DIPLOMARBEIT

Titel der Diplomarbeit

„The demonstration of reasoning by exclusion of individual common ravens (*Corvus corax*) is influenced by details of testing procedure"

verfasst von

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1. Introduction

Complex cognition has been suggested to have evolved because of problems animals had to face in their socio-ecological environment. As developing sophisticated cognitive skills should be costly such abilities would have to provide adaptive benefits. In consequence, cognitive traits should underlie the process of natural selection (Balda *et al.* 1996). A major approach to understand the evolution of cognitive abilities is the comparative approach where studying different species varying in the distance of phylogenetic relation and/or ecological pressures they encounter are compared to understand the variation of cognitive traits in terms of divergence, i.e. difference in closely related species facing different problems, and convergence, i.e. similarity in distantly related species facing similar problems (Balda *et al.* 1996). Corvids and primates face comparable ecological and social constraints which may have led to a convergent evolution of complex cognition in both taxa. Corvids and primates live in variable environments, are generalist foragers, and live in social environments of similar complexity. Thus, similar cognitive skills have been expected in corvids and apes (Emery & Clayton 2004; Emery 2006). In the last decade the ability of nonhuman animals to draw causal inferences by exclusion has gained increasing interest in the field of comparative cognition (Schloegl *et al.* 2009a; Hill *et al.* 2011; Pepperberg *et al.* 2013).

Causal reasoning is a process which enables individuals to solve problems where they have to deal with incomplete information and have to infer the missing parts of an incompletely perceived causal sequence of actions. For example, when individuals see the outcome of an action but did not perceive the action itself and thus, have to infer the missing event (Premack & Premack 1994). One type of causal reasoning is inference by exclusion, defined as selecting the correct of several options by logically excluding the alternatives (Call 2006), also referred to as "reasoning by exclusion" besides other terms within different fields of research (see Schloegl *et al.* 2009a for a review).

Three major experimental approaches have been used to study exclusion performances, namely language-based tasks, matching-to-sample-tasks and food-finding paradigms (Schloegl *et al.* 2009a). Initially linked to word-learning in humans (e.g. Huntley & Ghezzi 1993) exclusion performances were studied in language-trained animals. For example, language-trained chimpanzees (*Pan troglodytes*) (Beran & Washburn 2002) using so called lexigrams, *i.e.* geometric symbols to refer to objects, sea lions (*Zalophus californianus*) trained in a sign language (Kastak & Schusterman 2002), or a dog (*Canis familiaris*) knowing the verbal labels of toys which he was trained to fetch upon request (Kaminski *et al.* 2004) (but see Bloom 2004; and

Markman & Abelev 2004 for a critical view on the study; as well as Pilley & Reid 2011; and Griebel & Oller 2012 for follow up studies). In the approach of computer-assisted matching-to-sample paradigms subjects were trained to select pictures projected onto a touch screen and to associate two stimuli one of which was rewarded (S+) whereas the other was not (S-). Subsequently, subjects were presented with a new undefined stimulus together with an already associated stimulus (S-). Here, performing according to reasoning by exclusion subjects should choose the undefined over the defined comparison thereby possibly inferring that the new comparison might be rewarded (S+) and excluding the already as unrewarded defined alternative (e.g. Aust *et al.* 2008). As the before mentioned approaches had been criticized for their artificiality more natural food-finding paradigms were established which provided a less artificial approach without the necessity of extensive training on stimuli-relations (Call 2006; Schloegl *et al.* 2009b). In a paradigm first applied by Call (2004) with great apes, which I will refer to in the following as 'exclusion task', one piece of food was hidden in one of two opaque cups. Subjects thereupon received hints about the content of both cups (*both* condition), the baited cup only (*baited* condition), the empty cup only (*empty* condition) or none of them (*control*) in the visual (lifting the cover of cups) as well as the auditory domain (shaking the cups) (experiment 2, Call 2004). Subjects chose the baited cup significantly above chance not only when they saw or heard the food within the container (*both* and *baited*) but also when they were only shown the content of the empty cup (visual *empty*). Moreover, some of the subjects chose the baited cup significantly above chance when only the empty cup was shaken (auditory *empty*). Therefore, Call (2004) suggested that great apes are able to infer the location of hidden food in both domains.

Using inference by exclusion subjects might have logically excluded the empty cup as they have seen it empty and chose the second cup in expectation of finding a reward. Alternatively, the 'exclusion task' might have been solved by using the mechanism of avoidance, thereby rejecting the defined stimulus (the cup seen empty) without making inferences about the undefined stimulus (Aust *et al.* 2008; Schmitt & Fischer 2009).

Another food-finding paradigm commonly referred to as the 'apple-banana-task' introduced by Premack & Premack (1994) possibly provides the opportunity to disentangle the avoidance strategy from the reasoning strategy as it could only be solved via reasoning in the literal sense, *i.e.* by logically excluding potential alternatives (Call 2006), in contrast to avoiding an empty cache location (Tornick & Gibson 2013). In the original experiment chimpanzees accompanied by their trainer observed the experimenter placing an apple and a banana in two opaque

containers. The trainer blocked the subjects' view on the setup and distracted them for 2 minutes, whereupon the subjects saw the experimenter standing midway between the containers eating either an apple or a banana. Subsequently subjects were released to choose one of the containers. One of four subjects chose the container with the fruit other than the one she had seen being eaten by the experimenter in 10 out of 10 trials (Premack & Premack 1994). This performance was interpreted by Premack & Premack (1994) as indicative for the chimpanzee reasoning about the origin of the eaten fruit, thereby inferring that the fruit eaten by the experimenter (perceived outcome) might be the one initially placed inside the container (imagined event: experimenter took the fruit out of the container).

Call (2006) tested members of all great ape species, *i.e.* bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla*), and orangutans (*Pongo pygmaeus*), in a slightly modified version of the original 'apple-banana-task'. A piece of grape and banana were placed onto a sliding platform and covered with an opaque bin each. A small barrier was placed between the two bins and the experimenter retrieved one of the rewards to leave it behind the small barrier by reaching into one container, moving the hand to the barrier, showing the empty hand to the subject, and repeating this sequence with the other container. In the crucial condition the barrier was opaque and subjects saw the retrieved reward lying on the platform upon the removal of the barrier after manipulations. The experimenter then discarded the reward and subjects could choose a bin by touching it with one finger. Some subjects significantly chose the still baited over the empty bin suggesting that they drew the inference that the experimenter had removed the food from the bin (experiment 1, *inference* condition Call 2006).

Several species in addition to great apes have been tested and found to be able to solve the 'exclusion task' yielding different results regarding the tested domain (visual/auditory) (e.g. capuchin monkeys (*Sapajus libidinosus*, formerly known as *Cebus apella*) Sabbatini & Visalberghi 2008; Heimbauer *et al.* 2012; common ravens (*Corvus corax*) Schloegl *et al.* 2009b; olive baboons (*Papio hamadryas anubis*) Schmitt & Fischer 2009; lesser apes (family *Hylobatidae*) Hill *et al.* 2011; lemurs (*Eulemur macaco* and *Eulemur fulvus*) Maille & Roeder 2012; grey parrots (*Psittacus erithacus*) Pepperberg *et al.* 2013; clark's nutcrackers (*Nucifraga columbiana*) Tornick & Gibson 2013) (also see Hill *et al.* 2011 for a review on domainspecific differences)and for some species exclusion abilities were masked by local enhancement (carrion crows (*Corvus corone corone*) Mikolasch *et al.* 2011b) and social communicative cues(dogs Erdőhegyi *et al.* 2007). In contrast, solving the 'apple-banana-task' was restricted to few individual subjects (great apes

Call 2006; African grey parrots Mikolasch *et al.* 2011a; but see Pepperberg *et al.* 2013; Clark's nutcrackers Tornick & Gibson 2013). Therefore, the 'apple-banana-task' seems to be cognitively more demanding than the 'exclusion task'. For solving the 'apple-banana task' subjects would have to remember the location each food reward had been placed initially, use the shown food reward being discarded or eaten as cue to come up with the expectation that one of the two locations may be empty, and accordingly adjust their choosing behaviour.

Alternatively to the assumption that species lack the ability they were tested for, details of experimental procedure might have been not suitable for the species tested (Kamil 1987). Differences in testing procedure can yield different results. For example, in the field of perspective taking different studies yielded different results in the great apes. Hare *et al* (2000) tested chimpanzees in an experiment where two subjects, one subordinate to the other, competed over pieces of food visible to either both subjects, or to the subordinate subject only. Results suggested that subordinate individuals took into account the viewpoint of the competitor and chose the reward only they could see over the reward the competitor could see as well. Karin-D'Arcy & Povinelli (2002) failed to replicate those results with the same group of chimpanzees. Bräuer *et al* (2007) suggested that the difference in the two former studies might had been due to the differences in the spatial arrangement of the setup and conducted a study with a different group of chimpanzees. The study of Bräuer *et al* (2007) was conducted in a smaller testing compartment than used by Hare *et al* (2000) and yielded results similar to those of the latter study only after increasing the intensity of competition by putting the rewards closer to the door of the cage of the dominant competitor. Whether chimpanzees chose according to the knowledge about which of two food rewards a dominant specific could or could not see seemed to depend on the intensity of competition varied via the spatial arrangement of the setup according to the size of the testing cages (Bräuer *et al.* 2007). Recently, Pongrácz *et al* (2013) found, that different ways of pointing yielded different levels of performance of dogs in a two-way object choice task where a human pointing cue had to be used to find a food reward hidden in one of two bowls. Hereby, the compound of several features (presence of clicker sound at successful choice, food reinforcement dropped from the hand of the experimenter, duration of pointing until the released dog reached a defined distance from the bowls) but not the individual features on their own enhanced the performance of subjects to equally high levels of performance whereas with a momentary pointing cue alone (pointing expiring before the dogs were allowed to make a choice, food already placed in bowl) a "low performance" and a "high performance" group could be distinguished.

Schloegl *et al* (2009b) tested common ravens and keas (*Nestor notabilis*) on the 'exclusion task' in the visual domain following the procedure of Call (2004). They found that in the crucial condition ravens, but not keas, significantly chose the baited cup over the empty cup after they had been shown the content of the empty cup only. Ravens were subsequently also tested in a version of the 'apple-banana- paradigm' based on the method of Call (2006) which had been also applied to test African grey parrots (invisible condition, Mikolasch *et al.* 2011a). Two pieces of different food rewards were visibly put on a moveable platform and covered with opaque cups. An opaque barrier was placed in front of the cups and the experimenter retrieved one of the rewards. The experimenter showed the reward to the subject after she had removed the barrier and subjects were allowed to choose a cup. As subjects did mainly perform at chance level (Schloegl *et al*, unpublished) a preliminary study conducted by myself aimed to reveal whether a change of choosing modality would have an influence on the choosing behaviour of ravens. I introduced two different modalities of cup choosing (conditions). In the first condition (*point*) subjects had to choose by pointing at the chosen cup with the beak through wire mesh. In case of a correct first choice the experimenter handed over the reward to the subjects. In the second condition (*pilfer*) a wire mesh door was opened after the baiting procedure and subjects could retrieve the reward themselves. Choosing modality seemed to affect the behaviour of subjects, as they showed individual preferences for a side (right/left cup) in the *point* condition only. One of three subjects (Columbo) performed significantly above chance in the *pilfer* condition (binomial test, p=0.029) but the difference between the two modalities was not statistically significant (χ^2 = 0.812, df =1, p = 0.367). I observed following drawbacks during this preliminary study:

 i) In order to solve the 'apple-banana-task' subjects have to pay strong attention to the experimenter and the given hints throughout the procedure, but subjects frequently seemed not attentive to the experimenter during the procedure of my preliminary study. This observation raised the question whether there was a motivational problem involved.

ii) The way of manipulation in my preliminary study might have been confusing for the subjects because I used a small blind which only obstructed the cups and my forearms. Therefore, movements of my arms were observable and could also have indicated the exchange of the cups. In contrast, subjects in the study of Premack & Premack (1994) could not see the entire setup during the manipulations and in the study by Call (2006) the manipulations of the two containers were more obvious to the subjects. Though subjects could not exactly see which reward was removed, they observed the experimenter reaching in the containers, moving his hand between the containers and the blind, and showing the empty hand to the subjects after

each alternation (Call 2006).

iii) The consequence of choosing the empty cup first might have been not strong enough to evoke the use of more sophisticated strategies on side of the subjects.

Taking into account the ecology of species tested within a given paradigm might be crucial to provide results more representatives of the true abilities of subjects (e.g. Balda *et al.* 1996; Boesch 2008). Recently, grey parrots performed better with all 4 tested subjects choosing the still baited cup significantly above chance in a version of the 'apple-banana-task' that did not require them to remember the initial location of the different food rewards (Pepperberg *et al.* 2013). In contrast to an earlier study by Mikolasch et al (2011a) two differently coloured cups were used and subjects had initially learned to associate the colour of the cup with one particular type of food (Pepperberg *et al.* 2013). Pepperberg *et al* (2013) argued that parrots do not cache but eat fruits in the wild whereby the colour of the fruit might indicate degrees of ripeness and thus parrots might be able to be better in using colour-based than spatial hints. The ecology of ravens provides the possibility to test for the possible effect of the above mentioned drawbacks of my preliminary study. Food caching behaviour provides an ecologically highly relevant context for cognitive research as it is a natural behaviour also demonstrated in captivity with the benefit of possible experimental control (de Kort & Clayton 2006). Caching and sociality have been suggested to be important evolutionary driving forces for sophisticated cognitive abilities in Corvids (e.g. Balda *et al.* 1996; Emery & Clayton 2004; Emery 2006). Ravens can remember the exact locations of their own caches up to 2 weeks after caching (Heinrich & Pepper 1998) and also remember and raid caches they have seen others make (Bugnyar & Kotrschal 2002). During their first years after leaving their parents' care ravens come together in groups and share communal night roosts (Heinrich 2006). It has been suggested that coming together in a group is advantageous during the time before ravens found a pair-partner and establish a territory as they might have a bigger chance to get hold of food supplies within defended territories of established pairs (Heinrich 2006).Therefore, competition is a major factor in ravens' daily foraging situations where they have to compete with conspecifics as well as predators of different species such as wolves or eagles (Heinrich 2006). Ravens distinguish between possible competitors and individuals who did not gain knowledge about the exact location of caches and adjust their behaviour accordingly (Bugnyar & Heinrich 2005; Bugnyar & Heinrich 2006; Bugnyar 2010). The competition for food has been suggested to result in an "arms race for cognitive and deceptive abilities" (Bugnyar & Kotrschal 2002). Ravens developed counter strategies against caches being pilfered by conspecifics as well as against being caught in the act of pilfering caches of others (Bugnyar & Kotrschal 2002; Bugnyar & Heinrich 2005;

Bugnyar & Heinrich 2006; Heinrich 2006) and strategies for misleading competitors (Bugnyar & Kotrschal 2004).

Based on this background I aimed to clarify whether previous results were influenced by the experimental design used I modified the 'apple-banana-task' whereby I stepwise introduced factors of ecological relevance hypothesized of enhancing the motivation of subjects to apply possible skills to reason by exclusion. Moreover, I altered the clarity of given hints.

i) To enhance the ecological validity of the task as well as the attention of subjects during the experimental procedure I cached the food reward within small cavities I dug into the substrate of the experimental room and covered them with pieces of tree bark. Ravens reliably cache food in the wild as well as in captivity (Bugnyar & Kotrschal 2002; Heinrich 2006) whereby they put food into small gaps of surrounding structures or into the substrate and cover it with various materials ((Bugnyar & Kotrschal 2002). Ravens do also reliably pilfer caches they have seen being made by a human (Bugnyar 2010). Subjects were always highly attentive whenever a non-edible item or a piece of food was cached within the aviary, which was a commonly played game with subjects outside of experimental context.

ii) In the current study I used opaque curtains with closable peepholes and varied the visual access of subjects during manipulations on the caches to reveal whether the difference between the two approaches of not seeing the whole setup and seeing the movements without perceiving the exact action would have an impact on the performance of subjects.

iii) I introduced factors of competition to find out whether different levels of competition would have an effect on the performance of subjects. The subjects who participated in the present study were already territorial and living in pairs. It was not possible to provide a conspecific as competitor, which would have been the most natural approach, because subjects reacted aggressively against conspecifics other than the pair partner. Moreover, once a subject was used as competitor could subsequently not act as focal subject due to the fact that the competitor was observing the whole sequence of actions. Bugnyar *et* al (2007a) showed that ravens judge the competitive role of humans in a food caching context after experience with the respective human during play-caching with non-edible items. Hence, in the current study the experimenter or another human played the role of the competitor in case the subject chose the empty cache first. As the consequences of a wrong first choice with the experimenter putting the food reward into her pocket, the experimenter eating the food reward, and a second human competitor visibly present to the subject throughout the procedure taking out the food reward and eating it

might differ in intensity I applied different factors of competition stepwise in order of hypothesized degree of intensity.

iv) I varied the clarity of the presentation of the removed food reward. Ravens have been observed to show items to conspecifics in the wild and it has been suggested that this is used to draw the attention of others to external objects (Pika & Bugnyar 2011). I wanted to find out whether the change between an inadvertent and deliberate presentation of the removed food reward might change the performance of subjects.

My predictions were that ravens should similarly to great apes possess the capability for inferential reasoning, subjects should show their abilities more clearly in an ecologically more relevant caching context, making cues more clear should improve the possibility to use them, and that increasing levels of competition would enhance the subject's motivation and therefore also their performance.

2. Material and methods

2.1. Subjects

Three common ravens (*Corvus corax*) living in an outdoor aviary in the Cumberland Game Park, approximately 2 km south of the Konrad Lorenz Research Station in Grünau im Almtal in Upper Austria, participated in this study. Two subjects were females (Columbo: age 7 years, Gerti: age: 2 years) and one subject was a male (Rumo: age 3 years). Columbo and Rumo were handraised at the Konrad Lorenz Research Station, but Gerti was parent-raised by a pair of handraised ravens at the zoo in Wels and came to Grünau in May 2008.

A second male (Ilias: age 7 years) died during the course of the study and his data was omitted from the analysis. An additional pair of handraised ravens was available during the time of data taking in an outdoor aviary adjacent to the Konrad Lorenz Research Station, but they showed very strong neophobic reactions towards the setup. When the male finally started to approach the setup, the couple started breeding successfully and subsequently could not be tested.

Columbo and Rumo had already participated in a variety of cognitive studies, whereas Gerti was much less experienced with the interactive work with humans. For example, Columbo participated in studies on gaze following (Schloegl *et al.* 2007), social learning (Schwab *et al.* 2008), and perspective taking (Bugnyar 2010). All three subjects had been previously tested in the standard procedure of the 'apple-banana-task' as it was used in a study on African grey parrots (Mikolasch *et al.* 2011a). Moreover, Columbo and Rumo had participated in a preliminary study in July/August 2010 following the procedure of the *invisible* condition of Mikolasch *et al* (2011a), where I put two different but equally preferred food rewards on a wooden platform and covered them with opaque cups. Then, I put an opaque barrier between the birds and the cups and lifted both cups, whereby one of the rewards was removed. After removing the barrier I showed the removed reward to the bird and put the shown reward into my pocket.

2.2. Housing

The subjects were housed as couples within outdoor compartments of an aviary complex. Each pair of ravens (Gerti/Rumo, Columbo/Ilias) lived in an outdoor compartment established as their territory (TC in Figure 1) of 7 m height in the center of the compartments. This territorial compartments contained natural vegetation, a platform under roof cover for nesting, conifer trees, natural structures such as rocks and logs, and several perches. Two additional outdoor compartments were available for the separation of subjects: one middle outdoor compartment

(MOC in Figure 1) of similar design as the territorial compartments and accessible from both territorial compartments through wire-mesh doors, as well as an outdoor extension of the aviary (OE in Figure 1) accessible from the territorial compartment of Rumo and Gerti. A bigger, central testing compartment of rectangular shape (CTC in Figure 1) where subjects were tested individually was accessible through a gangway (G in Figure 1) from each territorial compartment. Two wire-mesh doors, one in the middle of each gangway, each leading to one smaller testing compartment (STC in Figure 1) were kept closed throughout this study. In the center of the aviary complex was an indoor room not accessible for the birds with two big plastic windows towards the central testing compartment and two small ones towards each territorial compartment (Figure 1).
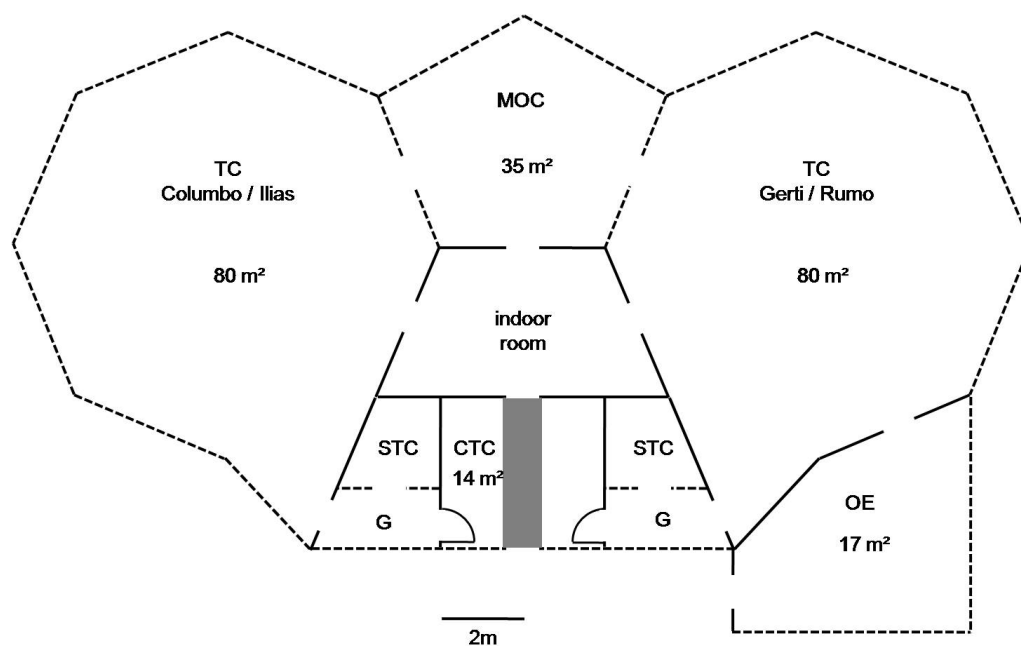
Figure 1: Sketch of the aviary complex in the Cumberland Game Park where subjects were housed. Broken lines indicate a structure built of wire-mesh. Solid lines indicate wooden structures. Bigger breaks in lines indicate doors. The two wire-mesh doorways where curtains had been put up to control for the subjects views are indicated with segments of a circle showing the opening direction. The grey rectangle represents a pathway of concrete leading through the central testing compartment, where the birds were tested individually. Testing compartments, gangways, and indoor room were roofed, outdoor compartments covered with nets. TC = territorial compartment (+ name of female/male of resident raven pair), MOC = middle outdoor compartment, OE = outdoor extension, CTC = central testing compartment, STC = small testing compartment, G = gangway.

Animals were fed a mixed diet of meat, fruits, dairy products, and bread twice per day after experiments. In each territorial compartment a big plastic bowl with daily changed fresh water for drinking and bathing was provided.

2.3.   Procedure

2.3.1. Food rewards

As food rewards I used pieces of self-made cake (1 cup oil, 2 cups sugar, 3 cups flower, 16g baking soda) colored in blue or yellow with flavourless food colouring (10 drops each) cut in small pieces, to assure they were clearly distinguishable and to avoid food preferences based on taste. Small pieces of dry cat food were used as small rewards in between, e.g. when subjects had to move to another compartment of the aviary complex.

2.3.2. Setup & general procedure

I tested the subjects individually in the central testing compartment of the aviary complex, which the subjects could enter from their territorial compartment via the gangway. A white canvas curtain was affixed to each gangway-door with a cut out peephole of 12cm in diameter 25cm above ground in the middle of the curtain. To manipulate the view of the subjects, these peepholes could be closed from the central testing compartment with a cover of canvas affixed to the curtain. Additionally, the curtains had a closeable rectangular window at human face-level.

In every trial I called the focal subject until it was visible to me in the gangway behind the peephole. I then cached food rewards in one or both of two caches (see below) and manipulated the caches as well as the peephole-covers depending on the given condition, with the subject staying in the gangway. Before opening the door for the subject to enter the experimental room and pilfer the caches I assured that the subject had a good view on the setup for approximately 5 seconds. If the peephole had been closed during the baiting or manipulations I opened the peephole, called the subject, and opened the door after the subject had been visible to me through the peephole. In order to avoid biasing the behavior of subjects by experimenter cues, I as soon as the subject entered the room moved to a position with my back to the main entrance looking straight ahead towards the indoor room where the camera had been put up.

The caches for the food rewards were two small cavities I dug in the ground cover of wood-chips on top of gravel with a distance of approximately 60 cm from each other and approximately 130 cm from the gangway-door for each pair of ravens. After caching the food rewards I covered each cache with a piece of tree bark measuring approximately 10 x 20 cm. Before each session, a camera was installed on a tripod in the indoor compartment behind a transparent plastic window. The view of the camera was adjusted in such a way, that the camera could record the experimental setup as well as the experimenter and the peephole (Figure 2).
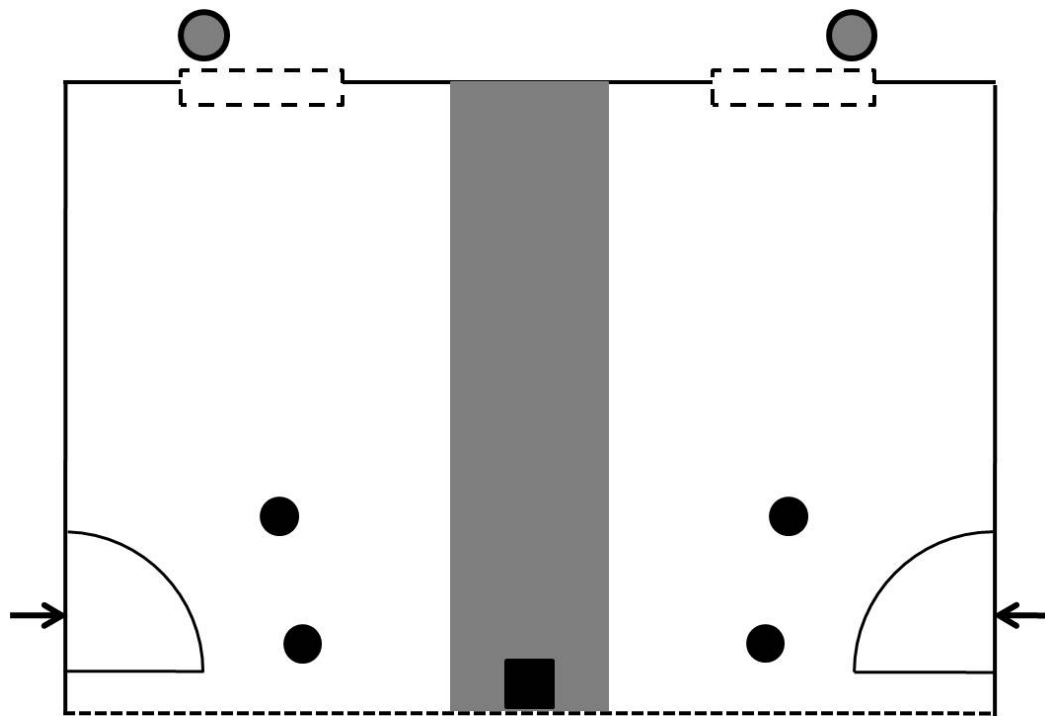
Figure 2: Sketch of the central testing compartment during testing.
Full black circles indicate the position of the caches, circles with grey center indicate the positions of the camera, and the full black square indicates the position of the experimenter when the subjects chose a cache. The direction of looking and entering the testing compartment of subjects is represented by black arrows. Segments of a circle indicate doors to the gangways including opening direction. The grey rectangle represents a pathway of concrete.

Side of the baited cache (left/right) and colour of the food reward (blue/yellow) were counterbalanced semi randomly within conditions with the constraints that the same side was not baited in more than 3 consecutive trials and the colour of the food reward which stayed within a cache as bait was not the same in more than 3 consecutive trials. Moreover, during initial baiting the yellow and blue reward were put into the left or right cache in 50% of trials, respectively.

A few exceptions to the rules of counterbalancing occurred due to experimenter error. In condition 1 'Baseline 1 – cue control' for Gerti the blue reward was used as bait in 3 more trials than the yellow and in this 3 trials it was put into the right cache. For Rumo in 'Baseline 1 – cue control' the left cache was baited in 3 more trials than the right cache and the yellow reward was used as bait in 3 more trials than the blue reward. Moreover, in condition 4 'Reasoning' for Rumo the left cache stayed baited after manipulation in 3 more trials than the right cache. For Columbo in condition 12 'Reasoning - all manipulations clear' the blue reward stayed in a cache as bait in 5 more trials than the yellow reward (Table 1). The conditions will be described in detail below.

Table 1: Exceptions to the rules of counterbalancing.
Number of trials in which the left/right cache was baited and the yellow/blue coloured cake were used as food rewards within the baited cache.

subject	condition	side of cache staying baited		colour of food reward in baited cache		total number of trials
		left	right	yellow	blue	
Gerti	Baseline I	10	11	9	12	21
Rumo	Baseline I	12	9	12	9	21
Rumo	Reasoning	19	16	18	17	35
Columbo	Reasoning all manipulations clear	18	17	15	20	35

2.3.4. Overview and sequence of conditions

The first two conditions were control conditions and subjects proceeded to testing if they i) did not use subtle cues to find hidden food ('Baseline 1 – cue control') and ii) did not prefer one over the other coloured food reward ('Baseline 2 – colour control'). The condition 'Exclusion' should reconfirm that ravens would reliably choose the baited cache if they see one of two caches empty. Subsequently, I presented the different reasoning-conditions in a sequence depending on the success of the birds in the previous condition. If the subject did neither choose the baited nor the empty cache first above chance, *i.e.* 50% of the cases, based on binomial testing I introduced a new factor hypothesized of altering the motivation of subjects. As the conditions differed gradually in the information available to the subject during manipulations I presented the conditions one after another (for details of conditions see below). When a subject chose one cache over the other (baited/empty) first significantly above chance in a reasoning-condition a condition of non-matching-control was presented. Prior to competition training, where subjects learned to be allowed to choose one cache only, subjects were allowed to approach and manipulate both caches. When the subject manipulated the cover of a cache with its beak after entering the testing compartment I considered the respective cache as the subject's first choice (Figure 3).
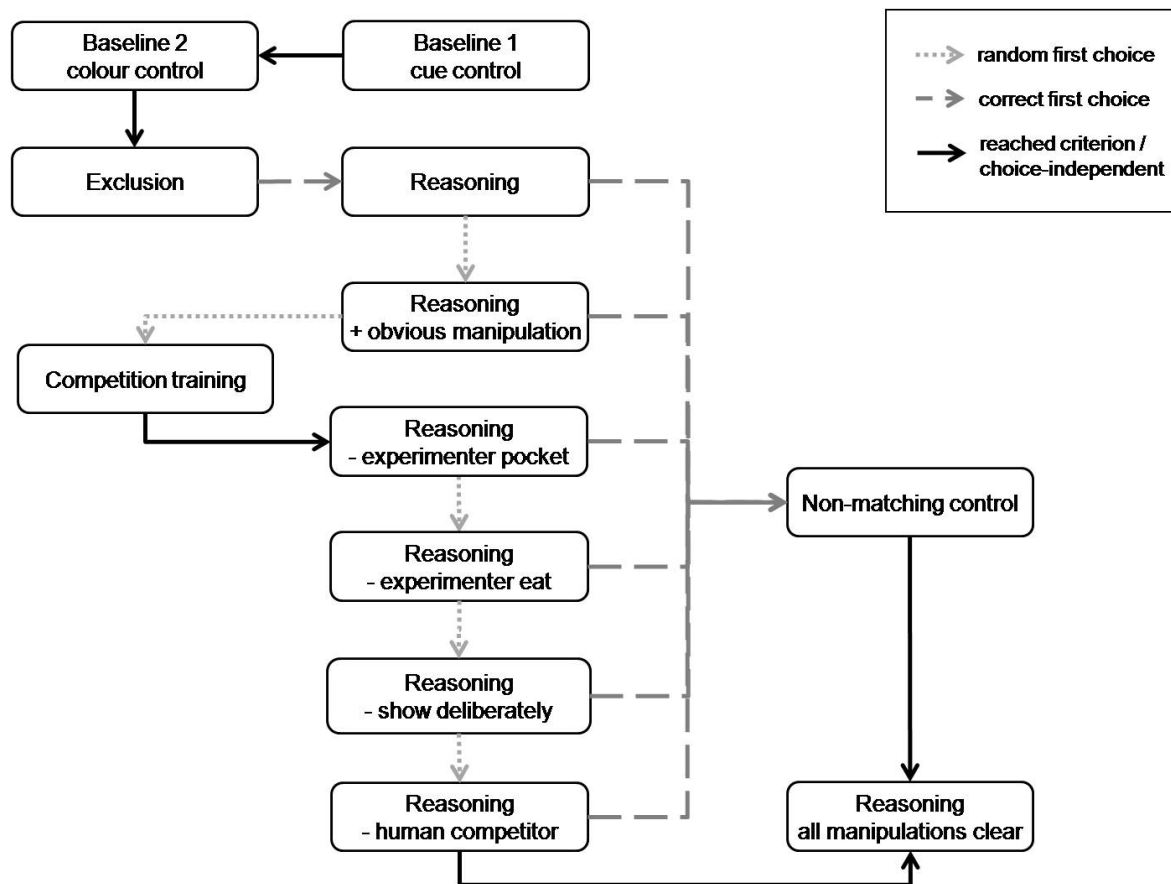
Figure 3: Possible sequences of conditions.
Dotted light grey arrows are pointing towards the subsequent condition if the subject chose randomly, *i.e.*
not significantly different from chance level (50%) using binomial test. The broken-lined dark grey arrows
indicate the subsequent condition if the subject chose the still baited cache first significantly above
chance. Black arrows indicate the following condition if a defined criterion was reached or the condition
was presented independent of success in the previous condition.

2.3.5 Amount of Sessions and trials

The period of data-taking was from 24th November 2010 to 8th May 2011, with a maximum of two sessions per day (morning/afternoon).

I considered a session every time a subject was available individually for testing or participated. Sometimes a subject could not be tested though appearing to be motivated to participate because the respective pair-partner had not cooperated in being separated to a different compartment of the aviary complex. Within one session I immediately set up a new trial after the subject had moved back into the gangway. In case the subject left to its territorial compartment I started the next trial as soon as the subject was back in the gangway and visible to me through the peephole. The subjects could quit working any given time by leaving into their territorial compartment as the door between the territorial compartments and the gangway was open during testing. If a bird had left I tried to attract the focal individual back by calling it or going to the territorial compartment and calling the subject. The session was terminated if it could not be continued after a maximum of 5 minutes. When the subject left and there was an obvious disturbance, like for example visitors of the game park in front of the aviary, I waited until the disturbance was over and then tried to call the subject to continue the session.

Each session consisted of a maximum of 7 trials. In the first two control conditions ('Baseline 1 - cue control', 'Baseline 2 - colour control') where a defined criterion, which will be specified in the detailed descriptions of conditions below, had to be reached for further testing I conducted a total of 21 trials resulting in a minimum of 3 sessions per condition. In condition 3 'Exclusion' as well as all reasoning-conditions, for which I used binomial tests to compare the subject's performance to chance-level (*i.e.* 50%), I conducted a total of 28 trials resulting in a minimum of 4 sessions per condition. When a subject chose the baited cache in 6 of 7 trials during the last session within a reasoning-condition an additional session was conducted to verify whether this performance was due to chance. Subjects received more than 7 trials within one session in 5 cases, all due to experimenter error. Moreover, subjects received different amounts of sessions within conditions as well as different amounts of trials per session as they could terminate participating any given time. The number of sessions within one condition ranged from 3-10 and the number of trials within one session ranged from 1-10 (for details see Table 2).

Table 2: Number of sessions and trials each subject received within each of the conducted conditions.
Given are range and median of the absolute frequencies of trials per condition. R. = Reasoning.

subject	condition	total amount of sessions	range trials/session	median trials/session	total amount of trials
Columbo	1 - cue control	9	1-4	2	22
Gerti	1 - cue control	5	1-6	5	21
Rumo	1 - cue control	5	2-7	3	21
Columbo	2 - colour control	8	1-5	2	21
Gerti	2 - colour control	3	7	7	21
Rumo	2 - colour control	4	3-7	5.5	21
Columbo	3 - Exclusion	10	1-7	2	28
Gerti	3 - Exclusion	4	7	7	28
Rumo	3 - Exclusion	4	5-9	7	28
Columbo	4 - Reasoning	9	1-5	4	28
Gerti	4 - Reasoning	4	7	7	28
Rumo	4 - Reasoning	6	1-7	7	35
Columbo	5 - R. obvious manipulation	5	2-7	7	28
Gerti	5 - R. obvious manipulation	4	7	7	28
Rumo	5 - R. obvious manipulation	5	2-7	7	28
Columbo	6 - Competition-training	28	2-7	7	175
Gerti	6 - Competition-training	22	3-7	7	147
Rumo	6 - Competition-training	12	3-7	7	77
Gerti	6a -Countertraining side-bias	4	7-8	7	29
Columbo	7 - R. experimenter pocket	4	7	7	28
Gerti	7 - R. experimenter pocket	4	7	7	28
Rumo	7 - R. experimenter pocket	5	7	7	35
Columbo	8 - R. experimenter eat	6	7	7	42
Gerti	8 - R. experimenter eat	5	7	7	35
Rumo	8 - R. experimenter eat	4	7	7	28
Rumo	8a - changed experimenter position	5	2-9	5	28
Columbo	9 - R. show deliberately	6	1-7	5.5	28
Gerti	9 - R. show deliberately	5	1-7	7	28
Rumo	9 - R. show deliberately	7	2-7	7	35
Columbo	10 - Nonmatching control show deliberately	4	7	7	28
Gerti	11 - R. human competitor	6	1-7	5	28
Rumo	11 - R. human competitor	7	1-9	3	28
Columbo	12 - R. all manipulations clear	6	2-7	7	35
Gerti	12 - R. all manipulations clear	4	7	7	28
Rumo	12 - R. all manipulations clear	7	2-7	5	35
Gerti	13 - Nonmatching control human competitor	4	4-10	7	28

2.3.6 Detailed description of conditions

The sequence of descriptions of the different conditions represents the sequence of presentation to subjects over the course of the study with the exception of the association-control. All descriptions referring to a side (left/right) apply to the side from the subjects' respective point of view.

2.3.6.1.   Preceding control conditions

1) Baseline 1 – cue control

This condition should assure that the subjects would not use possible undetected cues, like for example smell, to find out which one of two caches was baited.

I baited one cache out of sight of the subject, *i.e.* with the peephole closed. The subject was allowed to approach and manipulate both caches.

The criterion for further testing was reached when the subject chose the baited cache first in a maximum of 14 out of 21 trials.

Due to experimenter error Columbo received an additional 22nd trial in this condition. As the results of binomial testing including and excluding the additional trial were qualitatively the same I subsequently only present the results of the complete data. Gerti received the last trial of 'Baseline 1 – cue control' within the same session she received the first 7 trials of 'Baseline 2 – color control'.

2) Baseline 2 – colour control

This condition should control for food-preferences or color-preferences for one of the two food rewards.

In contrast to the first control condition for this condition I baited both caches with two differently colored rewards in full view of the subject, *i.e.* with the peephole open. I closed the peephole and opened it again after 10 seconds, as this was the time I approximately needed for manipulations in subsequent conditions. As soon as the subject was visible to me behind the peephole, I opened the door for the bird to pilfer the caches. The subjects were allowed to pilfer both caches.

The criterion for further testing was reached when the subject did not choose the reward of one colour first in more than 14 out of 21 trials.

3) Exclusion

This condition should reconfirm that ravens would reliably choose the baited cache if they see one of two caches empty.

I baited both caches with different food rewards and covered the caches in full view of the subjects. I closed the peephole, manipulated both caches, whereby I took out one of the rewards, and left the pilfered cache open with the piece of bark put clearly misplaced (approximately 30 cm from the cache) on the ground. I opened the peephole, called the subject until it was visible to me behind the peephole, and opened the door. Subjects were allowed to pilfer both caches.

Subjects met criterion for further testing if they chose the still baited cache first significantly above chance, *i.e.* a minimum of 20 out of 28 trials.

2.3.6.2.   Reasoning by exclusion, competition training, and non-matching control

The basic procedure in reasoning-conditions consisted of four sequences: baiting, manipulation, show and choice.

Baiting: In full view of the subjects (peephole open) I baited both caches and covered them simultaneously with the pieces of tree bark.

Manipulation: I lifted the bark of both caches in succession beginning with the left cache, thereby taking out one of the food rewards.

Showing: I showed the removed reward to the subject.

Choosing: I opened the door for the subject to enter the experimental room and pilfer the caches. Subjects were allowed to manipulate the cover of both caches in conditions prior to the competition training.

I conducted a series of conditions changing the way one of those four sequences was conducted for each condition by introducing factors expected to enhance the motivation of subjects to use their ability to reason by exclusion. Every time a change in the procedure had been introduced it stayed within subsequent conditions. In the following I will concentrate on describing the changes characteristic for each condition.

During reasoning-conditions I conducted a total of 28 trials within a minimum of 4 sessions with 7 trials each. If subjects did not choose the still baited cache first significantly above chance according to a binomial test the subsequent condition followed introducing a new change in one of the four sequences described above.

4) Reasoning

This condition aimed to reveal whether subjects would perform better when the experiment was embedded in a more naturalistic setup. Moreover, the subjects did not see the whole setup during manipulation, which was more similar to the original study of Premack & Premack (1994) opposed to using a small visual barrier as in my preliminary study following the procedure of Mikolasch et al (2011a).

During manipulation the peephole was closed obstructing the view of the subjects on the entire setup. During the sequence of showing I held the removed reward between thumb and forefinger of my right hand with my arm loosely hanging at the side of my body and my right body-side turned towards the peephole whereupon I put the reward into my pocket (inadvertently).

In the study of Call (2006) the used blind was a small barrier in between the two containers he used to hide the food rewards and subjects could see the experimenter moving his hand from the containers to the barrier. Comparably, for the next condition subjects could see that I approached the caches during manipulation but not what exactly I did there.

5) Reasoning - obvious manipulation

The procedure was the same as in the condition before with the difference that the peephole stayed open during manipulations and I manipulated both caches crouching down at the cache with the back towards the peephole using my body as a blind.

Up to this point subjects were allowed to pilfer both caches, which meant that the only consequence of choosing the empty cache first was that subjects had to approach the second cache afterwards to get a food reward. For the next condition I introduced the first factor of competition and trained the subjects that they were allowed to pilfer one cache only.

6) Competition Training – pilfer one cache only

During this training-condition the subjects learned that they were allowed to pilfer one cache only. If they chose the empty cache first, subjects would not receive a reward in the respective trial.

I baited one cache in full view of the subject. After 5 seconds I opened the door and the subject was allowed to pilfer one cache. If the subject chose the empty cache first I went to the baited cache, took out the food reward and put it into my pocket.

The subjects reached criterion for further testing when they chose the baited cache first significantly above chance within two consecutive sessions, *i.e.* 12 out of 14 trials.

As Gerti showed a consistent side bias to the right it was necessary to intersperse a sequence of counter-training against her side bias between sessions 16 and 17 of competition-training. During the counter-training I only baited the left cache. Criterion was reached as soon as Gerti chose the baited cache first within 3 consecutive trials within one session. After the counter-training sessions Gerti continued with 'Competition-training' until criterion was reached.

7) Reasoning - experimenter pocket

The basic procedure in this condition was the same as in condition 5 with the difference that subjects were now only allowed to pilfer one cache. When subjects chose the empty cache first I stepped forward, took out the food reward of the still baited cache and put the reward into my pocket.

Rumo received an additional session of 7 trials to check for possible within-condition learning because he chose the baited cache in 6 out of 7 trials during his last regular session.

As the ravens were familiar with me having food in my pockets the consequence of putting the reward into my pocket perhaps was not clear enough. Therefore, in the next condition I intended to enhance the level of competition by pretending to eat the reward.

8) Reasoning - experimenter eat

This condition was presented in the same way as the condition before with the difference, that when the subject chose the empty cache first I went to the still baited cache, took out the food reward, showed it to the subject, and pretended to eat it.

Due to experimenter error in 4 trials of session 3 for Gerti, I conducted an additional session of 7 trials with Gerti. As the results of binomial testing including and excluding the session with

experimenter error did not differ from each other I subsequently only present the results of the complete data. Due to experimenter error in one trial of session 1 and 3 trials of session 2 with Columbo she received 2 additional sessions within this condition because in all cases of experimenter error I did not pretend to eat the reward after the subject chose the empty cache first, but just put it into my pocket as in the last condition. As this was the crucial factor introduced in this condition I added 2 sessions to replace those without experimenter error. I subsequently only present the results of the complete data, because the results of binomial testing including and excluding the sessions with experimenter error did not differ from each other.

Rumo seemed to apply the strategy to always choose the cache closer to where I stood first and then quickly move to the other cache to get the reward even if his first choice was the empty cache. He chose the right cache from his view first in 26 out of 28 trials. Rumo reached the second cache faster and ate the food reward in 9 out of 14 trials where he chose the empty cache first. Therefore, Rumo received an additional version of this condition where I changed my position during choice to standing facing Rumo on the opposite side of the caches in equal distance from both caches and looking straight ahead. I maintained this position during choice for all subsequent conditions with Rumo.

Up to this point I showed the reward after manipulations to the subjects inadvertently. As subjects in the study of Premack & Premack (1994) actually saw the experimenter eating one of the possible food rewards I changed the presentation of the removed reward to make it more clear.

9) Reasoning - show deliberately

The main procedure was the same as in the previous condition with the difference that after manipulation I walked to a position between the two caches facing the subject, showed the removed reward by stretching my hand holding the reward between thumb and forefinger towards the subject, and pretended to eat the reward.

Rumo received an additional session with 7 trials to check for within-condition learning because he chose the baited cache in 6 out of 7 trials during the last regular session.

10) Reasoning - human competitor

In order to increase the factor of competition in this condition a real competitor was introduced. It was not possible to use another raven as competitor, because subjects acted aggressively against each other when another raven than the pair-partner was in a directly adjacent part of the aviary and I could not use the pair-partner as competitor due to the low number of subjects. As ravens have been shown to assess a human as competitor (Bugnyar *et al.* 2007a), for this condition another human served as a competitor.

The human stood in the gangway opposed to the gangway of the focal subject and was visible to the subject through a peephole at human face-level during the whole procedure of baiting, manipulation, and show. The procedure was the same as in condition 9. After the showing I first opened the door for the human competitor who slowly started moving towards the caches, and subsequently the door for the subject. If the subject chose the empty cache first, the competitor went to the still baited cache, took out the food reward, showed it to the subject and pretended to eat it.

As the space turned out to be too narrow to maintain my position next to the main entrance during choice, I moved further back in direction of the gangway the human had been in and stood behind the competitor.

11) Reasoning - all manipulations clear

After the whole sequence of conditions for each subject I added a condition where all manipulations were visible to the subject.

I baited both caches with different food rewards in full view of the subject. I approached the caches again, removing the food reward of one cache and lifting the cover of the other cache, facing the subject. After manipulations I walked to a position between the two caches facing the subject, showed the removed reward to the subject, and pretended to eat it. I opened the door for the subject to come in and pilfer the caches. If the subject chose the empty cache first I went to the still baited cache, took out the food reward, showed it to the subject, and pretended to eat it.

Due to experimenter error in 4 trials of session 3 and 3 trials of session 4, where I used the wrong list of counterbalancing which cache should be baited with which colour of food reward, Columbo received one additional session with 7 trials in this condition. As the results of binomial testing including and excluding the sessions with experimenter error did not differ from each other I subsequently only present the results of the complete data.

Due to experimenter error in 4 trials of session one Rumo received an additional session of 7 trials within this condition. In the respective trials I did not manipulate both caches before showing the food reward I had taken out to the subject. Instead, I took out the reward, showed it to the subject, and afterwards manipulated the second cache.

12)Non-matching control

When a subject chose the still baited cache first significantly above chance according to binomial test this condition was conducted to control for the possibility of subjects avoiding the cache including a food reward matching the one they had seen in my hand. Thus, the subjects might have used the seen food reward as a discriminative cue without drawing any inferences about its origin.

The procedure was the same as in the condition in which the subject reached significance with the difference that both caches stayed baited, *i.e.* when manipulating the caches I did not remove any of the two food rewards. During showing I stood midways between the caches facing the subject, took a food reward out of my pocket, showed it to the subject, and put the reward back into my pocket.

2.3.7. Analysis

I videotaped all trials and subsequently coded the performance of subjects from the videos, whereby first choice of the baited cache was a success. I considered a cache being chosen as soon as the subject touched the cover of the cache with its beak. As this was clear without ambiguity in every case I did not test for inter-observer reliability.

For statistical analysis I used SPSS 11.5 for Windows, with the level of significance set to $p=0.05$. All tests were non-parametric and two-tailed. For testing whether the baited cache, one of the food rewards, or any side of caches was chosen above chance I used binomial tests with a chance level of 50%. For testing whether there was a learning effect within conditions I compared the first and second half of trials or the first and last 14 trials (in case of uneven numbers of trials) using McNemar test. To assess whether subjects increased their performance over the course of the whole study for each subject individually I correlated the success rate, *i.e.* the relative frequency of choosing the baited cache first, with the number of conditions using Spearman Correlation. I excluded 'Baseline 2 – colour control' from the correlation as I did not register performance, because both caches were baited when the subjects were allowed to enter the experimental room and pilfer the caches. Moreover, I excluded condition 6 'Competition training' because it was a training condition where subjects had to reach a defined learning criterion and received as many trials as necessary to do so.

3.   Results

3.1.   Success

In condition 1 'Baseline 1-cue control' no subject chose the baited cache more often than expected by chance (binomial tests: each subject p>0.999; Table 3).

In condition 2 'Baseline 2-colour control' all subjects equally preferred both types of the coloured food reward (yellow/blue: Columbo 10/11, Gerti 10/11, Rumo 11/10; binomial tests: each subject p>0.999; n=21 trials for all subjects).

When seeing one cache empty (condition 3 'Exclusion') all subjects reached criterion and chose the baited cache significantly above chance (binomial tests: each subject p<0.001; Table 3).

All of the subjects did neither choose the still baited nor the empty caches first in more trials than expected by chance when they could not see the setup during manipulation (condition 4 'Reasoning'), and when they could see that the experimenter approached the caches again but without seeing the exact manipulations (condition 5 'Reasoning + obvious manipulation') (binomial tests: all subjects p≥0.572; Table 3)

In condition 6 'Competition training' Columbo, Gerti and Rumo needed 28, 22, and 12 sessions, respectively, to reach criterion of choosing the baited cache in 12 out of 14 trials within 2 consecutive sessions. Subjects received a total amount of 175 (Columbo), 147 (Gerti), and 77 trials (Rumo) within this condition.

In the additional counter-training against her side bias to the right Gerti received 3 sessions to 7 trials each and one session to 8 trials, *i.e.* a total of 29 trials, until she reached criterion to choose the baited cache, *i.e.* the cache to her left, in 3 consecutive trials within one session.

When the consequence of first choosing the empty cache was that I took the food out of the still baited cache and put it either into my pocket (condition 7 'Reasoning–experimenter pocket') or pretended to eat it (condition 8 'Reasoning - experimenter eat') no subject chose the baited cache first significantly above chance (binomial tests: all subjects p≥0.185; Table 3). After changing my position in the phase of choice with Rumo in condition 8a 'Reasoning experimenter eat – changed experimenter position' he did not show a preference for the still baited cache (binomial test: p = 0.851; Table 3)

Columbo chose the still baited cache significantly above chance (binomial test: p= 0.013) when I clearly showed the reward to the subject after manipulation (condition 9 'Reasoning - show

deliberately') whereas Gerti and Rumo did not significantly chose one cache over the other (binomial test: both p≥0.851) (Table 3).

When I took the reward that I showed the subject out of my pocket in condition 10 'Non-matching control - show deliberately', Columbo did not significantly chose one cache over the other (binomial test: p=0.851; Table 3).

Gerti chose the still baited cache significantly above chance (binomial test: p=0.036) when the first choice of the empty cache was followed by another human pilfering the baited cache (condition 11 'Reasoning-human competitor'), whereas Rumo did not chose any cache over the other significantly (binomial test: p=0.572) (Table 3).

When subjects could observe me taking out the food reward of one of the two caches (condition 12 'Reasoning - all manipulations clear') none of them chose the still baited cache above chance (binomial test: all not significant; Table 3)

Table 3: Performance of subjects in all conditions but competition-training.
Given are absolute and relative frequencies of choosing the baited or empty cache first as well as respective p-values of two-tailed binomial testing. For conditions of non-matching control "baited" resembles non-matching and "empty" resembles matching, *i.e.* first choice of the cache with the reward not matching or matching the shown reward. P-values ≤0.05 are given in bold typeface.

condition	subject	trials total (n)	absolute baited	absolute empty	relative baited	relative empty	binomial p
1 - cue control	Columbo	22	11	11	50	50	> 0.999
	Gerti	21	11	10	52	48	> 0.999
	Rumo	21	10	11	48	52	> 0.999
3 - Exclusion	Columbo	28	27	1	96	4	**< 0.001**
	Gerti	28	27	1	96	4	**< 0.001**
	Rumo	28	26	2	93	7	**< 0.001**
4 - Reasoning	Columbo	28	12	16	43	57	0.572
	Gerti	28	15	13	54	46	0.851
	Rumo	35	17	18	49	51	> 0.999
5 - R. obvious manipulation	Columbo	28	15	13	54	46	0.851
	Gerti	28	14	14	50	50	> 0.999
	Rumo	28	13	15	46	54	0.851
7 - R. experimenter pocket	Columbo	28	18	10	64	36	0.185
	Gerti	28	16	12	57	43	0.572
	Rumo	35	19	16	54	46	0.736
8 - R. experimenter eat	Columbo	42	24	18	57	43	0.441
	Gerti	35	19	16	54	46	0.736
	Rumo	28	14	14	50	50	> 0.999
8a - changed experimenter position	Rumo	28	15	13	54	46	0.851
9 - R. show deliberately	**Columbo**	28	**21**	7	**75**	25	**0.013**
	Gerti	28	15	13	54	46	0.851
	Rumo	35	17	18	49	51	> 0.999
10 - Nonmatching control show deliberately	Columbo	28	13	15	46	54	0.851
11 - R. human competitor	**Gerti**	28	**20**	8	**71**	29	**0.036**
	Rumo	28	12	16	43	57	0.572
12 - R. all manipulations clear	Columbo	35	20	15	57	43	0.5
	Gerti	28	15	13	54	46	0.851
	Rumo	35	20	15	57	43	0.5
13 - Nonmatching control human competitor	Gerti	28	16	12	57	43	0.572

To sum up, Columbo and Gerti performed above chance level in the conditions 'Reasoning - show deliberately' and 'Reasoning – human competitor', respectively, whereas they did choose randomly in the associated control-conditions ('Non-matching control'). Rumo did not choose the baited cup significantly above chance in any of the reasoning-conditions. All subjects chose at chance level in the condition in which they could see all manipulations, as well as in the preceding control for using inadvertent cues ('Baseline 1 – cue control'), but they chose the baited cache significantly more often when they had seen the other cache empty ('Exclusion') (Figure 4).
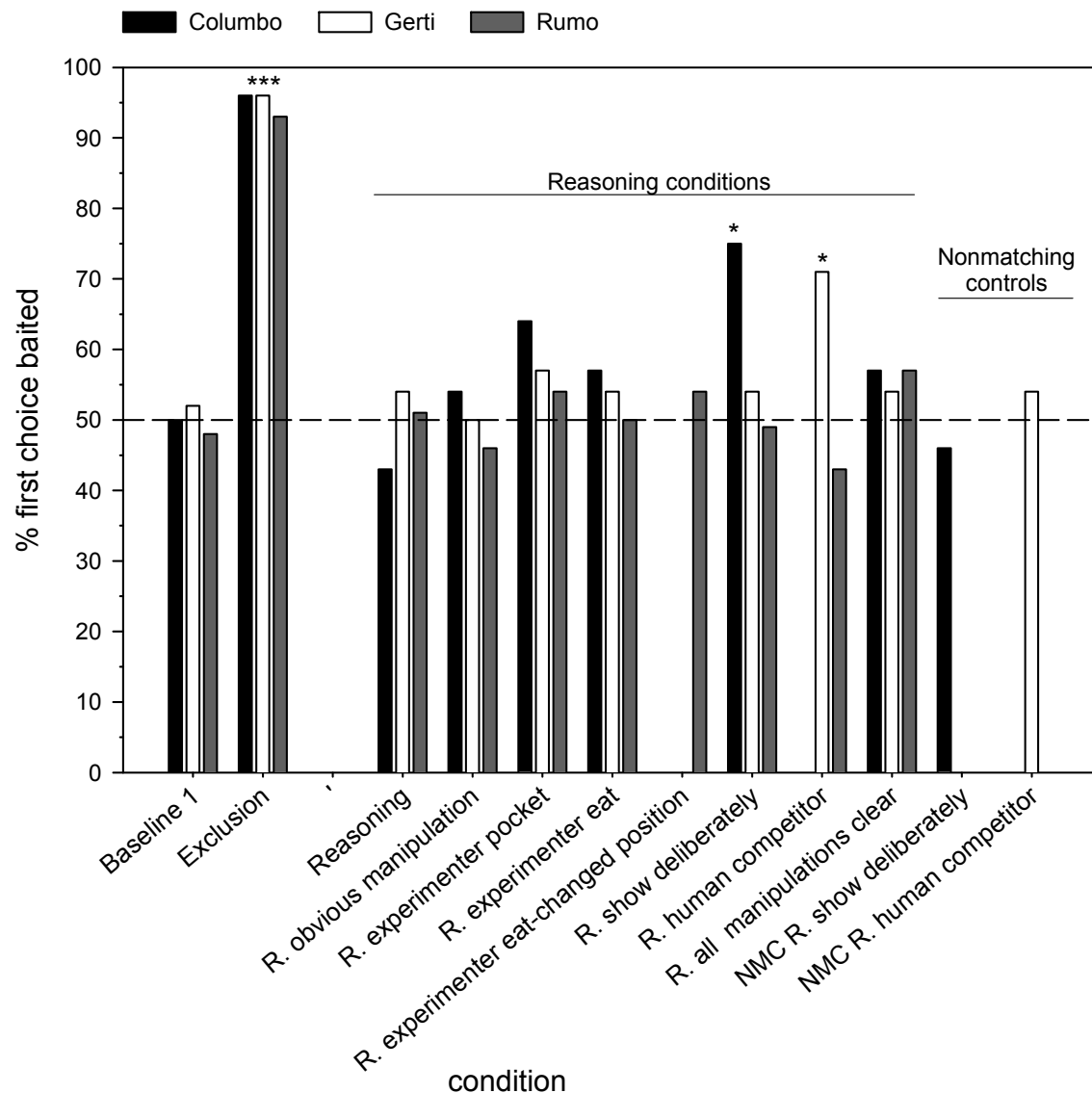
Figure 4: Relative number of trials in which the ravens Columbo, Gerti, and Rumo chose the still baited cache first for all conditions the success of first choice was recorded.
Asterisks mark significant differences from chance level (binomial tests) with * = p < 0.05, *** = p<0.0001; NMC = Non-matching control, R. = Reasoning, the broken line indicates chance level (50%).

3.1.1. Learning effects

None of the subjects chose differently in the first from the second half of trials within any condition (Mc Nemar: all p≥0.125).

The subjects did not increase or decrease in their relative frequency of choosing the baited cache first, or choosing the cache containing the reward not matching the shown reward first over the course of the study (Spearman Correlation: Columbo R=0.075, p=0.847, n=9 conditions; Gerti R=0.136, p=0.708, n=10 conditions; Rumo R=-0.012, p=0.973, n=10 conditions).

3.2. Side preferences

Columbo chose the right cache first significantly above chance in condition 2 'Baseline 2 – color control' (binomial test: p=0.007), condition 4 'Reasoning', condition 7 'Reasoning - experimenter pocket' (binomial test: both p<0.0001), and condition 12 'Reasoning – all manipulations clear' (binomial test: p=0.001). In all other conditions Columbo did not significantly prefer one over the other side of caches (top panel, Figure 5).

Gerti chose the cache to her right first significantly above chance in the conditions 'Baseline 1 – cue control', 'Baseline 2 –colour control', 'Reasoning', 'Reasoning clear manipulation', and 'Non-matching control - Reasoning - human competitor' (binomial test: all p<0.0001). In conditions 'Reasoning - experimenter eat', and 'Reasoning - show deliberately' Gerti switched to significantly choosing the cache to her left first (binomial test: both p<0.0001) (middle panel, Figure 5).

Rumo chose the cache to his right first significantly above chance in condition 1 'Baseline 1 – cue control' (binomial test: p=0.007), condition 2 'Baseline 2 – colour control', condition 4 'Reasoning', condition 12 'Reasoning - all manipulations clear' (binomial test: all 3 conditions p<0.0001), and condition 11 'Reasoning - human competitor' (binomial test: p=0.004). Rumo switched to significantly choosing the cache to his left first in condition 8 'Reasoning - experimenter eat' (binomial test: p<0.0001), but lost his side preferences after I had changed my position during choice in condition 8a 'Reasoning - experimenter eat – changed experimenter position' (binomial test: p=0.345). In condition 9 'Reasoning - show deliberately' Rumo again chose the cache to his left first significantly more often (binomial test: p=0.017). In condition 7 'Reasoning - experimenter pocket' (binomial test: p=0.5) as well as condition 12 'Reasoning – all manipulations clear' (binomial test: p=0.311) Rumo did not significantly prefer any side (bottom panel, Figure 5).
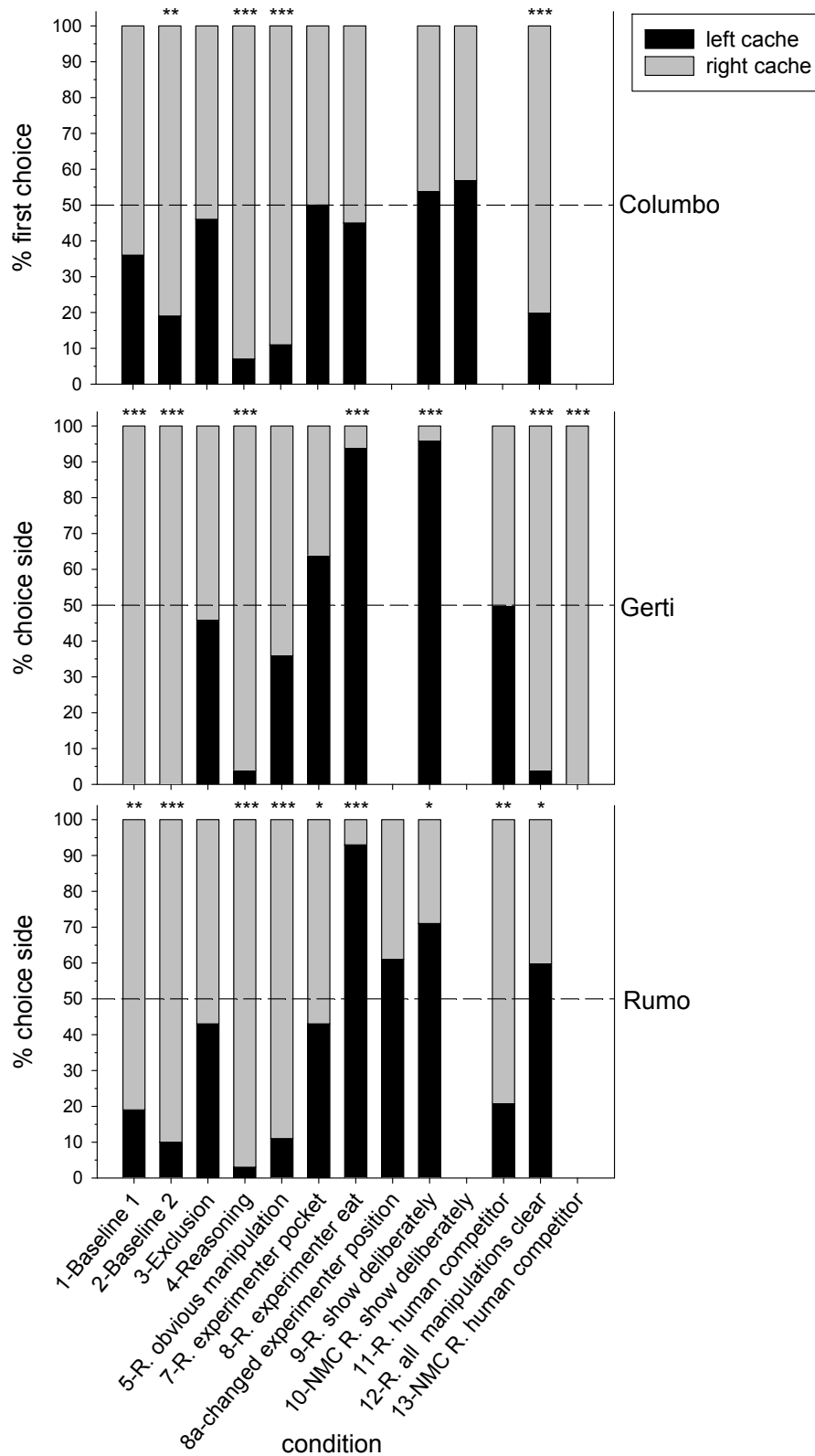
Figure 5: Relative frequencies of choosing the left/right cache first for all subjects in all conditions.
Asterisks mark significant differences from chance level (binomial tests) with *=p<0.05, **=p<0.01, and
***=p<0.001; NMC=Non-matching control, R.=Reasoning, the broken line indicates chance level (50%).

4. Discussion

Two of 3 common ravens (Columbo and Gerti) significantly chose the still baited over the empty cache first in different reasoning-conditions. Similar to other studies using the 'apple-banana-task' (Premack & Premack 1994; Call 2006; Mikolasch *et al.* 2011a; Tornick & Gibson 2013) ravens showed high individual differences suggesting that this mechanism is indeed demanding. Both conditions within which subjects reached significance included a more obvious manipulation where subjects could see me approaching the caches once again but did not exactly see what I did, a clear showing of the removed reward to the subject after manipulations (deliberately), and clear consequences of choosing the empty cache first (competition). The nature of the blind during manipulations of conditions within which subjects reached significance were more similar to the method of Call (2006) with observable movements of the experimenter's hand between bowls than to the original study of Premack and Premack (1994) where the setup was not visible to subjects during manipulation.

The setup with natural caches itself was not a sufficient factor for changing the performance of subjects. Columbo changed performance in the condition where the factor of clearly showing the reward to the subject was introduced. This was a factor also present in my preliminary study following the procedure of Mikolasch *et al* (2011a) where the rewards had been placed under opaque cups on a small moveable wooden platform on the floor and a small blind was used to obstruct the view on the cups during manipulation. Remarkably, Columbo reached significance in the condition most similar to the procedure applied in the preliminary study. Columbo then had chosen the still baited cup significantly above chance (71% of trials, binomial test p=0.029) when she was allowed to enter the room and turn over the cups on her own (*pilfer* condition). In contrast, the performance of Gerti changed as soon as a second human competitor was present who pilfered the still baited cache if she did not. This was the most natural competitive situation possible within this study. In the current study a conspecific as competitor which would have been the most natural type of competition could not be applied because of the small sample size and the territoriality of subjects. Subjects reacted aggressively towards conspecifics other than their respective pair partner and it would have been not possible to test a subject after being used as competitor. In contrast to Columbo, who had previously participated in an experiment where she was confronted with one human pilfering caches containing non-edible objects (pilferer) and another just looking at those caches (onlooker) (Bugnyar *et al.* 2007a), Gerti was much less experienced with humans as competitors. The change in performance within different conditions might be due to differing experience with participating in experiments and competition by humans. The prior experience with a human as competitor of Columbo might

have been the reason that the consequence of the experimenter taking out the reward of the still baited cache was a sufficiently strong consequence of a wrong first choice. However, the introduction of this factor of competition itself did not affect the performance of Columbo. Though Rumo did not change his preference for the still baited cache throughout all reasoning-conditions the introduced factor of competition where the experimenter pretended to eat the reward in case of a wrong first choice (condition 8 'Reasoning - experimenter eat') resulted in a change of strategy as Rumo tried to reach the second cache faster than his competitor.

The outstanding performance of subjects in condition 3 'Exclusion' was adequate to findings in a former exclusion-task (Schloegl *et al.* 2009b). Subjects chose the baited over the empty cache even more frequently in the current study compared to Schloegl *et al (2009b)* which might be due to the fact that the empty cache had been left open which made the still baited cache the only one left to be pilfered. Therefore, in contrast to the study of Schloegl et al (2009b) where both cups had been put back to their original position before the subjects were allowed to choose in the current study subjects did not have to remember the cache they had seen empty.

It remains unclear whether Gerti and Columbo really understood the underlying principle of the task, as both chose at chance level in the condition where all manipulations were clearly visible to them (condition 11 'Reasoning - all manipulations clear'). This is surprising as ravens have been shown to understand visible displacement from week 7 post fledging (Bugnyar *et al.* 2007b). In the study of Call (2006) subjects performed better in the *perception* – condition, where the experimenter visibly removed one of the two rewards, than in the *inference*-condition and 3 of 7 grey parrots chose the baited cup significantly above chance in the *visible* condition of Mikolasch et al (2011a). Condition 11 'Reasoning - all manipulations clear' had been the last condition of the study and was presented after a long period of intense testing in a repetitive manner. Hence, the birds might have lost their motivation to participate in this task. If this was true I would have expected them to quit participating more often during sessions within the last conditions. Against this hypothesis the subjects did not participate in less trials per session in condition 11 'Reasoning – all manipulations clear' when compared to previous reasoning-conditions. Still, it is possible that the attention of subjects towards the given hints ceased in the course of the study.

Also remarkable was the amount of sessions the subjects needed to reach criterion in condition 7 'Competition-training'. Ravens do remember and pilfer caches they have seen others make (e.g. Bugnyar & Kotrschal 2002) and ravens performed better in similar training sessions within earlier studies where ravens were trained to choose one of two bowls after they have seen the

experimenter put a food reward underneath one of them (Schloegl *et al* 2007; Schloegl *et al* 2009b). It is especially striking that Columbo, who had also participated in the studies mentioned above, needed the highest amount of sessions to reach criterion in the current study. In the studies of Schloegl *et al* (2007; 2009b) subjects received such conditions at the beginning of the study, as opposed to the current study with condition 7 'Competition-training' embedded within conditions presumably requiring more cogitation. Aust et al (2008) reported that one tested student searched for a more complex rule than reasoning by exclusion in a computer-based matching to sample task. The student's performance was consistently overshadowed by the attempt to find a more sophisticated strategy. Moreover, Aust et al (2008) found a pattern with dogs where the 3 of 6 dogs choosing according to reasoning by exclusion in the test conditions needed comparatively more time to learn the initial discrimination between two stimuli whereby one was rewarded and the other was not. The authors concluded that those individuals might have rather searched for a logical solution in contrast to relying on rote learning. Similarly, in the current study both ravens significantly choosing the still baited cache above chance in one of the reasoning-conditions needed more trials to learn to choose the baited cache during 'Competition training' with the baited/empty cache comparable to a simple positive/negative stimulus discrimination where subjects had to learn to choose the cache they had seen being baited for gaining a reward.

Columbo and Gerti might have learned to solve the task over the course of the study or within the condition they reached significance. However, the subjects did neither change their performance within any of the presented conditions nor over the course of the experiment. Though very fast learning can not be excluded, it is to mention that both subjects chose the still baited cache first on the very first trial in the respective condition. Another possibility would be a win-stay loose-shift strategy. In the condition Columbo reached significance she switched to choosing the baited cache in the subsequent trial whenever she chose the empty cache first within one session with only one exception where she chose the empty cache first in two subsequent trials within a session. For Gerti this pattern was not as clear, as she chose the empty cache first in 3 and 2 subsequent trials in two different sessions. Additionally, Columbo might have learned to solve the task within the preliminary study and applied this knowledge within the condition most similar to the former procedure. Against this hypothesis neither in the current study nor in the preliminary study a change of performance was found when comparing the first and second half of trials (preliminary study: McNemar, $p>0.999$).

Subjects might have used inadvertently given cues by the experimenter to find which one of the two caches was baited, *i.e.* clever hans effect (Pfungst 1998) . Then, the question remains why they did not use those cues in any of the other conditions given that the experimenter did not change and I consistently tried to avoid giving cues over the whole course of the study. Moreover, ravens performed poorly in finding food hidden underneath one of two cups when they received cues from the experimenter like looking at the baited cup, looking at the baited cup combined with vocalization, and looking at the baited cup combined with approaching it (Schloegl *et al.* 2008).

The significant success of Columbo and Gerti in one of the reasoning-conditions might also be due to the fact that subjects were tested repeatedly in the same kind of task with conditions only differing slightly leading to a total of 189 (Columbo), 203 (Gerti), and 252 (Rumo) respective trials in reasoning-conditions inreasing the possibility for finding a significance without biological relevance. Noteworthy, the subject receiving the highest total amount of trials within reasoning-conditions did not perform above chance level in any of these conditions.

All individuals showed significant side-biases. Possible influences might have been
a) the direction the door opened (they might have simply went to the cache accessible first after opening the door first)
b) local enhancement during manipulations (the experimenter approached the cache to the birds left first during manipulation)
c) the position of the experimenter during choice (experimenter stood at the entrance door to the left for Gerti and Rumo and to the right for Columbo).
The first cache accessible after the opening of the door was the left cache for Columbo. As Columbo chose the right cache significantly above chance in any condition she showed a significant side bias and she already showed a significant bias to the right in condition 2 'Baseline 2' where no manipulations could be observed only hypothesis c) remains. Gerti as well as Rumo changed the preferred side over the course of the study and the patterns do not clearly support any of the three hypotheses mentioned above. Against hypothesis b) Gerti did not prefer any side over the other during condition 'Reasoning - obvious manipulations' when she was able to observe the experimenter approaching the caches again for the first time. But the observed strategy of Rumo in condition 'Reasoning - experimenter eat' as well as the fact that he lost this side-bias after the experimenter changed position ('Reasoning - experimenter eat - changed experimenter position') also supports hypothesis c) that the position of the experimenter during choice had an effect. Rumo might have applied a mixed strategy of choosing the cache first

accessible after the opening of the door in conditions with milder competition and trying to be faster at both caches in situations of stronger competition. Ravens have been observed to speed up pilfering when competing with conspecifics that were also informed about the location of caches, especially when competing with a co-observer dominant to them (Bugnyar & Heinrich 2005).

Given the small sample size, the repetitive nature of this study, and the resultant low statistical power no clear general conclusion can be drawn. Some shortcomings of the current study emerged over the course of the study. Initially planned with six subjects only three ultimately could participate. Moreover, the amount of trials within conditions differed strongly which had not been planned initially. It might be interesting to test more subjects with the possibility to include competition with conspecifics over caches. Moreover, new paradigms might be found to add more perspectives on the abilities of reasoning by exclusion in common ravens as well as to add to the greater comparative picture. Following the principle of parsimony I would suggest that subjects rather used a less demanding mechanism for solving problems like the 'exclusion task' when possible and therefore more likely the mechanism of avoiding the location they had previously seen empty accounts for success in the study on exclusion performances in the visual domain by Schloegl et al (2009b) as well in the 'Exclusion' condition of the current study. However, this might not be as easy as it seems given that some species tested did not solve such tasks, for example lemurs (Maille & Roeder 2012), jackdaws (*Corvus monedula*) (Schloegl 2011), keas (*Nestor notabilis*) (Schloegl *et al.* 2009b), and pigeons (*Columbia livia domestica*) (Aust *et al.* 2008).

Taken together, the data suggest that at least some individual subjects were able to apply their skills more effectively in a paradigm considering ecologically relevant factors like a more natural situation of competition as well as containing more clarity regarding the given hints. Rather than being effective on their own the components within a given condition might have acted together within the respective condition to alter the subjects' performance in accordance with their individual prior experiences.

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6. Abstract

Corvids and apes are suggested to possess comparably complex cognitive abilities (Emery & Clayton 2004). Recently, common ravens (*Corvus corax*) were shown to be capable of solving a task on reasoning by exclusion but it remained unclear whether they did so relying on the mechanism of reasoning by exclusion in the narrower sense, *i.e.* logically excluding potential alternatives (Call 2006), or using avoidance without drawing inferences (Schloegl *et al* 2009b). Preliminary results using a version of the 'apple-banana-paradigm' introduced by Premack & Premack (1994) which is only solvable via reasoning by exclusion remained ambiguous. To clarify the potential effect of experimental setup on the performance of subjects I used the context of ecologically highly relevant food-caching and stepwise altered factors hypothesized of enhancing the subjects' motivation to use their skills. One of two different food rewards previously hidden in one of two caches in full view of the subjects was removed with the subjects' view totally or partially blocked. Subsequently, subjects were shown the removed reward and were allowed to enter the experimental room to pilfer both or one of the caches. Factors manipulated were 1) visibility of manipulations, 2) clarity of hint-presentation, and 3) competition in terms of consequence of choosing the empty cache first. Two of three subjects chose the still baited cache significantly above chance in conditions differing in the intensity of competition but subjects had difficulties solving less demanding elements. The intensity of the consequence succeeding a wrong first choice seemed to affect some subjects' behavior, but it seems to be a demanding task. It is concluded that ravens most likely used the mechanism of avoidance to solve previous experiments on exclusion.

7. Zusammenfassung

Es wird vermutet, dass Rabenvögel und Menschenaffen einander vergleichbar vielschichtige geistige Fähigkeiten besitzen (Emery & Clayton 2004). Vor kurzem wurde gezeigt, dass Raben (*Corvus corax*) eine Aufgabe des vernunftbedingten Ausschlusses lösen konnten. Es blieb jedoch ungeklärt ob sie die Mehrfachmöglichkeit logisch ausschlossen (Call 2006) oder diese ohne weitere Schlüsse zu ziehen vermieden (Schloegl *et al* 2009b). Ergebnisse eines Vorversuchs waren nicht eindeutig, in welchem eine Variante des sogenannten „Apfel-Bananen-Problems", eingeführt von Premack & Premack (1994), angewandt wurde. Dieses Problem ist nur durch Schlussfolgerung lösbar. Um den möglichen Einfluss der Versuchsbeschaffenheit auf die Leistung der Versuchstiere aufzuklären, führte ich einen vergleichbaren Versuch im Rahmen des ökologisch bedeutsamen Verhaltens des Futterversteckens durch und veränderte schrittweise Größen von welchen ich annahm, dass sie die Motivation der Versuchstiere ihre Fähigkeiten einzusetzen erhöhen würden. Ich entnahm eines von zwei unterschiedlichen Futterstücken, welche zuvor für die Versuchstiere beobachtbar in zwei unterschiedliche Verstecke gelegt worden waren, wieder aus dem Versteck wobei die Sicht der Versuchstiere vollständig oder teilweise eingeschränkt war. Anschließend ließ ich die Versuchstiere das entnommene Futterstück sehen, woraufhin sie den Versuchsraum betreten und beide oder eines der Verstecke plündern durften. Ich veränderte folgende Größen: 1) die Sichtbarkeit meiner Plünderung eines der Verstecke, 2) die Deutlichkeit des Hinweises auf das entnommene Futterstück, sowie 3) Konkurrenz bezüglich der Art der Folgen wenn die erste Wahl der Versuchstiere auf das schon leere Versteck fiel. Zwei von drei Versuchstieren wählten in verschiedenen Versuchsabschnitten, welche sich durch den Grad der Konkurrenz voneinander unterschieden, signifikant häufiger das noch bestückte Versteck. Es fiel den Versuchstieren jedoch ungewöhnlich schwer weniger anspruchsvolle Abschnitte des Versuchs zu bestehen. Das Gewicht der unmittelbaren Folge einer falschen ersten Wahl hatte möglicherweise einen Einfluss auf das Verhalten mancher Versuchstiere, insgesamt schien die Aufgabe jedoch eine herausfordernde zu sein. Ich schließe mit der Vermutung, dass Raben vorangegangene Versuche des vernunftbedingten Ausschlusses mit höherer Wahrscheinlichkeit mit Hilfe von Vermeidung der ungewollten Möglichkeit gelöst haben.

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2009   internship Field Station "La Gamba", Costa Rica

Flower preferences of nectar feeding hummingbird species

"Hummingbirds as Flower Visitors in the Field Station "La Gamba", Costa Rica"

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experiments on reasoning by exclusion with common ravens (*Corvus corax*)

"The impact of study design on the performance of ravens in a cognitive experiment"

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experiments on reasoning by exclusion with common ravens (*Corvus corax*)

"The demonstration of reasoning by exclusion of individual common ravens (*Corvus corax*) is influenced by details of testing procedure"

Research Interests

Animal behavior and cognition in interaction with their environment, comparative   aspect of cognition.

ornithology

Human-nature interaction and its effects on human behavior and cognition as well as human psychological welfare.

Human-nature interaction and its effects on nature conservation.

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1994 – 2000   training as classical ballet dancer, ballet conservatory St.Pölten

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1998 – 2010   voluntary service in the team of the youth- and pupil-center H2, St.   Pölten, Austria

2007   seminar on communication and presentation

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