. 2004: Finch physics: cognitive abilities related to tool-use in the woodpecker finch *Cactospiza pallida*. Anim. Behav. **67,** 689—697.

Tebbich, S., Taborsky, M., Fessl, B. & Blomqvist, D. 2001. Do woodpecker finches acquire tool-use by social learning? Proc. R. Soc. Lond. B – Biol. Sci. **286,** 2189—2193.

Thorpe, W. H. 1956: Learning and Instinct in Animals. Methuen and Co, London.

Tolman, E. C. 1936: The acquisition of string-pulling by rats – conditioned response or sign-gestalt? Psychol. Rev. **44,** 195—211.

Vince, M. A. 1956: String pulling' in birds. I. Individual differences in wild adult great tits. Br. J. Anim. Behav. **4,** 111—116.

Vince, M. A. 1958: "String-pulling" in birds. II. Differences related to age in greenfinches, chaffinches, and canaris. Anim. Behav. **6,** 53—59.

Vince, M. A. 1961: "String-pulling" in birds. III. The successful response in greenfinches and canaris. Behaviour **17,** 103—129.

Visalberghi, E. & Limongelli, L. 1994: Lack of comprehension of cause-effect relations in tool-using capuchin monkeys (*Cebus apella*). J. Comp. Psychol. **108,** 15—22.

Visalberghi, E. & Trinca, L. 1989: Tool use in capuchin monkeys: distinguishing between performing and understanding. Primates **30,** 511—521.

Vucetich, J. A., Peterson, R. O. & Waite, T. A. 2004: Raven scavenging favours group foraging in wolves. Anim. Behav. **67,** 1117—1126.

Weir, A. S., Chappell, J. & Kacelnik, A. 2002: Shaping of hooks in New Caledonian crows. Science **297,** 981.

Werdenich, D. & Huber, L. in press: A case of quick problem solving in birds: string-pulling in keas (*Nestor notabilis*). Anim. Behav., in press.

Received: August 11, 2004

Initial acceptance: December 8, 2004

Final acceptance: March 8, 2005 (M. Taborsky)