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MASTERARBEIT

Titel der Masterarbeit

String pulling and discrimination learning in jackdaws (*Corvus monedula*) and New Caledonian crows (*Corvus moneduloides*)

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1. General Introduction

Comparative cognition aims to understand "cognition across the animal kingdom, including how it works, what it is good for in nature, and how it evolved" (Shettleworth 2010, p. 6). Cognitive abilities as morphological traits are thought to have evolved as adaptations to the animal's physical and/or social environment. On the one hand species showing similar cognitive traits may be close relatives and sharing the skills because of common ancestry. On the other hand distantly related species may share similar cognitive abilities because they are facing similar cognitive problems. Bolhuis and Wynne (2009) question the "straightforward application of Darwinism to cognition". They further state that "evolutionary convergence may be more important than common descent in accounting for similar cognitive outcomes in different animal groups" (Bolhuis & Wynne 2009). Ignoring the evolutionary background in comparative cognition is surely not advised (Kacelnik 2009). Therefore comparing closely related species differing in their ecological niche on the one hand and comparing distantly related spices which are confronted with similar cognitive problems on the other hand is a standard approach in the field of comparative cognition to answer the question about the evolution of cognition.

The present study aimed to compare the cognitive skills of jackdaws (*Corvus monedula*) and New Caledonian crows (*Corvus moneduloides*), two closely related species which differ among other things in their foraging behaviour. New Caledonian crows are well known for their enhanced tool use abilities (e.g. Hunt 1996, Wire et al. 2002, Taylor et al. 2007). Jackdaws are not known to use tool. The ability to use tools is not wide spread in the animal kingdom. One widely accepted explanation for this notion is that tool use is cognitively demanding (e.g. reviewed in Emery & Clayton 2009). Hansell & Ruxton (2008) see "the lack of ecological contexts in which tools are superior to the already evolved anatomy of the animal" as explanation why relatively few species use tools and put tool using in the broader context of animal construction behaviour. However, if considering the first explanation one would expect that New Caledonian crows show enhanced cognitive abilities compared to jackdaws. The relevant cognitive aspects behind tool use are thought to involve learning about spatial relationships between objects, connectivity and weight (Teschke et al. 2011). Thus, if tool use is cognitively demanding, tool using species should show enhanced problem solving skills in which the appreciation of physical properties and relations between objects is crucial. It is clear that for fair and meaningful comparisons of a tool using and a non-tool using species another task than tool use has to be addressed. For this reason the present study aimed to test

the ability of jackdaws and New Caledonian crows to discriminate two objects on the basis of either visual, acoustic or weight cues in a string pulling context which allows the animals to seek information on their own before making the decision where to pull up a string completely (see study 2). The ability to pull up strings is wide spread within birds, which gives this approach the possibility to become a standard test of discrimination learning in different modalities and to investigate information seeking in a comparative manner.

Vertical standard sting pulling represents a physical problem dealing with connectivity and means-end relationships. Providing different variations of the string pulling problem, like slanted and crossed strings (e.g. Heinrich 1995,Werdenich & Huber 2006), over length strings (Shuck-Paim et al. 2009, Amann et al. unpublished), and/or counterintuitive setups (Heinrich & Bugnyar 2005), has the potential to further investigate the cognitive mechanism the animals use when solving the problem. As a precondition all the subjects had to be proficient in pulling up a string, but because of a different main focus of the study, no further variations were provided. Nevertheless the acquisition of the solution to the string pulling problem revealed interesting results, which therefore are presented separately (see study 1).

Study 1

String pulling in jackdaws and New Caledonian crows: differences in discovering and consolidating the solution

Abstract

The ability to retrieve a reward by pulling up a string is a classic example of problem solving in birds. It is thought that birds of different species use different cognitive mechanisms to solve this problem. Vertical string pulling requires well co-ordinated and repeated actions of pulling up the string and stepping on it until the reward can be reached. The aim of this study is to show that it is important to analyse separately when the birds start with string pulling and how they consolidate to apply this correct method and whether and how they improve in conducting a smooth sequence of pulling and stepping on the string. Jackdaws and New Caledonian crows were investigated in this study. The jackdaws had fewer problems performing a smooth sequence of pulling and stepping on the string once they stepped on the pulled up string, but the latency to start with string pulling decreased more gradually from trial to trial. In contrast, the New Caledonian crows had greater difficulties performing the required motor pattern of pull-stepping, but after 4-5 trials the latency of first pull-step showed a sudden decrease. This suggests a kind of understanding of the problem (means-end understanding) or quick learning in the crows. However, 7 out of 14 jackdaws and 2 out of 5 New Caledonian crows never succeeded. This suggests a kind of chance discovery of the correct method of stepping on the string once it is pulled up in the successful individuals. Once the correct method was discovered the birds appeared to instantaneously exploit their discovery. The results are discussed in respect to facilitating innate behavioural components, operant conditioning and means-end understanding.

2.1 Introduction

One of the oldest examples of problem solving in birds is the classic string pulling paradigm. This behaviour was first documented by Albertus Magnus in 1250 and later by Plinius in 1554 (citied in Seibt & Wickler 2006). In the past hundred years or so this phenomenon has been studied experimentally, because it allows direct species comparisons of problem-solving abilities. The string pulling task shows potential understanding of cause-effect and means-end relationships (e.g. Heinrich & Bugnyar 2005, Werdenich & Huber 2006). Means-end behaviour is defined as reaching a goal by a deliberate and planned sequence of actions where obstacles preventing the goals from being achieved have initially been removed (Willatts 1999). In the case of string pulling the obstacle is represented by the distance between the subject and the desired out-of-reach reward (Huber & Gajdon 2006); it has to be overcome by pulling up the string (means to an end). So far many mammals (e.g. Tolman 1937, Osthaus et al 2005, Whitt et al. 2009) as well as birds (Dücker & Rensch 1977, Heinrich 1995, Heinrich & Bugnyar 2005, Funk 2002, Seibt & Wickler 2006, Werdenich & Huber 2006, Schuck-Paim et al. 2009, Taylor et al. 2010) have been tested.

The mechanisms proposed for explaining the successful performance in the string pulling task are numerous, but they can be assigned to two main categories: i) "low-level" explanations, like innate behaviour, trial and error learning or conditioning, and ii) "high-level" explanations, like insight and goal-directed means-end understanding. Blue tits, reared under controlled conditions, started to pull up strings spontaneously, even if no reward was present (Altevogt 1954). Because blue tits show a well established coordination of beak and foot movements, which is part of their innate feeding behaviour, Altevogt (1954) argues that "there is no need to apply terms like insight or understanding to this (string pulling) pattern of behaviour". A study on string pulling in goldfinches and siskins found individual as well as species differences (Seibt & Wickler 2006). 62% of the siskins but only 23% of the goldfinches who had no previous experience successfully managed to pull up the string. Although both species use their beaks and feet in a coordinated manner, string pulling competence seemed to depend on their experience with handling branchlets (experienced branchlet-handlers were more successful) and on trial-and-error learning in combination with potential operant conditioning (Seibt & Wickler 2006). However, keas (parrots endemic to New Zealand) solved the string pulling problem spontaneously, some even without showing explorative or inefficient actions, and at group-level they did not improve along the experiment (Werdenich & Huber 2006). Such quick problem solving may be based on means-end understanding and/or some level of anticipation

(Werdenich & Huber 2006). Heinrich & Bugnyar (2005) showed that naive ravens suddenly performed the whole sequence of pulling-up the string and stepping on the pulled-up loop. However, only experienced individuals were able to pull down a string in order to make the reward come up. These results lead the authors to suggest 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" (Heinrich & Bugnyar 2005). Taylor et al. (2010) postulate a different explanation for spontaneous-like string pulling: operant conditioning mediated by a perceptual-motor feedback cycle – "pulling the string moves the meat towards an individual, and stepping on the string holds it in a position closer than before the pull".

Physical problems, such as vertical standard string pulling, which require specific motor patterns, hold two aspects: the discovery and the execution of the solution. The ability to find the correct solution to a given problem seems to be more a cognitive task (e.g. goal-directed instead of random exploration and understanding of means-end relations). Executing the solution, on the other hand, is additionally influenced by the birds' motor abilities, such as well established beak-foot coordination. Furthermore problem solving can be divided into two phases, a discovery-phase and a consolidation-phase (improving the technique of problem solving once it is found). A gradual improvement in starting to perform the correct solution would suggest trial-and-error learning or conditioning, whereas an abrupt increase in performance would point more to a kind of sudden understanding of the problem. It is important to keep these aspects of starting to perform string pulling apart from how string pulling is performed as a whole sequence of actions, because it is possible that a subject shows the solution-approach spontaneously while the observed learning effects are due to poor motor skills. On the other hand an animal could execute the solution "perfectly" and thereby solve the problem quickly, but only because its motor repertoire includes the required motor pattern, e.g. well established beak-foot coordination in case of string pulling, which favours the solution.

This theoretical framework can be applied to the string pulling paradigm. Heinrich (1995) described the most common solution in ravens as several repeats of pulling the string up and stepping on the pulled-up loop. The crucial behaviour of the whole sequence of string pulling is stepping on the pulled-up loop of string (Heinrich 1995, Seibt & Wickler 2006). The aspect of discovering the solution in string pulling can therefore be defined as completing the first pull-step sequence; the following pull-step sequences until reaching the reward represent a successful execution of the solution. However, the stepping action is also favoured by good

overall beak-food coordination. Therefore it seems important to analyse exactly, when the behaviour of stepping on the pulled up loop occurs, to be able to disentangle the two aspects of the string pulling paradigm. The first time an animal steps on the pulled-up loop and the actions which follow immediately thereafter, seem to be relevant in describing the animals' understanding of the solution (solution-discovery). If a subject shows very little to none explorative behaviour and starts immediately pulling up the string and stepping on the pulled up loop this would point to anticipatory problem solving and/or means-end understanding. However, stepping on the string could also occur by chance while exploring the setup. If in such a case the animal continues showing pull-step sequences or at least tries to do so, one would argue a kind of "understanding" or quick learning of the importance of this behaviour for the solution of the problem. The study aims to disentangle the two aspects of problem solving by analysing the animals' action patterns until they managed to secure the reward for the first time (after Werdenich & Huber 2006). Furthermore possible learning effects are evaluated by analysing the individual's performance over trials.

So far jackdaws have not been systematically tested on the string pulling problem and the conclusions drawn from the "anecdotal" results are contradicting. Hertz (1926) tested one jackdaw and concluded from his observations that string pulling was already in the animal's motor repertoire. Thrope (1945) however suggested insightful behaviour as being on work when solving the string pulling task. Finally Drücker & Rensch (1977) studied one jackdaw and concluded that the string pulling ability was due to associative learning. A further aim of this study is therefore to investigate the string pulling problem systematically in jackdaws by studying more individuals and analysing their behaviour in detail. Although New Caledonian crows' ability to solve the string pulling task has already been tested (Taylor et al. 2010), it seems worth replicating the study in parts and applying the same methods to both species, jackdaws and New Caledonian crows in order to allow direct species comparison. String pulling like tool-use represents a manipulative task. New Caledonian crows are well known for their remarkable tool use abilities (e.g. Hunt 1996, Weir et al. 2002). Using sticks as tools to extract invertebrates is a typical feeding behaviour of New Caledonian crows (Kenward et al. 2004). Comparing New Caledonian crows to jackdaws, a species which is phylogenetically closely related but does not show any tool use or other sophisticated manipulative behaviour is especially interesting.

2.2 Methods

2.2.1 Subjects and housing

The study was conducted with two corvid species: jackdaws (*Corvus monedulas*) and New Caledonian crows (*Corvus moneduloides*). All subjects were housed at the research station of Dr. Auguste von Bayern, Leutstetten (Germany) in collaboration with the "Behavioural ecology research group", University of Oxford (Great Britain). 14 adult jackdaws and 5 adult New Caledonian crows participated in the study. All animals were individually marked with coloured leg-rings.

Jackdaws

The jackdaws were kept in two large outdoor aviaries which were connected to one another. Seven of the Jackdaws were housed in aviary A (12 x 10 x 2.8 m; with a total of ten jackdaws) and seven in aviary B (15 x 9 x 2.8 m; with a total of twelve jackdaws). Both aviaries were equipped with branches and wooden perches, nest boxes, plastic tables and chairs, and live *Sambucus nigra* bushes. The ground was partially covered with wood chips and uncovered concrete under the most frequented roosts to facilitate cleaning. The subjects were tested individually in visually isolated test-compartments (ca. 3 x 1.5 x 2.8 m, L x W x H). To reduce stress the test-compartment was arranged in such a way that the subject could interact with its pair-partner. However, only the focal subject could view the test setup.

The main diet consisted of a mixture of boiled rice, minced beef-heart and quark, softened cat-pellets, fruits (e.g. oranges, apples, bananas) and cereal with mealworms. Fresh water was provided every day in big bathing tubs. The birds were deprived of food 2-3 hours before testing.

New Caledonian crows

Four of the five subjects were wild caught and the female Uék was hand-reared in captivity (for details see Kenward et al. 2004, 2006). The subjects were housed in pairs (Annie-Claude and Boycott, Ebony and Tino, Uék was kept alone because her partner had died) in outdoor aviaries (ca. 60 m^3 each) with associated indoor rooms (ca. 8 m^3 each). The birds were kept inside during the night for reasons of safety and warmth (especially in wintertime). A small test

compartment was attached to each of the indoor rooms, so that every individual could be tested individually in visual isolation. The indoor bedding material consisted of newspaper, which was renewed on a daily basis. To facilitate cleaning the outdoor compartment consisted of an uncovered concrete floor. Each outdoor compartment contained several big branches, a big plastic tub containing stones and gravel of different sizes as well as a few tree trunks which contained several holes, in which the animals could insert sticks. The indoor rooms were equipped with two branches, an artificial nest-basket and some toys (e.g. plastic cars, sticks, cubes, bricks with holes, etc.). Furthermore, two heating lamps guaranteed species-adapted temperatures year round and a solar-colour lamp with 13:11 light-dark cycle was also installed in each indoor compartment.

The main meals were provided in the indoor compartment and consisted of small stripes of beef-heart, softened cat-pellets, and a mixture of rice, minced beef-heart and quark. Additionally the crows received mealworms and pieces of fruit (oranges, papaya, bananas). Water was accessible at libitum in the indoor enclosure. A bathing tub was provided in the outdoor aviary once a week. To ensure the subject was highly motivated all food, except for the fruit, was removed 2-3 hours before testing.

2.2.2 Apparatus and procedure

Unless otherwise stated the apparatus and procedure was the same for both species. A natural straight perch (ca. 5 cm in diameter) was fixed in the test compartments. A brown cotton cord, 4 mm in diameter, was used as string. Habituation trials (jackdaws: 5 min/trial; New Caledonian crows: 10 min/trial) were provided to habituate the subjects to the separating procedure as well as the presence of the experimenter in the test compartment (this was not the case in New Caledonian crows) and the string. Jackdaws had to successfully retrieve a mealworm from a 14 x 14 cm platform (platform trials), which was fixed on the perch, three times in a row and then to solve three consecutive short-string trials: a 4 cm long string with food on its end was fixed pendiculary on the perch. The birds could directly reach the reward, without the need of showing a pull-step. New Caledonian crows were confronted only with short-string trials and had to solve three trials in a row. After passing the habituation phase, the birds were tested in string pulling with a 40 cm (jackdaws) or 50 cm (New Caledonian crows) long string. The length of the string required both species to do about five pull-step sequences in order to reach the reward. Subjects received a maximum of 6 trials per session and one session per day. A trial ended if the reward was successfully reached or after 10 min

(20 min for New Caledonian crows) had elapsed. A session was terminated if a subject failed during two consecutive trials. The experiment ended after 16 successful trials. The reward could potentially be reached by flying directly to it. To prevent the birds from obtaining the reward in this way a cage (87 x 40 x 60 cm, L x W x H) was fixed directly under the perch in which the string was hanging. The cage was not introduced unless the individual showed the "flying"-method twice. To be sure that the subjects were not disturbed by the cage a second habituation phase was conducted (three platform trials and three short string trials). If a subject was not successful in reaching the reward by showing the pull-step technique within eight trials it received stepwise training with increasing string length (for jackdaws: 9, 12, 17, 25 cm; for New Caledonian crows: 12, 17, 25 cm, one individual needed additional 35 cm and 40 cm steps) with the cage present. To proceed to the next step an individual had to be successful in three consecutive trials. All trials were videotaped for detailed analysis.

2.2.3 Analysis

The analysis was divided in two sections: i) a detailed observation of the behaviour shown in the subject's first attempt to reach the reward and ii) analysis of performance over trials. The action list after Werdenich & Huber (2006) was used for behavioural observations (Table 1). To analyse the performance during trials in detail the following latencies and times were obtained from the videos: solution time (cumulative time of interacting with the string until reaching the reward); pull-step latency (cumulative time of interacting with the string until first pull-step), duration pull-stepping (cumulative time of interacting with the string from end of first pull-step until reaching the reward). Furthermore the number of drops (defined as performing at least one pull-step sequence and then letting the string fall again) were also registered. If a subject flew off the perch or interrupted its interaction with the string for about 3 seconds time measure was stopped and continued when the animal restarted interacting with the setup. A repeated ANOVA with trial-number (successful trial 1-16) as within-subject factor and species (jackdaws and New Caledonian crows) as between-subject factor was calculated to analyses the subjects' performance over trials. The variable numbers of drops was analysed separately for the two species using a Friedman test, because this data was not normally distributed.

The trials were analysed in a random order (trial number and individuals) to ensure that the possible influence of decreasing accuracy over time was eliminated. All statistical tests were made with SPSS.17 and the alpha-level was set at 0.05. The data was transformed using a logarithmic function (log10) for all parametric tests to ensure a normally distributed dataset. A

second analysis of a random selection of ten percent of the trials showed high intra-observer reliability (correlation after Pearson: r=0.997, p<0.001, linear regression-coefficient: β=1.033, p<0.001).

Table 1: Action list and action sequences in the attempts to secure the reward (after Werdenich & Huber, 2006). *) actions directed towards the string

Action number	Action
Efficient actions	
1	Lands on perch/cage
2*	Reaches for string with beak
3*	Pulls up string with peak
4*	Places string on perch/cage
5*	Uses one foot to hold string on perch/cage
6*	Uses both feet to hold string on perch/cage
7*	Pulls up string until body is upright and therefore gains more string
8*	Grabs string directly with foot
9*	Takes one or more steps sideways on perch/cage holding string with beak
10*	Lets go of string with beak to reach down again
11*	Gains reward after having pulled up string
21*	Flights towards reward
22*	Grabs reward by flying to it
Inefficient actions	
12*	Tries to place string on perch/cage but does not succeed
13*	Tries to place foot on string but does not succeed
14*	Drops string after having pulled it up
15	Sits/moves on perch/cage
16	Flies off perch/cage
Exploratory actions	
17*	Nibbles/pecks string
18	Nibbles/pecks perch/cage
19*	Touches string
20*	Nibbles/pecks on fixation of the string

2.3 Results

2.3.1 Task acquisition (discovery-phase)

Jackdaws

All 14 jackdaws showed interest in the setup and interacted with the string (Table 2). However, only Spinni succeeded in his first trial. Nine individuals were successful in retrieving the reward at least once. The jackdaws showed two methods to solve the task: i) flying directly to the reward from the ground or the sidewalls of the test-compartment, ii) classic standard string pulling. Two individuals showed the flying-method only and three individuals exclusively showed the pull-step method (Table 2). Csoka and Karacho solved the task twice by flying directly to the reward, but switched to the pull-step method when confronted with the cage-setup. Tschok and Orange-re first succeeded with the pull-step method, and then spontaneously changed to the flying-method. Interestingly Orange-re did not change back to the pull-step method, when the flying-method was prevented by adding the cage. After stepwise training, the individual solved the task again by pull-stepping.

Table 2: Performance of jackdaws and New Caledonian crows in the first 10 trials/presentations of vertical standard string pulling.

jackdaws	1	2	3	4	5	6	7	8	9	10
Spinni	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Tschok			✓	✓	✓	✓	✓	✓	✓	
Orange-re			X	✓	X	✓	✓	f, x	X	✓
Radja			X	X	✓		✓	✓	✓	✓
Krakehl	f, x						✓	✓	✓	✓
Karacho	X	X	✓	✓	X		X	X	✓	✓
Csoka	X		X		✓	✓	X		✓	✓
Dohli	X		X			f	f			s
Jackie	X		X						s	s
Xenia			✓		X	X			s	s
Orange-li			✓			f		✓	s	s
Krawall			X	X	X				s	s
Poldi	X	X	X	X					s	s
Rani	X	X	X		X	X	X	X	s	s

NC crows	1	2	3	4	5	6	7	8	9	10
Uek	✓	✓	✓		X	✓	✓	✓	✓	✓
Anniclaude		✓	✓	✓		✓	✓	✓	✓	✓
Ebony		X			X	✓		✓	✓	✓
Tino	X	X		X			X		s	s
Boycott	X		X		X			X	s	s

✓ success by showing pull-step sequences
X interacted with the string, but no success
✓ success by directly flying to the reward
 not interacted with the string
f attempt to reach the reward by flying
s stepwise training

A detailed analysis of the jackdaws' actions showed that until they first pulled up the string entirely (7 solvers) or before they were given stepwise training (7 non-solvers) the only difference between the solvers and non-solvers was, that the non-solvers never stepped on the pulled-up string (action 5 or 6, Table 1). Interestingly five out of the seven solvers executed the complete action-sequence of pulling up and stepping on the string without showing any drop (action 14, Table 1) after having stepped on the pulled up string for the first time. Only Radja and Karacho dropped the string once after they had stepped on the pulled up string for the first time. A comparison of the total number of actions involving the string (*actions, Table 1) until the last action before the first successful bout of pull-step sequences not interrupted by drops (solvers) or after 8 trials of unsuccessful attempts to solve the task by pulling up the string (non-solvers) showed no difference between the solvers (median 14, 1st Quartile 9, 3rd Quartile 73) and non-solvers (median 27, 1st Quartile 14.5, 3rd Quartile 33; Mann-Whitney test: n_1=7, n_2=7, U=24.000, exact p=1.000, Figure 1). This suggests that the non-solvers were as interested in the string as the solvers were. Importantly, even the occurrence of action 3 (pulls up the string with the beak) did not differ between the solvers (median 3, 1st Quartile 1.5, 3rd Quartile 17.5) and non-solvers (median 4, 1st Quartile 1, 3rd Quartile 5.5 Mann-Whitney test: n_1=7, n_2=7, U=19.500, exact p=0.535, Figure 1).
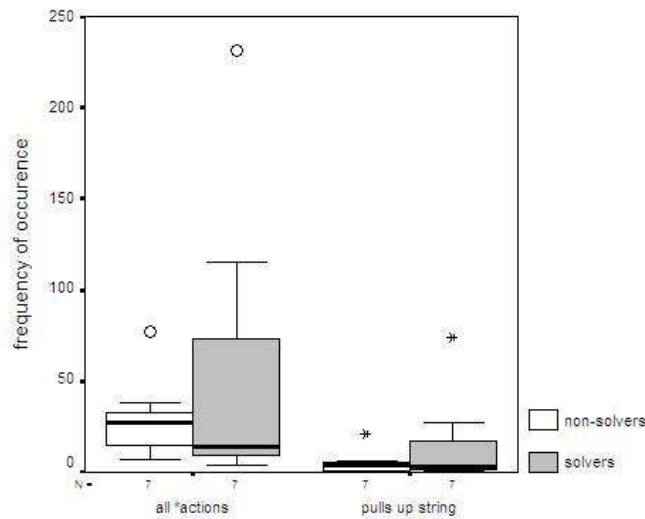
Figure 1: Box-plots of the jackdaws' total number of all *actions (actions directed towards the string, Table 1) and "pulls up string" actions (action 3, Table 1) until showing the first errorless string pulling performance (solvers, grey) or starting with stepwise training (non-solvers, white). *Boxes* represent the interquartile range (IQR), *bars* within *boxes* are median values and *whiskers* indicate the lowest and highest value still within 1.5 IQR of the lower and upper quartile respectively the 5th and 95th percentile.

New Caledonian crows

All five New Caledonian crows showed interest in to the setup, but again only one individual succeeded in the first trial. Over the curse of the experiment the three females, but none of the two males, solved the task without the need of stepwise training (Table 2). They pulled up the string entirely using the pull-step method. They were never observed reaching the reward by flying directly to it. A detailed analysis of the actions the New Caledonian crows performed until they pulled up the string entirely (solvers) or started with the stepwise training (non-solvers) showed some difference between these two groups. Because of the small sample size these differences are just reported in a descriptive manner. The three successful females seemed more interested in to the setup than the two unsuccessful males. The females showed a lot more actions involving the string before they reached their first bout of successful uninterrupted pull-step sequence than did the two non solving males (solvers/females: Anniclaude 91 actions, Ebony 51, Uek 43; non-solvers/males: Boycott 12, Tino 13). The same results were found for the pull-up action (action 3, Table 1). Ebony and Uek, each, pulled the string up 8 times and Anniclaude 18 times in the mentioned period, whereas Tino pulled it up just twice and Boycott never. In contrast to the successful females, the two unsuccessful males never stepped on the string. Unlike the jackdaws, the cows did not show a stable performance of the whole pull-step sequence after having stepped on the pulled up string for the first time. However, after they stepped on the string for the first time they immediately continued pull-stepping, but with less proficiency than the jackdaws. All three successful crows showed relatively more efficient actions (see Table 1) after their first pull-step than before (% efficient actions before first pull-step and after first pull-step: Uek 50.0, 91.3; Anniclaude 58.8, 83.8; Ebony 38.1, 73.3). Uek dropped the string twice, Ebony three times and Anniclaude six times after having stepped on the pulled up string for the first time.

2.3.2 Performance over trials (consolidation-phase)

In order to detect any learning effects the subjects' performance over trials was analysed. The six jackdaws (Orange-re was excluded because it showed the pull-step technique only once without stepwise training) and the three New Caledonian crows, which solved the string pulling problem reliably without getting stepwise training, significantly decreased their solution time (repeated ANOVA: $F_{1,16}=3.836$, p<0.001, Figure 2a). There was no species effect repeated ANOVA: $F_{1,16}=2.070$, p=0.193), but a significant interaction of the variables trial and species (repeated ANOVA: $F_{1,16}=2.664$, p=0.002) found. The fact that the subjects became

faster in solving the problem could be caused by finding sooner the correct solution-approach (first pull-step) in each trial and/or by improving the required motor pattern of pull-stepping. Therefore the solution time was split in two variables: the pull-step latency – representing the solution-approach, and the duration of pull-stepping until the reward is reached– representing the solution-execution. The pull-step latency (repeated ANOVA: $F_{1,16}$=3.750, p<0.001, Figure 2b) as well as the duration of pull-stepping (repeated ANOVA: $F_{1,16}$=2.301, p=0.007, Figure 2c) significantly decreased in the course of the experiment. Whereas no species effect (repeated ANOVA: $F_{1,16}$=1.65, p=0.242) and no interaction of the variables trial and species (repeated ANOVA: $F_{1,16}$=1.213, p=0.274) was found for the pull-step latency, further analysis of the duration of pull-stepping showed a significant species effect (repeated ANOVA: $F_{1,16}$=66.675, p<0.001) and a strong interaction of the variables trial and species (repeated ANOVA: $F_{1,16}$=3.810, p<0.001). Right from the beginning the jackdaws performed more or less perfectly and therefore could not became faster in executing the pull-step sequences (repeated ANOVA: F=0.640, p=0.832). Only in few cases they made release errors (drops, Figure 2d). The New Caledonian crows in contrast decreased their duration of pull-stepping over trials (repeated ANOVA: F=3.302, p=0.003) by significantly decreasing the number of drops to nearly zero (Friedman test: n=3, Chi²=25.075, p=0.049, Figure 2d).
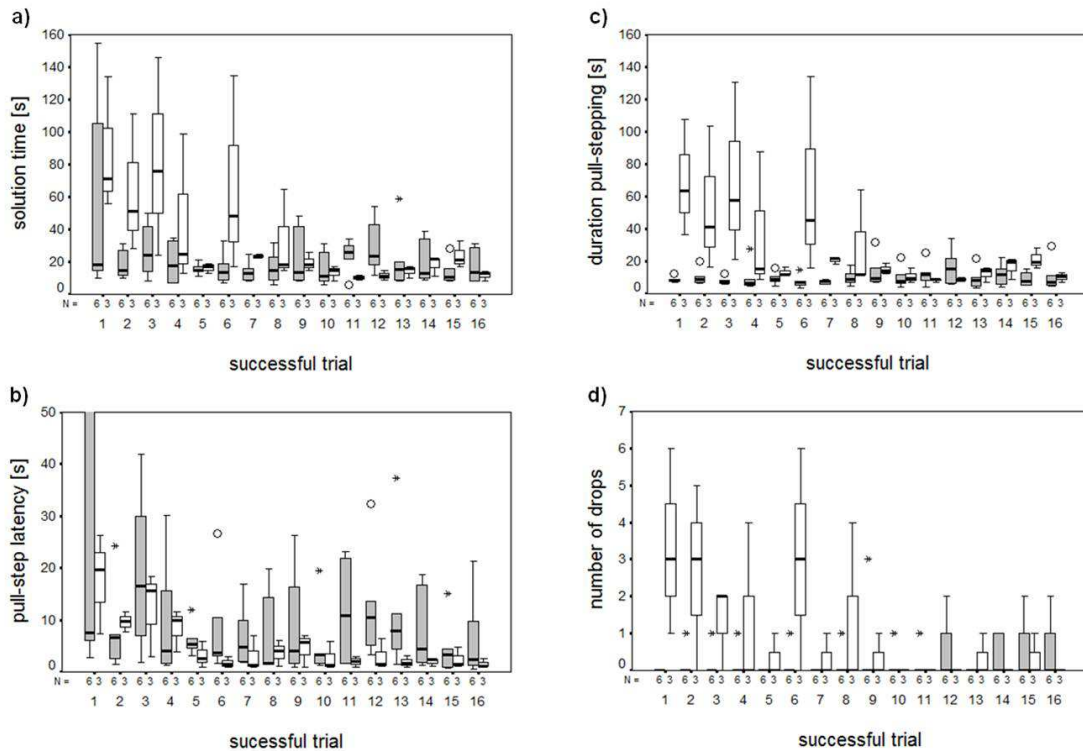

Figure 2: Box-plots showing the performance of pulling up a string in jackdaws (grey) and New Caledonian crows (white) over the first 16 successful trials. *Boxes* represent the interquartile range (IQR), *bars* within *boxes* are median values and *whiskers* indicate lowest and highest value still within 1.5 IQR of the lower and upper quartile

respectively. a) Solution time: time interacting with the string until reaching the reward, b) pull-step latency: time interacting with the string until first pull-step (missing values of successful trial one for jackdaws: upper quartile 105 s, upper whisker 155 s), c) duration pull-stepping: time interacting with the string from end of first pull-step until reaching the reward, d) number of drops.

2.4 Discussion

The analysis of the solution time showed a strong trial effect in all individuals but more detailed investigations revealed that this effect had different causes in the two species. The results suggest that the jackdaws had no big problems executing the required action pattern of pulling up the string and stepping on the pulled up loop (duration pull-stepping, Figure 2c), but it took them some time to start with it (pull-step latency, Figure 2b). Over the trials they seemed to learn that pull-stepping is the correct approach to the solution, which is shown by the decreasing pull-step latency. Therefore one could argue that the jackdaws did not seem to have any motor problems but their solution-finding improved gradually. This suggests a kind of trial-and-error learning in finding the correct solution approach as opposed to a means-end understanding. The New Caledonian crows, in contrast, had difficulties in performing the pull-step action (see number of drops and duration pull stepping, Figure 2). However, from trial five on they more or less immediately started to pull up the string and step on it in each trial. The perfect pull-step technique however, was reached later around trial eight. The New Caledonian crows seemed to have recognized after four trials that pulling the string up and stepping on it is the correct approach to the solution, but they seemed to have considerable motor problems executing this solution. One could therefore interpret these results as a kind of means-end understanding or quick learning with motor problems.

As already mentioned jackdaws as well as New Caledonian crows used more or less only one method to secure the reward, apart from some jackdaws flying directly to the reward, which was prevented by installing a cage. In contrast keas showed in total nine different pulling-methods to reach the reward (Werdenich & Huber, 2006). All of these techniques were food directed and similar efficient. Even more striking, the keas' behaviour remained flexible, as they performed the different methods throughout the trials. The authors explain this diversity in methods used with the keas' playful exploration of objects. Jackdaws and New Caledonian crows are by far more neophobic, which might restrict their experiences made during exploration.

However, in some aspects the jackdaws' performance remains contradicting. Seven out of fourteen jackdaws solved the string pulling problem at least once without help. Although just one individual (Spinni) solved the task on its first trial, the detailed analysis of the action patterns nevertheless showed that the subjects performed the string pulling kind of "spontaneously". After having stepped on the pulled-up loop for the first time five out of the seven solvers performed the whole sequence of pulling up and stepping on the string without errors and the remaining two solvers made just one error. Heinrich (1995) proposed four ways in which a precise behavioural sequence of numerous steps, like string pulling, could be achieved: i) random chance, ii) programming present already at birth, iii) learning both the sequence and its effects, and iv) insight. It seems likely that the solvers started to show interest to the setup and tried different actions until by chance they stepped on the pulled-up string. This behaviour was then "recognized" immediately as the crucial one for solving the task, because all the subjects who stepped on the pulled-up loop immediately continued performing pull-steps. The behaviour of stepping on the pulled-up string "could have been achieved by random chance rather than insight. However, insight may have followed so that the random "discovery" could be instantly exploited" (Heinrich 1995). For Seibt & Wickler (2006) such a mechanism does not seem to differ from operant conditioning. Similarly Taylor et al. (2010) proposed operant conditioning via a perceptual motor feedback cycle. Pulling as well as stepping on the string are reinforced because both actions hold a positive feedback (Taylor et al. 2010). A further possibility could be that the action pattern of pull-stepping is to some extend innate, like discussed for blue-tits (Altevogt 1952), siskins and goldfinches (Seibt & Wickler 2006). It could be that the action pattern of pull-stepping has to get started by a specific stimulus, which in this case could be the first pull-step itself. If that would be the case, the action pattern should go on even if the reason for it is not present. This could also explain the self-rewarding component of string pulling, which was suggested for some species (e.g. Altevogt 1952, Shuck-Paim et al. 2009). However, jackdaws' foraging behaviour does not represent any action patterns analogical to string pulling, apart from fixing objects with their feet (Dwenger 1989, personal observations), which weakens the argument of an innate motor program of string pulling in this species. Nevertheless there might be some facilitating prerequisites present – like beak-foot coordination when fixing food items with the foot and single actions like pulling and stepping – which have to be chained together to a behavioural sequence in order to reach the goal. Epstein et al. (1984) could show that pigeons were able to spontaneously chain together separately trained behaviours and so made their solution look "insightful". Thus, the potential of one-trial-learning of chaining together different behaviours should not be underestimated in respect to string pulling.

Although the jackdaws had no problems performing string pulling, they did not seem to transfer the knowledge of "knowing that pull-stepping is the correct approach" to the next trial. They gradually improved in finding the correct solution approach. As soon as they rediscovered the correct solution by stepping on the pulled up string in each consecutive trial, they again immediately performed the whole action sequence, without showing any irrelevant actions. It seemed as if they would experience a kind of "Eureka-moment" after the first pull-step in each trial. Further evidence for this explanation comes from the results of the stepwise training of the non-solvers. From the moment they stepped on the string for the first time, they solved the string pulling problem in every trial in which they showed clear interest in the setup. All seven non-solvers learned the required action sequence of pulling up and stepping on the string, which shows that by providing shorter strings, which increase the subject's motivation and interest, the chance of stepping on the pulled-up loop is increased and therefore the solution is facilitated.

The five New Caledonian crows behaved differently from the jackdaws. The three female crows were able to solve the task without getting stepwise training. However, after having stepped on the pulled-up loop for the first time it took them several attempts to secure the reward (first solution times ranged from 56-134 s and number of drops ranged from 2-6). These results are in contrast to the findings of Taylor et al. (2010) where all four New Caledonian crows solved the string pulling problem immediately (first solution times ranged from 6-37 s, 40 cm long string) and showed no drops in their first trial. However, Medina et al. (unpublished data) tested 12 adult New Caledonian crows which showed no spontaneous-like string pulling performance (first solution times ranged from about 28-43 s, number of release errors ranged from about 6-11, 40 cm long string). Neophobia cannot be the explanation why the crows in the present study did not solve the problem immediately because all of them interacted intensively with the string. The finding that the crows tried to chain together the behaviours of pulling up the string and stepping on it immediately after their fist pull-step sequence, shows that they recognized the pull-step pattern as being the solution. However, at the beginning they had considerable more problems than the jackdaws in performing the required motor pattern. Jackdaws have well established beak-foot coordination, especially in food context. They can often be observed holding pieces of food with one or both feet to rip off small parts (Dwenger 1989, personal observations). New Caledonian crows are also known to use their feet (Weir et al. 2002, personal observation), but more in tool use context (tool manufacturing, tool holding). However, to position the large Zophoba-larva, which was used as a reward, in line with the beak, the New Caledonian crows never used their feet to fix the

larva. Instead they put the larva carefully on the perch still holding it loosely with the beak to then try to grasp it on its anterior or posterior end to be able to swallow it down in one piece. The jackdaws, on the other hand, always fixed the larva between the perch and one of their feet to tear off little parts which they could easily swallow. These observations suggest that the jackdaws use their beak and feet in a well coordinated manner in a food context, which could facilitate their performance with the motor pattern of string pulling (Altevogt 1954), whereas New Caledonian crows less often show behaviours involving both beak and feet.

The role of operant conditioning mediated by a perceptual-motor feedback cycle (Taylor et al. 2010) in string pulling remains questionable, because large inter-species as well as inter-individual differences in string pulling were found (Vince 1961, Seibt & Wickler 2006). Taylor et al.'s (2010) suggestion to explain these contradicting results is that spontaneous string pulling of naive individuals was so far found only in corvids (Heinrich 1995, Heinrich & Bugnyar 2005) and psittacids (Pepperberg 2004, Werdenich & Huber 2006, Schuck-Paim et al. 2009, Krasheninnikova & Wanker 2010), two families with enlarged forebrains compared to other birds (cited in Emery & Clayton 2004). Possibly "bird species with larger associative brain areas are able to integrate information between perceptual and motor pathways quicker than species with smaller associative brain areas" (Taylor et al. 2010). However, this explanation does not account for the inter-individual differences which were found in siskin and goldfinches (Seibt & Wickler 2006), and in the present study. The important difference between the successful and unsuccessful subjects was that the former never stepped on the pulled up string. This was also the case in the two *Carduelis* species (Seibt & Wickler 2006). The action of "stepping on the string", if discovered by chance or based on cognitive abilities like understanding of cause-effect relationships (Heinrich & Bugnyar 2005) or imagination (Emery & Clayton 2004), has to be "recognized" as crucially relevant for solving the problem or could serve as a stimulus for starting an innate motor program. When considering operant conditioning this action does not need to be "understood", but would be favoured because of its rewarding nature. Taylor et al. (2010) argue that the reinforcing aspect of stepping is that the reward fixed on the end of the string remains closer to the subject. Pulling the string up and holding it still with the beak would lead to the same positive feedback. The crucial difference between holding the string with the foot or the beak is that in the former case the beak is free to make another pull, which brings the reward even closer. Therefore an animal has to understand or learn the advantage of using the foot, if this behaviour is not innate. However, the role of perceptual-motor feedback cannot be neglected. Amann et al. (unpublished data) confronted keas, experienced in string pulling with an over-length task, in

which the subjects had to pull up 60 cm of over-length string until the reward moved closer. They also gave the keas a hooked task, in which 60 cm of over-length string, threaded through the reward and hidden under a platform, had to be pulled up before perceiving any movement of the reward. The males failed on about half of the trials and only one female succeeded once in each condition. The keas could see the reward at any time, but there was no feedback perceivable during the first pull-step sequences because of the over-length. Summarizing, finding the correct solution seems to require a kind of understanding of the advantage to use the feet in combination with the beak, whereas the execution of the solution might be facilitated by a positive perceptual-motor feedback cycle leading to accelerated problem solving via operant conditioning.

Detailed observations and analysis of the discovery and execution of problem solving in combination with clever variations of experimental setups have the potential to provide further insight into the underlying mechanisms of problem solving in animals.

Study 2

Comparing jackdaws' (*Corvus monedula*) discrimination performance in three sensory modalities

Abstract

The aim of this study was to compare jackdaws' performance in a visual, acoustic and weight discrimination task where a baited and a non-baited canister were tight at the end of two separate strings hanging from a perch. The subjects were required to pull the strings in order to gain access to the discriminatory features in all three tasks. In the visual task, the two canisters differed in colour. In the acoustic task, pulling at the string resulted in an auditory cue or not, and in the weight task, the two canisters differed in weight. The cue co-varied with the presence of food in the visual task (arbitrary relation), whereas the cue was caused by the content of the canister in the acoustic and weight task (causal relation). For the intuitive group, the acoustic or the heavy canister was baited. For the counterintuitive group, the silent or the lighter canister contained the food. The results showed that jackdaws spontaneously adopted the crucial method of switching from one string to the other before making their choice in 10.3% ±5.4 (mean, ±SD) of the trials. In contrast to the assumption that causally structured discrimination tasks should be easier to learn than tasks which hold an arbitrary relation, jackdaws did not show better performance in the intuitive than in the arbitrary or counterintuitive tasks. Rather, the individuals developed a preference for the counterintuitive lighter canister, and the individuals of the "counterintuitive" group switched more often from the wrong to the correct canister in the weight task than they did *vice versa*. This suggests that jackdaws are capable in discriminating objects solely on the basis of weight. Although the experimental setup has the potential of becoming a standard method for comparative research in discrimination learning and causal reasoning, the performance of the birds is poor overall and possible reasons for this are discussed.

3.1 Introduction

Successful and efficient foraging is based "on being selective and exercising keen powers of discrimination" (Terborgh 1983, p. 83; cited from Visalberghi & Néel 2003). An individual could perceive the relation between a given cue and the food reward in two possible ways: (i) as co-variation – cue co-varies with presence of food or (ii) as causation – presence of food causes cue (Hanus & Call 2008; Schrauf & Call 2009, 2011). Call (2004) tested all four species of great apes in a discrimination task, giving them visual or auditory information about the content of two opaque containers where only one was baited. The subjects performed above chance level if the cue was caused by the presence or absence of the food item, e.g. shaking one container produced noise depending whether the reward was in the container or not. However, if the cue co-varied with the food (such as tapping noisily on the rewarded container) and thus was not causally related to it, the individuals performed at chance level. Studies on capuchin monkeys (*Cebus apella*, Sabbatini & Visalberghi 2008) and olive baboons (*Papio hamadryas anubis*, Schmitt & Fischer 2009) using basically the same paradigm reported similar results regarding the distinction between causal and arbitrary structured discrimination problems. Up to date it remains open whether similar abilities of detecting and exploiting causal relations can be found also in non-primates.

Recently, birds have become more and more of interest in cognitive sciences. Especially research on corvids has provided evidence that this avian taxon shows remarkable cognitive abilities in the physical as well as the social domain, which can be compared with those of primates (see Emery & Clayton 2004 for review). On one hand jays and ravens developed remarkable cognitive skills regarding food caching and pilfering (e.g. Emery & Clayton 2001; Emery et al. 2004; Bugnyar & Kotrschal 2002, 2004). On the other hand New Caledonian crows show sophisticated tool-use abilities (e.g. Hunt 1996; Weir et al. 2002; von Bayern et al. 2009). Jackdaws however show no special additional abilities in the physical domain, which might have triggered cognitive adaptations ("adaptive specialization hypotheses", de Kort et al. 2006). Although the common ancestor of all corvids is thought to be a moderate food cacher (de Kort & Clayton 2006), the non-food storing and non-tool using jackdaws seem a good model species to test for cognitive skills, which could be of a common repertoire within the Corvidae.

In studies on inference by exclusion, the subjects are given cues that are causally related to food. In a study on ravens and keas, Schloegl et al. (2009) compared the inference by exclusion performance of these two species. In one experiment the subjects had to choose between two

blows under one of which a reward was hidden. The ravens choose the baited bowl above change level regardless if they have been shown the content of both, the baited or the empty bowl only. In contrast, the keas failed in the condition in which they saw just the content of the empty bowl, and therefore would have had to infer that the food was hidden under the other bowl. In a follow up study Schloegl (2011) tested jackdaws on the same paradigm with the result that they did not choose by inference by exclusion, which supports the argument that inference by exclusion abilities may have evolved in the context of food caching (as special adaptation). Coming back to the distinction between causal versus arbitrary structured discrimination task, the setup used in these two studies can be seen as a causal structured discrimination task in the visual domain, because the visual cue, upon which the decision had to be made, was caused by the presence or absence of the reward.

So far studies on discrimination were focused mainly on the visual modality. Less is known whether animals can also use acoustic and/or kinaesthetic information (e.g. weight) as cue for their decisions. A few studies have been conducted on the use of weight information in primates. McCulloch (1941) managed to train five chimpanzees to discriminate between two objects differing only in weight. It took them a median of 1100 trials to perform above chance level. In a similar study by Schrauf & Call (2009) two out of five orang-utans and three out of five bonobos, but none of the two gorillas learned to discriminate two objects just by their weight after about 300 trials. In both studies the discrimination task held an arbitrary structure, because the experimenter defined a priori which of the two objects (the lighter or the heavier) was the correct one and rewarded the subject if the right decision was made. Beside great apes, capuchin monkeys where shown to use weight information in food finding as well as in tool selection. To investigate the capuchins' ability to use sound and weight information to infer the fullness of a nut shell, Visalberghi & Néel (2003) manipulated the content of nut shells. The subjects selectively chose the heavier nut shells using weight and sound by tapping on the nuts. Furthermore it was shown that capuchin monkeys are able to select the most efficient stones (Visalberghi et al. 2009) or artificial hammer tools (Schrauf et al. 2008) for cracking open nuts based solely on weight. In contrast to the presented studies on great apes, these three studies on capuchin monkeys deal with discrimination problems structured in a causal way. Hanus & Call (2008) could show that chimpanzees are sensitive to the effect of weight. The chimpanzees inferred the location of the food by the effect the food's weight had on a balance. The subjects had not to assess the weight of the cups, but had to base their decision on the visual outcome caused by the food's weight. Apart from the primate-studies, there are hardly any studies investigating the use of kinaesthetic information

in other taxa. To best of our knowledge, there is only one study which could show, that two bird-species can discriminate two objects solely on weight. Heinrich et al. (1997) showed that Black-capped Chickadees (*Parus atricapillus*) and Red-breasted Nuthatches (*Sitta canadensis*) discriminate in favour of heavier over lighter sunflower seeds. They even reject normal seeds when confronted with manipulated heavier filled seeds. The ability to discriminate objects on the basis of weight can be advantageous and increase efficiency in foraging and therefore should be found in species feeding on encapsulate food such as nuts and seeds.

The aim of the present study was to compare jackdaws' discrimination ability of arbitrary and causally structured tasks and to investigate whether the subjects will seek information about both options in a comparative way before making their final decision. Vertical standard string pulling was chosen as basic setup. The subject had to discriminate two containers that differed only in the visual, auditory, or weight dimension. The two containers were tight to the suspended end of the strings fixed at a perch, so that each container hung inside an opaque cylinder. Thus, the opaque cylinder concealed the visual dimension of the container and lifting the container by pulling the string was required to assess the dimension in all three tasks (thereby perceiving the container's colour, or hearing the "bell" being moved in the container, or assessing the weight of the container). This setup was chosen because it allowed comparing all three tasks directly and it forced the subjects to manipulate the objects/strings in all three discrimination tasks in order to perceive the discriminatory cues (active information seeking).

Independent from each other and for the same reasoning, Schrauf & Call (2011) developed a very similar setup for testing great apes' ability to use weight as a cue. Schrauf & Call (2011) showed that chimpanzees were able to select the baited cup solely on the basis of weight (causal condition). Five out of nine subjects chose the correct (heavier) cup at least in 12 out of 16 trials. In an arbitrary visual task (the two cups differed in colour) all but one individual failed, and thereby confirmed their hypothesis, that causally structured discrimination problems should be easier to learn than arbitrarily structured once.

3.2 Methods

3.2.1 Subjects and housing

Subjects were 12 adult hand-reared jackdaws, which were kept in two big outdoor aviaries at the research station of Dr. Auguste von Bayern, Leutstetten (Germany), in cooperation with the "Behavioural ecology research group", University of Oxford. All subjects were well experienced in pulling up strings by showing the pull-step technique (for details see study 1). Each aviary was furnished with branches and wooden perches, nest boxes, tables, chairs, and live *Sambucus nigra* bushes. The ground was covered partially with wooden chips and, under the most frequented roosts, with concrete to facilitate cleaning.

The main diet consisted of a mixture of boiled rice, minced beef-hart and quark, softened cat-pellets, fruits (e.g. oranges, apples, bananas) and cereal with mealworms. Once a week the birds were given bread softened in milk. Fresh water was provided every day in big bathing tubs. The birds were deprived of food 2-3 hours before testing.

3.2.2 Apparatus and procedure

In order to test the subjects' performance in the different discrimination tasks, two preparatory phases were carried out before conducting the main experiment. The main apparatus consisted of a natural straight wooden perch (5 cm in diameter), which was fixed in each test compartment. A wire-mesh cage (87 x 40 x 60 cm, l x w x h) was nailed directly to the lower side of the perch, so that the bird could interact with the setup while standing on the perch. The string (brown cotton cord 4 mm in diameter), was tight to the perch and hung into the cage. To facilitate pulling up the string, 5 cm of the wire-mesh was cut off on both sides of the perch. This arrangement allowed the individuals to easily reach down to grasp the string, but they could not enter the cage (Figure 1). The animals were tested in a visually separated compartment in each of the two aviaries. Because all subjects were pair-bonded and therefore separation from the partner induced high levels of stress, it was important to ensure that the pair could interact even while testing. In one of the aviaries, this was done by keeping the focal-subject's partner in a compartment next to the test-compartment, whereas in the other aviary, the arrangement of the different compartments allowed the pair to interact without the need of separating both from the group. Although the focal-subject could interact with its partner, the experimental-setup was positioned in the test-compartment of both aviaries in a

way that it could not be seen by the partner. Separation of the focal subject was achieved in most of the cases by waiting until the individual flew in the test compartment or by gently chasing it into it. Both procedures seemed not to be very stressful for the birds, as they usually immediately started to investigate the setup.
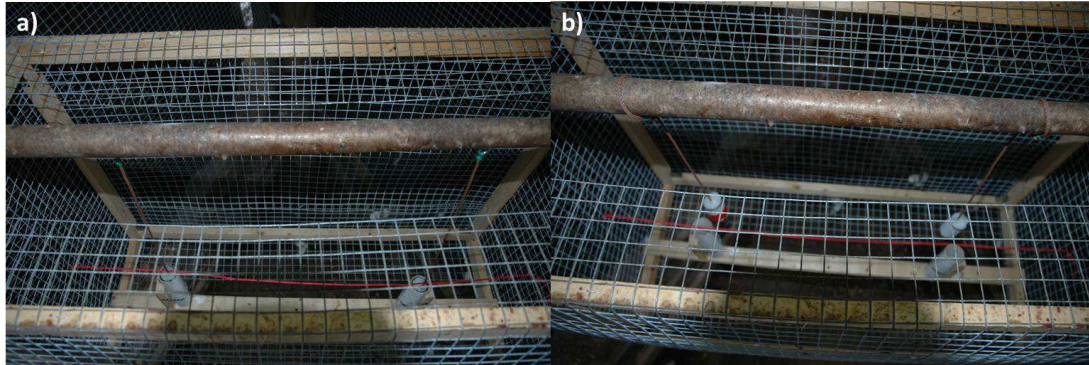

Figure 1: Experimental setup from bird's-eye view of the visual task. a) both canisters inside the cylinder, discriminatory feature not visible; b) after pulling the canisters out of the cylinders the discriminatory feature perceivable.

Training phase

The aim of the training phase was to habituate the subjects to a two choice task. Two 40 cm long strings were tight to the perch 40 cm apart from each other. A black open film-canister was attached at the free end of both strings. One of the canisters was baited by fixing a *Zophoba*-larva clearly visible on top of it. The jackdaws received one session per day with six trials per session. In a session, each canister was baited three times. The side of the rewarded string was assigned by coin flipping. A trial ended when the individual reached the reward or when 10 min had elapsed. The first string at which an individual pulled was defined as first choice. The criterion of successfully completing the training phase was set at 15 correct first choices within 18 consecutive trials (binomial test: p=0.008). The p-value of making 15 correct choices out of 18 consecutive trails by chance is lower than 0.005 (simulation of 10000 trials with a 50% probability of making a correct choice).

Canister handling

After passing the training phase the subjects were trained to pull up a baited canister when the reward was not visible. A 40 cm long string was fixed in the middle of the perch and the black

film-canister which was attached on its free end was baited inside with a *Zophoba*-larva. The subjects had to successfully retrieve the reward by pulling up the canister in three consecutive "visible" trials, in which the larva was just partially covered by a piece of synthetic wool. Thereafter they had to solve a total of six "not visible" trials on two consecutive days within 5 min per trial. In "not visible" trials, the reward was covered completely by the piece of wool, which the subjects had to tear out of the canister in order to get the reward. If a subject showed no interest because of not seeing the reward, it got a "help" trial – the canister with the completely covered reward was fixed 3-4 cm under the perch and thus could be reached without the effort of pull-stepping. This increased the individuals' motivation of manipulating the canister. After a successful "help" trial, the "not visible" trials were provided again.

Discrimination tasks

The canisters, which held the discriminatory feature and were tight on the free end of a string, were inserted in a slightly bigger cylinder which covered its visual appearance. Just by pulling on the string and thereby lifting the canister out of the cylinder, the discriminative stimuli of the canister could be perceived (see Figure 1 and Figure 2). The two containers in the visual task differed in colour. One canister was completely white, whereas the lower half of the other canister was red and just the upper half was white. In the acoustic task both canisters were green, but inside one canister several small nails were freely hanging, which produced an acoustic cue if the canister was moved jerkily. To guarantee the sound production a red string was fixed horizontally about one centimetre above the cylinders, so that by pulling the canister out of the cylinder the canister staggered because it hit the string. The "silent" canister of the acoustic task contained some little stones, which were glued on the bottom of it, to exclude any weight differences. Therefore both canisters of the acoustic task weighted 20 g. The two canisters of the weight task were coloured in blue. The light and the heavy canisters weighed 8 g and 32 g, respectively. The weight of the heavier canister was achieved by gluing several little stones on the bottom of the canister. The cylinders for each task had the corresponding colour of the canisters.
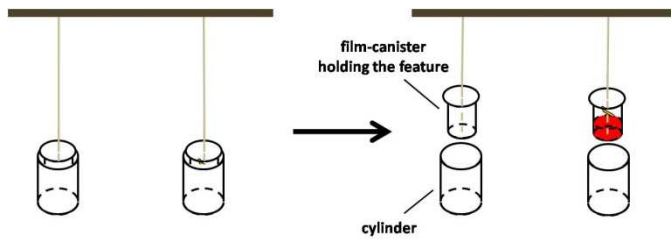
Figure 2: Schematic drawing of the experimental setup (visual discrimination task shown). The discriminatory feature is only perceivable after pulling the canister out of the cylinder.

The subjects were randomly assigned to two different treatment groups with the restriction of having the same ratio of the sexes and aviary-provenience in the two groups. For treatment group 'intuitive', the canister coloured in white-red (visual task), the sound producing canister (acoustic task), and the heavier canister (weight task) where baited, whereas in treatment group 'counterintuitive', the reward contingencies were *vice versa* (see Figure 3).
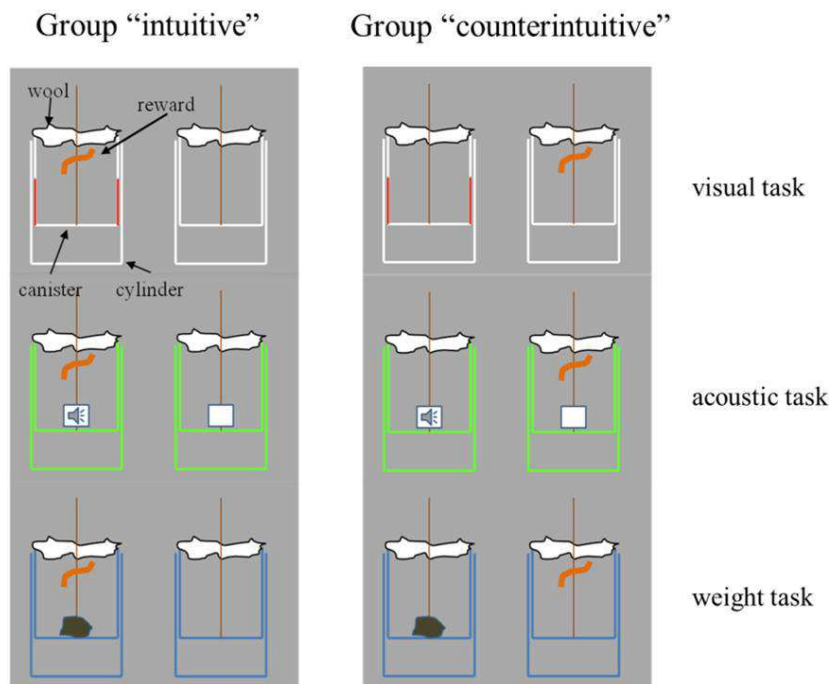
Figure 3: Schematic drawing of the two canisters of the visual, acoustic and weight task for group "intuitive" and group "counterintuitive".

Subjects were given a maximum of six trials per session and one session per day. Two trials of each task were provided in one session, with the restriction of not having the same task consecutively within and between sessions. The baited side was assigned pseudo-randomly with the following criteria: i) within one session each side was baited three times, ii) one

specific side was baited in not more than two consecutive trials within and between sessions, and iii) within seven sessions the left/right side had to be baited equally often in each of the three tasks (each side was seven times baited per task in seven session). The first string that was pulled up entirely (canister could be grasped with the beak) was defined as first choice. A trial ended when the correct string was pulled up entirely or when 10 min had elapsed. Because some individuals seemed to have a bias to pull up the string on the side which they had not pulled up in the previous trial, all subjects got one extra minute after having pulled up the correct string as first choice, what allowed them to possibly pull up also the wrong string. This procedure removed the bias of pulling up the strings alternating between the trials. If a subject showed a strong side preference (same side as first choice in at least 5 consecutive trials across tasks and sessions), the string which was not preferred was baited in the following trials until the subject choose again the other side two times. After such a "correction" phase, the baited side was again assigned pseudo randomly, as described above.

The experiment started at the beginning of January 2010, but had to be stopped about one month later, because the breeding season was starting. In this period, the birds were involved in on-going fights for nest boxes and mates. Several test sessions had to be interrupted because either the focal subject's partner was involved in some aggressive interactions or its nest box was occupied by another pair. For this reason, I was able to conduct a restricted number of trials per task only.

3.2.3 Analysis

All trials were videotaped for detailed analysis. The performance in the training phase of males and females was compared by carrying out a Mann-Whitney U test. In the discrimination experiment the following behaviour was recorded for each trial: i) correct first choice: pulling the baited canister completely up without touching the wrong string (C), ii) wrong first choice: pulling the unbaited canister completely up without considering the correct string (I), and iii) rostripulating one string (e.g. making few pull-steps) and then switching to the other string (IC: correct string-switch, CI: wrong string-switch). In order to perform better than at chance level, one would expect that in about half of the correct trials (entirely pulled up the correct string first), the subject should by chance pull first the wrong string and then switch to the correct one after having perceived the discriminatory feature. For this reason, the crucial trials are the ones in which the subjects showed switches either to the correct or incorrect string. The number of correct and wrong first choices and the number of correct and wrong string-

switches were measured for each subject in each task. Binomial tests with 0.5 as test proportion were carried out.

To rule out if the subjects had more difficulties to pull up the heavier canister, the first trial of the weight task was analysed in more detail: the latency to reach the first-choice canister was measured and the number of pull-step sequences for reaching the canister was counted. Measures of subjects that pulled up the heavier or lighter canister in the first trial where compared with Mann-Whitney U tests.

All tests were two tailed and alpha-level was set at 0.05.

3.3 Results

3.3.1 Training phase

Eleven of the twelve jackdaws reached the criterion of 15 correct first choices out of 18 consecutive trials (see Table 1). The number of trials to criterion ranged from 15 (smallest number possible) to 42 trials. However, all successful individuals except Csoka managed to reach the criterion within 24 trials. Orange-re was quite nervous when being separated, most likely because another pair attempted to take over his nest-box, and therefore had to be excluded from the study. Regarding the performance in the training phase, no differences between males and females were found (Mann-Whitney U test: $N_1=7$, $N_2=4$, $U=10.5$, $p=0.527$). The individuals that were assigned randomly to group "intuitive" in the later discrimination task needed significantly more trials to reach criterion in the training phase than the individuals that were assigned to group "counterintuitive" (Mann-Whitney U test: $N_1=5$, $N_2=5$, $U=0.0$, $p=0.008$).

Table 1. Name, sex, performance in training phase, number of help-trials and assignment to discrimination group of the subjects.

Individual	Sex	Aviary	Training phase (trials to criterion, min. 15/18)	Help-trials* (Canister handling)	Treatment group
Csoka	F	1	42	6	intuitive
Jackomo	F	2	21	0	intuitive
Karacho	F	1	24	0	intuitive
Radja	M	2	18	11	intuitive
Tschok	M	1	21	1	intuitive
Dohli	F	1	16	1	counterintuitive
Jackie	F	1	16	0	counterintuitive
Spinni	M	1	15	0	counterintuitive
Xenia	M	2	17	2	counterintuitive
Rani	F	2	16	1	counterintuitive
Krakehl	F	2	20	-	-
Orange-re	?	2	-	-	-

*If subjects were not interested in the string with no reward visible, they were given help-trials in order to train them to pull up strings (see chapter Canister handling in section Methods for details). Numbers represent the number of help-trials a subject needed to pull up strings reliably.

3.3.2 Canister handling

Out of the eleven individuals who passed the training phase, four succeeded in the canister handling without the need of help-trials (Jackie, Spinni, Karacho and Jackomo). The other seven jackdaws did not show interest to the setup when there was no reward visible. After one to eleven help-trials, six of them pulled up the canister even if the reward was not visible (see Table 1). Only Krakehl did not succeed in this task and had to be excluded at this point.

3.3.3 Discrimination tasks

Nine of the remaining ten jackdaws showed interest to the setup. Only Rani was not willing to participate in the experiment. After seven sessions of no interest, she was excluded from the experiment.

The nine subjects were given in total a mean of 33.7 trials ± 2.4 SD of the visual task, 33.2 ±2.4 trials of the acoustic, and 33.1 ±2.8 trials of the weight task.

Table 2 presents the trial by trial performance of each individual in each task. Overall, the success-rate of both groups did not exceed chance-level. In the first part of the experiment, Xenia was significantly correct in the weight task (Table 2, Binomial test p=0.021). In four of these trials, she abandoned her first incorrect string choice and switched to pull up the correct container. Jackomo was significantly incorrect in the same task (Table 2, Binomial test p=0.001). There were no differences in the percentage of correct trials between the first and second part of the experiment, except for Jackie and Spinni in the visual task, and Karacho in the weight task where they showed a decrease in performance. Jackomo improved its significantly incorrect performance in the first half to random performance in the second half of trials in the weight task.

Table 2: Trial by trial performance and comparison of success-rate in visual, acoustic and weight task.

Visual

	% correct trials 1st part	2nd part	total
"intuitive"	55.0 ±8.1	55.0 ±6.6	55.2 ±5.6
Csoka	62.5	52.9	57.6
Jackomo	50.0	56.3	53.1
Karacho	43.8	55.6	50.0
Radja	56.3	46.7	51.6
Tschok	62.5	65.0	63.9
"counterintuitive"	53.1 ±18.8	36.4 ±11.7	43.3 ±2.5
Dohli	31.3	50.0	40.0
Jackie	68.8	25.0*	44.4
Spinni	68.8	28.6	45.9
Xenia	43.8	42.1	42.9

Acoustic

	% correct trials 1st part	2nd part	total
"intuitive"	41.3 ±13.0	46.4 ±7.8	43.9 ±9.4
Csoka	56.3	47.4	51.4
Jackomo	25.0	33.3	29.4
Karacho	43.8	50.0	47.1
Radja	50.0	53.8	51.7
Tschok	31.3	47.4	40.0
"counterintuitive"	45.3 ±3.1	59.7 ±12.8	52.4 ±5.8
Dohli	43.8	69.2	55.2
Jackie	50.0	50.0	50.0
Spinni	43.8	47.4	45.7
Xenia	43.8	72.2	58.8

Weight

Trial	% correct trials 1st part	2nd part	total
"intuitive"	38.8 ±22.3	39.5 ±16.8	38.5 ±11.9
Csoka	31.3	23.5*	27.3*
Jackomo	6.3*	53.3	29.0*
Karacho	62.5	21.1*	40.0
Radja	37.5	41.7	39.3
Tschok	56.3	57.9	57.1
"counterintuitive"	64.1 ±13.9	43.9 ±10.1	53.5 ±7.9
Dohli	56.3	35.7	46.7
Jackie	68.8	35.0	50.0
Spinni	50.0	55.5	52.8
Xenia	81.3*	50.0	64.7

Black boxes represent trials where the incorrect canister was pulled up first; grey boxes represent trials where the correct canister was pulled up first; exclamation marks represent the occurrence of at least one string-switch in the

Over all tasks, the percentage of trials in which the individual jackdaws switched between the strings was 10.3% ±5.4 (mean ±SD). Spinni switched only two times. Tschok switched quite often in all three tasks, but he did so nearly exclusively in the second part of the experiment (see Table 3). When the birds switched from one string to the other, they did so only once in almost all of these trials. Only in five cases, multiple switching was observed: Tschok did so once in the visual and once in the acoustic task, Dohli once in the weight task and Xenia once in the acoustic and once in the weight task. In all events, the subjects switched from the correct string to the wrong and then back to the correct which was finally pulled up entirely. Five subjects (Jackomo, Radja, Dohli, Jackie, Spinni) switched more often in the first part and four individuals (Csoka, Karacho, Tschok, Xenia) did so more often in the second part of the experiment. Comparing the two parts of the experiment for each task separately, there was no clear pattern found. Only three subjects (Csoka, Karacho and Tschok) showed in all three tasks a higher percentage of string-switches in the second part of the experiment. The other six animals switched in the first part of the experiment more often, less often or equally often depending on the task (see Table 3). It is striking that in the weight task none of the subjects of group "counterintuitive" switched in the second part of the experiment.

Table 3: Distribution of switches throughout the experiment.

Visual

	c/w	trials 1st part (1–16)	trials 2nd part (17–37)	% trials with switches 1st part	% trials with switches 2nd part
"intuitive"	2/2			5.0 ±5.2	13.0 ±12.5
Csoka	0/0			0.0	5.9
Jackomo	1/0			6.3	6.3
Karacho	0/1			6.3	11.1
Radja	1/1			12.5	6.7
Tschok	0/0			0.0	35.0
"counterintuitive"	4/1			7.8 ±3.1	5.1 ±7.4
Dohli	0/1			6.3	0.0
Jackie	2/0			12.5	0.0
Spinni	1/0			6.3	4.8
Xenia	1/0			6.3	15.8

Acoustic

	c/w	trials 1st part (1–16)	trials 2nd part (17–37)	% trials with switches 1st part	% trials with switches 2nd part
"intuitive"	5/2			8.8 ±9.5	15.4 ±10.8
Csoka	0/0			0.0	21.1
Jackomo	2/2			25.0	5.6
Karacho	1/0			6.3	11.1
Radja	1/0			6.3	7.7
Tschok	1/0			6.3	31.6
"counterintuitive"	4/1			7.8 ±6.0	17.2 ±19.4
Dohli	1/0			6.3	7.7
Jackie	2/0			12.5	16.7
Spinni	0/0			0.0	0.0
Xenia	1/1			12.5	44.4

Weight

Trial	c/w	trials 1st part (1–16)	trials 2nd part (17–37)	% trials with switches 1st part	% trials with switches 2nd part
"intuitive"	1/3			5.0 ±6.8	16.8 ±14.0
Csoka	1/1			12.5	23.5
Jackomo	0/2			12.5	13.3
Karacho	0/0			0.0	10.5
Radja	0/0			0.0	0.0
Tschok	0/0			0.0	36.8
"counterintuitive"	11/1*			18.8 ±8.8	0.0 ±0.0
Dohli	2/1			18.8	0.0
Jackie	4/0			25.0	0.0
Spinni	1/0			6.3	0.0
Xenia	4/0			25.0	0.0

Black fill represent wrong trials, grey fill represent correct trials, white fill represent trials with no switches from one string to the other and exclamation marks represent the occurrence of at least one string-switch in the respective trial. 1st part: trial 1-16. 2nd part: trial 17 till end of testing. Numbers in bold represent group means (±SD). c/w: correct/wrong string-switch. Correct string-switch is defined as switching from the incorrect to the correct string before having pulled up the incorrect string entirely. Wrong string-switch is defined as switching from the correct to the incorrect string before having pulled up the correct string entirely. Numbers in bold of column "c/w" represent group sums. The difference between correct and wrong string-switches was compared to a 0.50 chance distribution using the Binomial-test. * indicate significant results according to binomial test (p≤0.05). Binomial-tests were carried out for the group-sums only.

For the following more detailed analysis, only the string-switches of the first part of the experiment were considered. This decision is supported by the fact that it is not clear which influence the upcoming breeding season and the on-going fights and stress had on the task performance of the subjects. At the time the fights for nest boxes and breeding partners became more and more frequent, all subjects had completed at least 16 trials per task. Schrauf & Call (2011) who tested great apes with nearly the same setup in a visual and weight

discrimination task provided 16 trials per task as well. In the first part of the experiment, the numbers of trials in which string-switches were made, showed a tendency to differ between the different discrimination tasks in group "counterintuitive" (Friedman-test: N=4, X^2=5.69, p=0.058), but not in group "intuitive" (Friedman-test: N=5, X^2=1.53, p=0.465). In the weight task, subjects of group "counterintuitive" switched in 18.8% ±8.8 (mean ±SD) of the trials compared to 7.8% ±3.1 (mean ±SD) in the visual task and 7.8% ±6.0 (mean ±SD) in the acoustic task. Table 3 presents the number of correct and wrong string-switches for each individual in the first 16 trials per condition. Overall, subjects showed significantly more correct than wrong string-switches (Binomial test: 27 correct switches against 10 wrong switches, p=0.009). However, on group level, only group "counterintuitive" switched significantly more often from the incorrect string to the correct than *vice versa* (Binomial test: 19 correct switches against 3 wrong switches, p=0.001). This result was not caused just by one individual. All four subjects switched more often to the correct than to the wrong string (Wilcoxon test: Z=-1.826, p=0.068). Looking at each task separately, group "counterintuitive" showed significantly more correct string-switches than wrong once in the weight task only (Binomial test: 11 correct switches against 1 wrong switch, p=0.006; significant even after Bonferroni-correction for alpha-level inflation, corrected α=0.008). Again all four subjects of group "counterintuitive" switched more often from the incorrect string to the correct than *vice versa* (Wilcoxon test: Z=-1.857, p=0.063). A comparison between the two groups revealed that group "counterintuitive" showed significantly more correct switches in the weight task than group "intuitive" (Mann-Whitney U test: N_1=5, N_2=4, U=0.5, p=0.016, Fig. 3A).

It is possible that switching to the lighter canister is a result of individuals avoiding the effort of pulling up the heavy canister. There was no difference in the reaching latency (Mann-Whitney U test: N_1=5, N_2=4, U=7.0, p=0.556) or in the number of pull-step sequences to reach the canister (Mann-Whitney test: N_1=5, N_2=4, U=3.5, p=0.111) between the five individuals (Csoka, Karacho, Tschok, Jackie and Spinni) which pulled up the heavy canister and the four individuals (Jackomo, Radja, Dohli and Xenia) which pulled up the light canister in their first trials of the weight task.
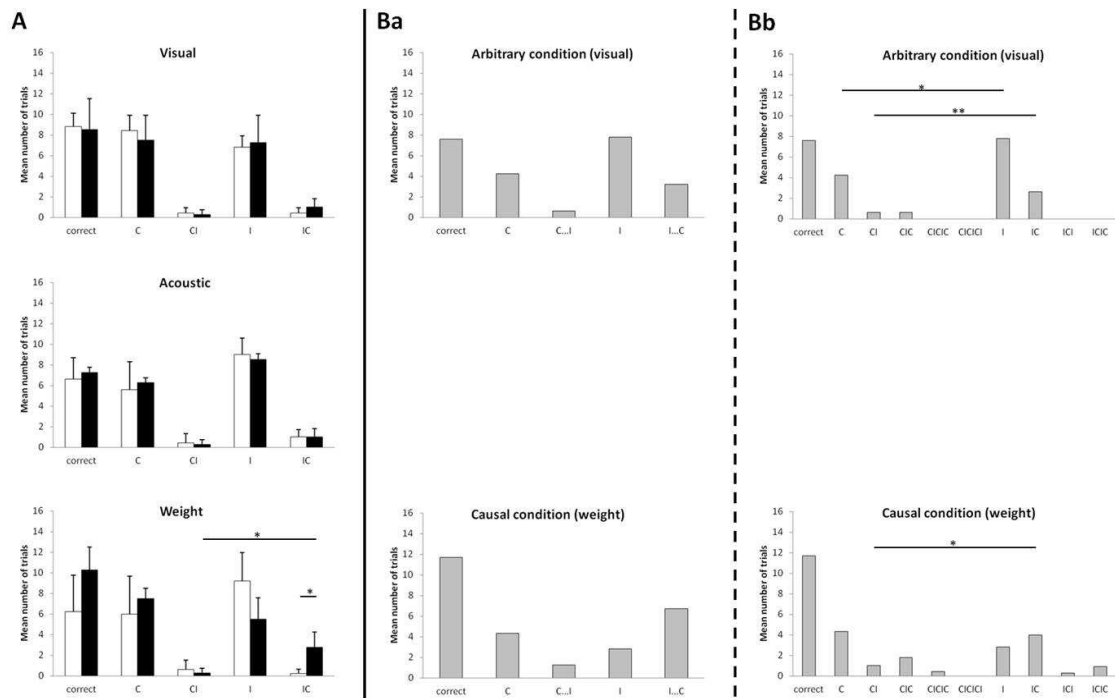
Figure 4: (A) Jackdaws; (Ba, Bb) Chimpanzees (Schrauf & Call, 2011). Mean (+SD) number of trials individuals showed one of the following pulling patterns: correct: total of correct trials; C: correct; I: incorrect; C or I: only pulled at one string, no string-switches; CI or IC: one string-switch; CIC or ICI: two string-switches; ICIC: three string-switches; CICIC: four string-switches; CICICI: five string-switches. First letter indicates the string subjects started to investigate, last letter indicates the string subjects ended up with (after Schrauf & Call, 2011). White bars: jackdaws of group "intuitive", black bars: jackdaws of group "counterintuitive", grey bars: chimpanzees. (Ba) Multiple string-switches of the chimpanzees were summed up to correct string-switch (I...C) and wrong string-switch (C...I) accordingly. (Bb) Original data from Schrauf & Call (2011).

3.4 Discussion

The following discussion of the results is mainly focused on the first part (first 16 trials per task) of the experiment, because the upcoming breeding season seemed to distract the birds. In the period when the second part of the experiment was conducted several trials were interrupted by fights through the wire mesh partition of the focal subject with a group-member or the focal subject got distracted by aggressive interactions in the aviary. Furthermore Schrauf & Call (2011) used a very similar setup testing chimpanzees' ability to use weight to find hidden food providing them 16 trials only. Therefore the results of the first part of the experiment are well comparable to Schrauf & Call's (2011) findings.

Overall the jackdaws did not perform above chance-level in any of the three discrimination tasks within the first 16 trials. However, right from the beginning the individuals of both groups switched from their first investigated string to the other one, which then was pulled up entirely. This switching-behaviour is required to seek information on both possible options to then make the correct decision. The analysis of the string-switches showed that in some tasks they have appreciated the relevant discriminatory feature. Despite the small number of such string-switches, it is interesting that most of these switches occurred in the weight task of group "counterintuitive", for which the lighter canister was the baited one. Furthermore, the subjects of this group switched significantly more often to the correct canister than *vice versa*. Interestingly, it seemed that all jackdaws taken together showed a bias to the lighter canister (out of the first 16 weight-trials all subjects as one group chose the lighter canister in 10.0 ±2.87 trials, mean ±SD; Wilcoxon test: N=9, Z=1.827, p=0.068). The bias to the lighter canister and the switching behaviour of group "counterintuitive" in the weight task suggest that jackdaws seem to be able to use kinaesthetic information. The ability to asses an object's weight and to make use of this information is especially useful in foraging context. For animals feeding on wrapped food, e.g. nuts, it can be very advantageous assessing the value of the content before starting with an energetically costly opening procedure (Visalberghi & Néel 2003). No reports where found that Jackdaws would crack open nuts. However, jackdaws are known to eat oak-seeds and pray on bird eggs (Dwenger 1989; von Blotzheim & Bauer 1993). Oak-seeds as well as bird eggs do not represent the main diet (Dwenger 1989). Therefore it can be argued that there is no big advantage for jackdaws to possess the ability to discriminate an object's weight or to be sensible to auditory cues in foraging context, both of which would give information about how valuable a food item is. However, the common ancestor of all corvids is thought to be a moderate food-cacher (de Kort & Clayton 2006), for which weight discrimination abilities could have been beneficial. Therefore, even in a non-food storing corvid, like the jackdaws, rudimentary abilities of weight discrimination could be present. It would be interesting to test e.g. Eurasian jays (*Garrulus glandarius*) and Spotted Nutcrackers (*Nucifraga caryocatactes*), two species which are specialised food cachers and are also highly dependent on their caches (de Kort & Clayton 2006), or American crows (*Crovus brachyrinchos*), which are known to crack open nuts by dropping them from several meters on to a suitable surface (Cristol & Switzer 1999) on the presented setup. According to optimal foraging theory, they should assess the value of the nut (e.g. its weight) before caching or dropping it.

One aim of the study was to investigate if jackdaws recognise the causal structure of a discrimination task and therefore would be better in such a task compared to an arbitrary structured one. No evidence was found that the subjects learned the visual discrimination, in which the cue and the reward held an arbitrary relation, although all subjects as one group switched significantly more often from the wrong string to the correct one over than *vice versa* (Binomial test: 20 correct string-switches against 5 wrong string-switches, p=0.004). The same poor performance was found in the acoustic task, in which pulling at one string produced noise. In this case there was a causal structure of pulling at the string and the production of the noise. However, not the reward caused the noise production, but iron nails inside the canister. Also in the weight task, the jackdaws showed a quite poor performance. However, as already mentioned above, all individuals as one group showed a preference for the "counterintuitive" light canister. Taken together, in contrast to the chimpanzees (Schrauf & Call 2011) no evidence was found, that jackdaws established a correct stimulus-response association faster/easier in the causal structured tasks than in the arbitrary or counterintuitive tasks.

Schrauf & Call (2011) argue that the tested chimpanzees are aware of the causal relation of the cue and the reward in the weight task, because they performed above chance level within 16 trials only in the causal condition (weight task) and not in the arbitrary condition (visual task). Even if the chimpanzees showed a significant higher preference towards the heavier cup than the jackdaws (mean (±SD) number of trials subjects chose the heavier cup: chimpanzees 11.7, ± 3.57; jackdaws: 6.0, ±2,87; Mann-Whitney test: $N_1=9$, $N_2=9$, U=9.0, p=0.004), no difference was found if comparing the chimpanzees' bias to the heavier cup to the jackdaws' bias to the lighter cup (Mann-Whitney test: $N_1=9$, $N_2=9$, U=29.0, p=0.340). As already mentioned, if subjects were able to recognise the causal structure of the discrimination task, they should choose the heavier canister more often. However, if an animal is not aware of this causal structure it is thought to choose randomly until it managed to learn the discrimination by associative learning, if the individual is able to perceive the weight difference at all.

A bias to the lighter canister can be explained by the subjects avoiding the heavier canister because pulling up the heavy canister could be harder and energetically more expensive. Avoidance of the heavy canister seems not to explain the bias for the lighter canister in jackdaws because individuals pulling up the heavy canister did not need more time or more pull-step sequences until reaching the canister than the ones which pulled up the lighter canister.

Although Schrauf & Call (2011) convincingly argue by citing different studies why it seems unlikely that for the chimpanzees the weight task was simply easier to learn within this setup, their argumentation would have been much stronger, if they would have confronted the subjects with the counterintuitive condition, in which the lighter cup is the baited one.

Also in regard to the number of successful individuals the jackdaws' performance in the weight task is comparable to the chimpanzees'. In the study of Schrauf & Call (2011) five out of nine chimpanzees managed to solve the weight discrimination. The criterion used by Schrauf & Call (2011) was set at 12 correct choices out of 16 trials, which seems rather weak (two tailed Binomial test: p=0.077). If applying a stronger criterion (13 out of 16, two tailed Binomial test: p=0.021) still four chimpanzees succeeded in the weight task. However, there were not significantly more chimpanzees which reached the Schrauf & Call's (2011) criterion than jackdaws of the "counterintuitive" group (chimpanzees: 5 out of 9, jackdaws: 1 out of 4; Fisher's exact test: p=0.335).

Comparing the jackdaws with the chimpanzees in regard of their string-switching behaviour reveals a quantitative as well as a qualitative difference. The chimpanzees of Schrauf & Call (2011) showed a higher percentage of trials with string-switches than the jackdaws and especially in the weight task a considerable number of multiple switches occurred (see Figure 4). The jackdaws hardly ever switched more than once per trial. The lack of multiple switching in the jackdaws suggests that they did not directly compare the two canisters in neither of the three tasks, but that they may base their decision on the information of the first investigated string ("if correct stay, if wrong switch"). A possible explanation for the low percentage of trials with string-switches in jackdaws could be that jackdaws had difficulties in stopping the pull-step action once it was started. Jackdaws are very proficient in pulling up strings and seem to have no motoric problems once they have started the action pattern, suggesting an innate component of the string-pulling behaviour (see study 1). Furthermore, the distance between the two strings was in both studies 40cm. It is very likely that for chimpanzees switching was less costly than for jackdaws, because for the apes it might have been possible to grasp both strings from more or less the same position. The jackdaws in contrast, had to move all the 40cm from one string to the other in order to be able to pull them up. On the one hand might the costs of switching have been higher for jackdaws, one the other hand making the wrong decision resulted in no reward for the chimpanzees, but only a delayed reward for the jackdaws. As jackdaws are proficient in pulling up the canister and got the opportunity to get the reward even being wrong in their first choice, comparing the two strings might have not paid off, because being wrong was not that costly.

In order to perceive the discriminatory feature, the setup required the individuals to investigate the strings not only in the weight and acoustic task, but also in the visual task. From a theoretical point of view the subject could switch to the other string either because it recognised that the first investigated string was the wrong one or because it wants to compare both strings, before making a decision. The discrimination between the correct and wrong canister in the visual and acoustic task can be seen as absolute (the feature is present or not), whereas in the weight task the discrimination is more gradual (both canisters have a mass, but one weighs more than the other). For this reason it could be argued that it is likely that in the weight task individuals switch to compare the different outcomes, whereas in the visual and acoustic tasks they switch to avoid the wrong one. However, in all trials of the weight task the weight of the two different canisters was the same. Thus, subjects could have learned the absolute values. Because of this uncertainty it seems more appropriate to talk about changes or switches, not about comparisons.

The poor performance and negative results of the present study should not be taken as evidence that jackdaws are not able to perceive and understand causal relations between elements. Although Schrauf & Call (2011) and we developed independently from each other very similar experimental setups, the experimental procedure were quite different. The chimpanzees were either tested first on the weight task followed by the visual task or *vice versa*, to rule out any carrying over effects from one task to the other. In contrast, all jackdaws got the three different tasks intermixed within one session, which allowed to test three different tasks and divide the subjects in two groups with opposite reward contingences. The disadvantage of this procedure is that the subjects may have been confused which feature they should attend to (visual, acoustic, weight). Furthermore, the correct canisters of group "counterintuitive" held some similar features (unicoloured, silent and light) in all three tasks. In group "intuitive" the baited canisters differed between the tasks (two colours, noisy or heavy). This difference may have affected the performance of the subjects. For further studies it is advised to test one task after the other, although this requires more subjects to control for effects of testing order.

To conclude, the study showed that jackdaws are sensible to weight differences. Apart from the procedural shortcomings, the developed experimental setup seems to have the potential to study animals' understanding of causal structured discrimination problems and behaviour of information seeking. Furthermore, it has the potential of becoming a standard test for comparing discrimination abilities in different sensory modalities and for meaningful species comparisons.

4. General Discussion

The comparative string puling study showed that not all the individuals are able to solve the string pulling task without help. Interestingly the ratio of successful individuals was quite similar in the two species. Half of the Jackdaws and three out of five New Caledonian crows managed to pull up the string. In the second study the jackdaws' performance in the different discrimination tasks is comparable to that of chimpanzees especially if focusing on the string-switching behaviour. As shown above the differences seem to be more quantitative than qualitative. However, beside these species differences the individual variation was quite extensive in both of the studies.

Thus, the question emerges: Did successful jackdaws of the first study perform different than unsuccessful jackdaws in the second study? In other words, are some individuals consistently better over a series of different tasks? The performance of individuals in cognitive tasks is not only influenced by their cognitive abilities but also by non-cognitive factors like e.g. age, sex, housing-conditions; and previous experience (reviewed in Thornton & Lukas 2012). However, there might be also cognitive traits, which like behavioural syndromes would be stable over time and contexts, and on which natural selection would work. Thus, considering individual variation across different cognitive tasks "can play a crucial role in elucidating the organization, development and evolution of cognitive processes, and along the way offer answers to longstanding questions regarding the general or modular nature of intelligence"(Herrmann & Call 2012). As pointed out already success in the string pulling problem seemed to depend on chance discovery during exploration. Given the poor overall-results of the discrimination study, it seems more adequate to compare the subjects switching-behaviour, which is crucial to solve the task, as also shown by Schrauf & Call (2012), to the string-pulling performance of study one. There were no differences in the percentage of trials with string-switches in the second study between the successful and unsuccessful string-pullers of study one (% (mean ±SD) of trials with string-switches, successful string-pullers: 9.3 ±6.4; unsuccessful string-pullers: 11.6, ±5.4, Mann-Whitney test: n_1=5, n_2=3, U=6.000, p=0.786). These results should not be taken as evidence that there might not be smarter and less smart individuals in general. The two studies were not designed to test for a kind of "general intelligence" trait in jackdaws.

However, coming back to the interpretation of individual variance in cognitive datasets there is still the question: Why are some individuals of the same species better than others? So, what is causing success in problem solving? Do species or even individuals which solve a certain

physical problem show higher cognitive abilities? And can we therefore conclude that they are more intelligent? Caution and awareness of possible overinterpretation are needed when trying to answering such questions. As shown in the present study, success in pulling up the string (study 1) and thereby reaching the reward seemed to depend mainly on the discovery of stepping on the pulled up loop. There might be some cognitive mechanisms involved by which the subjects realize or appreciate the stepping action as relevant for securing the reward. However, the first pull-step action seems to occur by chance and only thereafter cognitive mechanisms might play a role how and to what extent this random discovery is exploited. Thus, in some cases different experience while exploring the problem might be a key factor explaining differences in problem solving. This argument is further supported by a study done by Benson-Amran & Holekamp (2012) on innovative problem solving in spotted hyenas. They showed that successful individuals were more persistent and also more diverse in their explorative behaviour than unsuccessful individuals. The present study showed further, that motivation is clearly influencing the subject's performance in pulling up the string. In the training phase (two choice task) of study 2 subjects clearly showed a preference to pull up the rewarded string instead of the unrewarded string. When the subjects then were confronted with a string where no reward was visible (canister handling of study 2) their performance dropped dramatically. Seven out of eleven subjects were first not interested at all in pulling a string up if no reward was visible. It is very likely that their motivation decreased because of not seeing the reward. In study one all the unsuccessful individuals started to pull up the string after being confronted with shorter strings. It can be argued that providing shorter strings, which increase the subject's motivation and interest, facilitated the solution. Persistence, diversity of explorative behaviour, motivation and neophobia (e.g. Auersberg et al. 2011) are examples of influencing non-cognitive factors of problem solving. This makes comparative cognition a complex and multidimensional issue.

Studies on problem solving usually want to test for specific cognitive abilities or mechanisms and therefore often concentrate on the question, if a species is able to solve a given problem or not. The string pulling study as well as the discrimination study showed that it can be worth looking at the results in more detail. It is not only relevant if an animal is able to master a task but especially how it approaches the problem and how it manages to solve it. As pointed out in the first study, physical problems hold two aspects: finding the correct solution and executing it. As study one showed different species might show difficulties in both or only either of the two aspects. Thus, the approach of analysing the finding and the execution of the solution separately has the potential to bring further insights. The discrimination study showed a

further aspect, namely the information seeking behaviour, which should be studied in more detail. In discrimination tasks usually all the relevant information is presented to an animal and then they are forced to make their decision. The approach in the present discrimination study allowed the subjects to base their decisions on the experiences and information they got, while investigating the setup. It would be interesting studying the influence of these two different approaches on the subjects' performance in discrimination tasks.

At the moment studies on animal physical cognition seem to be focused on species with larger relative brain sizes, like e.g. corvids, parrots and primates. As string pulling and discrimination learning are wide spread in the animal kingdom it would be very interesting testing also species with smaller relative brain sizes, like e.g. small passerines, with the same approach of analysis (string pulling) and experimental design (discrimination learning). As the two presented studies showed, testing several species on the same problem with the same study design makes it possible to figure out qualitative as well as quantitative species differences of cognitive abilities, which then can give us a better picture of the evolution of intelligence.

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7. Zusammenfassung

Die Fähigkeit eine Schnur hochzuziehen, um an ein Stück Futter, das am Ende der Schnur befestigt ist, zu gelangen (string pulling), ist ein klassisches Experiment zur Untersuchung von Problemlösung bei Vögeln. Es scheint, dass Vögel unterschiedliche kognitive Mechanismen anwenden, um dieses Problem zu lösen. Dies konnte durch verschiedene Varianten des klassischen vertikalen „sting pulling" Problems gezeigt werden. Das Ziel der ersten Studie war, die Wichtigkeit der genauen Analyse aufzuzeigen, wie die Individuen an das Problem herangehen und zu welchen Lösungsausführungen sie kommen. Desweiteren sollten beide Phasen der Problemlösung, das erstmalige Entdecken und die Konsolidierung der Problemlösung, genauer untersucht werden. Hierfür wurden Dohlen (*Corvus monedula*) und Neukaledonische Krähen (*Corvus moneduloides*) getestet. Beide Arten lösten das „string pulling" Problem mit der klassischen Abfolge folgender Handlungen: Schnur mit Schnabel hochziehen, auf den hochgezogenen Teil der Schnur mit dem Fuß zwecks Fixierung drauf steigen, mit Schnabel erneut hinunterreichen, um weiteres Stück der Schnur hochzuziehen. Die Dohlen hatten kaum Schwierigkeiten in der Lösungsausführung, sprich den erforderlichen Bewegungsablauf auszuführen, nachdem sie zum ersten Mal je Versuchsdurchgang auf das hochgezogene Stück Schnur mit einem Fuß gestiegen waren. Das Finden des richtigen Lösungsansatzes (erstes Fixieren der Schnur mit dem Fuß je Versuchsdurchgang) dauerte in den ersten Versuchsdurchgängen noch länger, verbesserte sich aber kontinuierlich. Im Gegensatz dazu, schienen die Neukaledonischen Krähen mehr Probleme zu haben, die erforderliche Bewegungskette von Hinaufziehen und Draufsteigen auszuführen. Nach 4-5 Versuchsdurchgängen aber zeigten die Krähen den korrekten Lösungsansatz sprunghaft schneller. Das könnte auf eine Art von Verständnis über die Zusammenhänge von Schnur, Belohnung und erforderlichen Bewegungsablauf (z.B. „means-end understanding") oder auf schnelles Lernen schließen lassen. Wie auch immer, 7 von 14 Dohlen und 2 von 5 Krähen waren nicht erfolgreich. Das wiederum deutet darauf hin, dass die erfolgreichen Individuen, den korrekten Lösungsansatz von Hinaufziehen und Fixieren mit dem Fuß „zufällig" entdeckt haben. Diese Entdeckung wurde dann aber sofort als die richtige Lösungsmethode erkannt und benutzt. Die Ergebnisse werden in Bezug auf den Einfluss von angeborenen Verhaltensweisen, operanter Konditionierung und Verständnis über Ziel-Mittel-Beziehungen („means-end understanding") diskutiert.

Das Ziel der zweiten Studie war es, die Diskriminationsleistung von Dohlen in einer visuellen, akustischen und gewichtsbezogenen Aufgabe zu vergleichen. Hierzu wurden zwei Döschen, eines mit und eines ohne Belohnung, mit einer Schnur an einem Ast befestigt. In allen drei Aufgaben mussten die Individuen die Döschen zuvor etwas hochziehen, um die Unterscheidungsmerkmale wahrnehmen zu können. In der visuellen Aufgabe hatten die beiden Döschen unterschiedliche Farben. Zogen die Vögel in der akustischen Aufgabe an der Schnur so war ein Geräusch wahrzunehmen oder nicht. In der Gewichts-Aufgabe unterschieden sich die Döschen in ihrer Masse. Bei der visuellen Diskriminationsaufgabe co-variierte das Diskriminationsmerkmal „Farbe" mit der Belohnung, es bestand also eine arbiträre Beziehung zwischen Merkmal und Belohnung. Im Gegensatz dazu wurde das Diskriminationsmerkmal in der akustischen und Gewichtsaufgabe vom Inhalt des Döschens verursacht (kausale Beziehung). Für die „intuitive" Gruppe war jeweils das laute bzw. das schwere Döschen mit einer Belohnung versehen. Bei der „kontraintuitiven" Gruppe war hingegen das lautlose bzw. leichte Döschen belohnt. Die Ergebnisse zeigten, dass die Dohlen spontan von Beginn an zwischen den beiden Schnüren wechselten, bevor sie sich für eine entschieden. Dieses Verhalten ist essentiell, da erst nach zumindest einmaligem Ziehen an der Schnur das Diskriminationsmerkmal, auf wessen Basis eine korrekte Entscheidung getroffen werden kann, wahrgenommen werden kann. Solche Wechsel von einer Schnur zur anderen kamen in insgesamt 10,3% ±5,4 (Mittelwert, ±Stabw.) der Testdurchgänge vor. Entgegen der Annahme, dass kausal strukturierte Diskriminationsaufgaben leichter erlernt werden sollten als jene mit arbiträrer Beziehung zwischen Merkmal und Belohnung, zeigten die Dohlen keine bessere Leistung in den kausal intuitiven Aufgaben verglichen mit den arbiträren bzw. kontraintuitiven. Vielmehr entwickelten die Individuen beispielsweise eine Präferenz für das kontraintuitive leichtere Döschen. Des Weiteren wechselten die Vögel der „kontraintuitiven" Gruppe in der gewichtsbezogenen Aufgabe häufiger von der falschen Schnur zur richtigen als umgekehrt. Dies deutet darauf hin, dass Dohlen im Stande sind, Objekte lediglich auf Grund ihres Gewichtes zu unterscheiden. Obwohl der Versuchsaufbau das Potenzial hat, eine Standardmethode in der vergleichenden Kognitionsforschung in den Bereichen Diskriminationslernen und Wahrnehmung von Kausalzusammenhängen zu werden, sind die Ergebnisse zum Teil etwas dürftig und mögliche Gründe dafür werden diskutiert.

8. *Curriculum Vitae*

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Education

since 2008	Master course of "Ethology, Neurobiology and Cognition" and Master course of "Nature Conservation and Biodiversity Management" at the University of Vienna, Austria
2005-2008	Bachelor course of Biology at the University of Innsbruck, Austria
2000-2005	High school "Realgymnasium J. Ph. Fallmerayer", Bressanone, Italy

Research Experience

2012	MSc Thesis: Investigating the decline of the Warbler finch on Santa Cruz Island, Galapagos. Supervisor: Dr. Sabine Tebbich (University of Vienna, Austria)
2010	Research practical: The attitude to nature and nature conservation at the urban fringe. Supervisor: Dr. Thomas Wrbka, Dr. Stefan Schindler (both University of Vienna, Austria)
2009-2012	MSc Thesis: String pulling and discrimination learning in jackdaws (*Corvus monedula*) and New Caledonian crows (*Corvus moneduloides*). Supervisor: Uni. Prof. Mag. Dr. Ludwig Huber, Dr. Gyula K. Gajdon (both University of Vienna, Austria), Dr. Auguste von Bayern (University of Oxford, Great Britain)
2009	Research practical: How much do keas (*Nestor notabilis*) rely on perceptual motor feedback when solving the string pulling task. Supervisor: Dr. Gyula K. Gajdon (University of Vienna, Austria)

2008	BSc Thesis: Development of a method to force the occurrence of chimerea in regeneration of *Dorvillea bermudensis* (Annelida). Supervisor: Mag. Dr. Bernhard Egger (University of Innsbruck, Austria)
2006	BSc Thesis: Differences of the activity-pattern of Northern Bald Ibises (*Geronticus eremita*) during Zugunruhe. Supervisor: Dr. Johannes Fritz (University of Vienna, Austria)

Employment History

since 2012	Coordination and textual elaboration of information boards for two nature parks and one national park of the province of Burgenland, Austria
2011-2012	Textual elaboration of the exhibition "Love in the reeds" on the reproductive strategies of reed breeding birds, Purbach am Neusiedler See, Austria
Summer 2010	Construction assistant at the new research station "Haidlhof" of the Department of Cognitive Biology, University of Vienna, Austria
2010	Certificated National Park Ranger of the "Nationalparks Austria"
since 2009	Guide at the Neusiedlersee – Seewinkel National Park, Austria
2006	Hand rearing of two Night herons (*Nicticorax nicticorax*) for the Austrian documentary "UNIVERSUM"
2006-2008	Collaborator of the research project "waldrappteam" (Dr. Johannes Fritz). Research assistant, public relations, communication with the Italian partners, assistant at two human led migrations

Scholarships

2011	Scholarship (Förderungsstipendium) of the University of Vienna, Austria, for the field trip to Galapagos
2011	Performance Scholarship for the academic year 2009/2010 of the University of Vienna, Austria
2009	Performance Scholarship for the academic year 2007/2008 of South-Tyrol, Italy

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Publications

Schindler S., Cimadom A., Wrbka T. (2011): The attitude to nature and nature conservation at the urban fringe. *Innovation – the European Journal of Social Science Research*, 24, 379-390.

Talks

Cimadom A., Tebbich S., Fessl B., Hood-Novotny R. (2012): The need of basic biological information to effectively control an invasive parasitic fly (*Philornis downsi*) on the Galapagos Islands. 6th European Conference of Behavioural Biology, Essen.

Languages

German: native language

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