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"Problem Solving and Tool Use in Ravens and Carrion Crows"

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Abstract

Innovative and flexible tool use as well as other technical problem solving skills are frequently regarded as indicators of advanced cognitive abilities because they suggest technical intelligence and causal reasoning. However, this assumed connection of problem solving and causal reasoning is not yet fully resolved.

The present study seeks to empirically investigate this supposed relationship by studying technical problem solving and tool use in common ravens (*Corvus corax*) and carrion crows (*Corvus corone*). Tool use has hardly been reported for these two species in the wild. Therefore, if ravens and carrion crows can solve tool related problems, this might suggest that tool use abilities result from domain-general cognitive capacities rather than from domain-specific cognitive skills that have evolved for tool use per se.

At first, the study examined if captive ravens and crows innovatively and flexibly used stone tools to solve a technical problem solving task. For this purpose, we tested if the birds spontaneously dropped stones through an open tube into a transparent box causing a platform to collapse and gaining a food reward. Thereafter, we investigated how different kinds of pre-experience with the functional characteristics of the box influenced the subjects' stone dropping performance. Therefore, one test group could release the platform by directly pushing it down from above though a shortened tube with the beak. Another test group received experience in collapsing the platform by pulling a string from below. Thereafter, the birds' stone-dropping performance was re-tested. In a third step, we examined if the birds made a transfer between different tools and could use sticks instead of stones to collapse the platform.

The results showed that four out of eight crows and one out of ten ravens used stone tools without having ever applied them in experimental settings before. The remaining crows could use the experience of both pushing and pulling to make a transfer to dropping stones, which implies that they had learned something about the respective physical properties of the box. In contrast, the remaining ravens were neither successful in pushing nor in pulling the platform down, even after extensive possibilities to explore the box. All birds that had been successful with the stones also attempted to insert sticks into the tube. For some test conditions, the experiment revealed motivational differences between the ravens and crows, which suggest that the ravens rather tried to solve technical tasks with physical force, whereas the crows rather tended to apply the tools.

The study shows that both ravens and crows can spontaneously drop stone tools into an apparatus. Furthermore, it indicates that some of the crows may have some appreciation of causalities underlying the task, which supports the assumption that tool use in the wild is no prerequisite for an advanced technical intelligence and physical cognition.

Zusammenfassung

Innovativer und flexibler Gebrauch von Werkzeugen sowie andere Fähigkeiten zur Problemlösung im technischen Bereich legen technische Intelligenz und das Verstehen von Kausalzusammenhängen nahe. Aus diesem Grund werden diese Verhaltensweisen bei Tieren häufig als Zeichen von hohen kognitiven Fähigkeiten gedeutet. Der genaue Zusammenhang von Problemlöseverhalten und kausalem Verständnis ist jedoch noch nicht vollständig geklärt.

Vorliegende Arbeit versucht, diesen Zusammenhang empirisch zu untersuchen, indem die Fähigkeiten zur technischen Problemlösung von Kolkraben (*Corvus corax*) und Aaskrähen (*Corvus corone*) getestet werden. Für diese zwei Arten gibt es kaum Nachweise von Werkzeuggebrauch in freier Wildbahn. Sollten Raben und Krähen trotzdem in der Lage sein, technische Probleme mit Hilfe von Werkzeugen zu lösen, weist dies darauf hin, dass Problemlösefähigkeiten im technischen Bereich keine domänenspezifischen kognitiven Leistungen sind, die sich zum Werkzeuggebrauch per se entwickelten, sondern das Resultat allgemeiner Intelligenz.

Aus diesem Grund wurde in einem ersten Schritt untersucht, ob Raben und Krähen Steine innovativ als Werkzeuge zur Lösung eines technischen Problems einsetzen. Dazu wurde getestet, ob die Vögel spontan und ohne jegliche Vorerfahrung mit der Testapparatur Steine durch eine Röhre in eine transparente Box fallen ließen, wodurch eine Plattform kollabierte und eine Belohnung freigesetzt wurde. In weiterer Folge wurde getestet, wie verschiedene Arten der Vorerfahrung mit den funktionellen Eigenschaften der Testapparatur die Leistungen der Vögel beeinflussen. Hierfür bekamen jene Tiere, die mit den Steinen nicht erfolgreich waren, die Chance, die funktionellen Eigenschaften der Box auf verschiedene Arten zu erkunden. Eine Testgruppe konnte die Plattform durch ein verkürztes Rohr direkt mit dem Schnabel von oben hinunterdrücken. Eine zweite Testgruppe konnte die Plattform mit einer Schnur von unten aus der Verankerung lösen und herunterziehen. Nach dieser Vorerfahrung mit der Box und dem Kollabieren der Plattform wurden die Vögel erneut mit den Steinen getestet. In einem weiteren Testschritt wurde untersucht, ob die Vögel einen Transfer zwischen verschiedenen Werkzeugen, nämlich Steinen und Stäbchen, machen.

Die Ergebnisse zeigen, dass vier von acht Krähen und einer von zehn Raben Steinwerkzeuge verwendeten ohne sie jemals zuvor in Experimenten benutzt zu haben. Die verbleibenden Krähen konnten sowohl die Vorerfahrung durch Hinunterdrücken als auch jene durch Herunterziehen der Plattform dazu nutzen, einen Transfer zur Benutzung der Steinwerkzeuge zu machen. Dies impliziert, dass diese Krähen etwas über die technischen Eigenschaften der Box lernten. Im Gegensatz dazu waren die verbleibenden Raben trotz ausgedehnten Möglichkeiten zur Erkundung der Box weder im Hinunterdrücken noch im Hinunterziehen der Plattform erfolgreich. In weiterer Folge machten alle Vögel, die mit den Steinen erfolgreich waren, auch Versuche, die Stäbchen ins Rohr zu stecken. Darüber hinaus zeigten sich in den Experimenten Unterschiede in der Motivation der Raben und Krähen. Diese Unterschiede deuten darauf hin, dass die Krähen eher dazu geneigt waren, Werkzeuge zu benutzen, während die Raben die technischen Aufgaben eher mit physischer Kraft zu lösen versuchten.

Die Resultate belegen, dass sowohl Raben als auch Krähen spontan Steine in eine Testapparatur fallen lassen können und weisen darauf hin, dass einige Krähen den Mechanismus der Apparatur und die dahinterliegenden Kausalzusammenhänge verstanden haben. Dies unterstützt die Annahme, dass auch Vogelarten, die in freier Wildbahn keine Werkezuge benutzen, hohe technisch-kognitive Fähigkeiten besitzen können.

1. Introduction

For a long time, the ability to use tools has been regarded as a uniquely human trait and has been used to argue that humans are cognitively superior to non-human animals. However, in the last few decades, numerous studies could show that various non-human animal species are also able to use tools (e.g. Bentley-Condit & Smith 2010; Lefebvre et al. 2002). Nevertheless, it is still unclear what exactly non-human animals understand about the physical properties and the underlying principles of tool use tasks.

1.1. Tool Use

Tool use is commonly defined as "the external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool" (Shumaker et al. 2011: 5), which is a slightly extended and altered version of a definition by Beck (1980: 10). With regard to this definition, many animals, ranging from mammals, mostly primates, over birds to insects use tools (e.g. Bentley-Condit & Smith 2010; Lefebvre et al. 2002). For example, chimpanzees use stones for nut-cracking (Boesch & Boesch 1990) or sticks to poke for termites (Goodall 1986), dolphins use sponges for foraging in the sand (Krützen et al. 2005), New Caledonian crows use pieces of leaves for extracting food from holes (Hunt 1996) and ant-lions throw sand at escaping prey (Pierce 1986).

1.2. The Evolution of Cognitive Mechanisms and Tool Use

The evolution of cognitive mechanisms is largely influenced by selective pressures acting on species' morphological, physiological and behavioural traits as well as by ecological characteristics. Therefore, cognitive processes, including the abilities to use tools and to understand the underlying physical principles, are adaptations to specific environmental conditions (e.g. Biro et al. 2013; Shettleworth 2009 b; Teschke et al. 2013). As tool use skills are linked to the environmental conditions they evolved in, they differ across species both in quality and quantity (Auersperg et al. 2011; Santos et al. 2006).

A major theory concerning the evolution of intelligence and cognition is that feeding strategies determine mental development. Especially tool-mediated extractive foraging, i.e. the act of locating, acquiring and processing foods embedded in a matrix or a container with the help of tools, is regarded as an important driving factor for sophisticated cognitive abilities (e.g. King 1986; Parker & Gibson 1977; Parker & Gibson 1979). This so-called extractive foraging hypothesis is supported by the fact that many species that use tools are extractive foragers (e.g. chimpanzees: Boesch & Boesch 1990; Goodall 1986; King 1986; orang-utans: Fox et al. 2004; Lethmate 1982; capuchin monkeys: King 1986; Ottoni & Izar 2008; New Caledonian crows: Hunt 1996). However, the distribution of tool use in the wild cannot be explained by ecological factors alone (Boesch & Boesch 1990; van Schaik, Deaner & Merrill 1999).

The extractive foraging hypothesis also states that brain size increased in the course of the evolutionary adaptation to feeding ecology (e.g. Parker 2015). In primates as well as in birds, the amount and complexity of tool use behaviours correlate with brain size (Lefebvre et al. 2002; Lefebvre et al. 2004; Reader & Laland 2002; Seed & Byrne 2010). However, extractive foraging and tool use are no prerequisites for large brains as there are also species that have large brains, but do not use tools (e.g. parrot species: Liedtke et al. 2011). An alternative explanation for the evolution of intelligence is the social cognition hypothesis that focuses on complex social behaviour and argues that "increases in neocortex size are related to changes in group size rather than changes in ecological niche or patterns of resource exploitation" (Dunbar 1992: 483).
Beyond that, it is unclear to what extent the evolution of tool use abilities relates to the evolution of general cognitive skills such as causal understanding. For example, also species that do not use tools in the wild can employ tools in experimental settings (e.g. Auersperg et al. 2011; Bird & Emery 2009; Santos et al. 2006; Tebbich et al. 2007). This suggests that instead of domain-specific cognitive capacities that have evolved as adaptations to specific ecological niches, species can use domain-general cognitive skills to solve technical problems (e.g. Santos et al. 2006; Teschke et al. 2011).

1.3. Causal Reasoning and Insight

Tool use is frequently associated with insightful behaviour, in particular with causal reasoning skills (Bird & Emery 2009; Byrne 1997; Emery & Clayton 2009; Kacelnik 2009; McCormack et al. 2011; Shettleworth 2009 a; Shettleworth 2012; Thorpe 1964). Insight is usually described as "the sudden production of new adaptive responses not arrived at by trial behaviour […] or the solution of a problem by the sudden adaptive reorganization of experience" (Thorpe 1964: 110). This assumed connection between tool use, causal understanding and insight leads to a lot of debates about how much tool-using animals comprehend about the mechanisms that underlie the solutions to technical problems (e.g. Chappell 2006).
On the one hand, technical problem solving skills and seemingly "insightful" behaviour might suggest causal reasoning abilities, which in turn seem to indicate an advanced intelligence (Thorpe 1964; von Bayern et al. 2009). On the other hand, tool use behaviour could result from much simpler cognitive mechanisms such as genetic predispositions, associative learning or shaping (Lind et al. 2009; Seed & Byrne 2010; Tebbich et al. 2010). This, however, would mean that the respective animals do not necessarily have a causal understanding of the actions they perform and are also unable to create causal interventions (Taylor et al. 2014).
Nevertheless, there are claims that the difference between humans' and animals' understanding of tool use is just quantitative, and not qualitative. Chappell (2006) argues that while no non-human animal employs tools with the complexity and variety like humans do it, humans also do not always possess an in-depth understanding of the principles underlying their actions.
Although there are plenty of discussions concerning this issue, only few investigations give a reasonable account of the cognitive mechanisms that motivate tool use (Kacelnik 2009; von Bayern et al. 2009).
Two of these studies that have already addressed the issue of insightful behaviour in animals and have tried to unravel the extent of animals' understanding of tool use tasks have motivated the present study in particular and shall therefore be described in more detail.
In the first one, a study done by Bird and Emery (2009), rooks, a species for which there are no reports of tool use in the wild, were presented with a box containing a platform that collapsed and

released a food reward when slight pressure was applied through a vertical tube on top of the box. After being trained to nudge stones into the tube from a ledge next to the opening of the tube, the rooks succeeded in dropping stones onto the platform. Thereafter, they transferred to pushing the platform down with sticks. Although their behaviour was termed “insightful” problem solving by the authors, the birds were trained without previously being given the chance to solve the task spontaneously by themselves. Also, without groups of naïve controls, it is impossible to know what the birds had learned about the causal mechanisms of the original task and it remains possible that they were simply able to transfer from previously associatively reinforced behaviours. Therefore, within this experiment, one cannot argue that the rooks have understood the underlying concept of the collapsibility of the platform.

A follow-up study was conducted by von Bayern and colleagues (2009) on New Caledonian crows, a species that habitually uses tools in the wild. This study examined how pre-testing experience affected the crows’ performance in a problem solving task. None of six New Caledonian crows spontaneously dropped stones through a tube into a box, but after being trained to nudge stones into the tube, the two trained crows immediately brought stones to the box and dropped them down the tube. To investigate whether subjects had learned something about the collapsibility of the platform, another group of four crows was trained to push the platform down with their beaks directly through a shortened tube and to thus release the platform without the use of stones. Also two of these birds subsequently generalized to correctly using the stones to collapse the platform. This makes the authors conclude that the crows have learned about some functional properties of the task, namely that the platform has to be collapsed to obtain a reward (Shettleworth 2009 a; von Bayern 2009). However, it cannot be argued that the New Caledonian crows have understood the underlying principle of the apparatus because it would be enough for them to know that the platform has to be touched from above to be rewarded. Therefore, it cannot yet be assumed that the birds were able to make causal interventions (Taylor et al. 2014).

An adequate control would be to give the subjects another type of pre-experience, in which they do not have to collapse the platform from above, but can instead collapse it from below. If the birds still succeed in making a transfer to using stones, this can be taken as a sign that the subjects have understood the physical properties of the apparatus.

1.4. Ravens and Crows

Common ravens and carrion crows are both highly interesting model species to test technical problem solving skills of non-habitual tool users. They belong to the corvid family, a family of which members have a large brain relative to their body size (Emery 2006), which is comparable to primates (Emery & Clayton 2004). Corvids were shown to have advanced cognitive abilities in many previous experiments (e.g. Emery & Clayton 2004; Lefebvre et al. 2002), they have great innovation scores (Lefebvre et al. 1997) and they exhibit remarkable innovative and flexible behaviour (Auersperg et al. 2011). Therefore, it might be possible to also find that corvids are able to understand the underlying principles of technical problem solving tasks.

However, when looking at the species level, physical problem solving, tool use and technical flexibility are normally not associated with common ravens or carrion crows, but rather with New Caledonian crows (e.g. Chappell & Kacelnik 2002; Chappell & Kacelnik 2004; Hunt 1996; Hunt & Gray 2004 a; Hunt & Gray 2004 b; Taylor et al. 2007; Taylor et al. 2009; Weir et al. 2002). Differences in tool use behaviour might result from differences in these species’ foraging behaviour. In contrast to

New Caledonian crows, which are extensive extractive foragers, both common ravens and carrion crows are typical scavengers (Marzluff et al. 2007) and there are no reports that they regularly use tools in the wild.

Still, they are explorative and manipulative, which might be influenced by the fact that they frequently cache their food (Auersperg et al. 2015; Bugnyar et al. 2007; Jacobs et al. 2014). Ravens were for example shown to spontaneously perform a sequence of pulling on strings and stepping onto the pulled up loops to reach food attached to the end of these strings (Heinrich & Bugnyar 2005). Also, there is ample anecdotal evidence for crows dropping nuts on streets to have them cracked by automobiles (*C. corone*: Nihei & Higuchi 2001; *C. brachyrhynchos*: Grobecker & Pietsch 1978, but also Cristol et al. 1997). However, to my knowledge, no direct studies on tool use in both ravens and carrion crows have been conducted. Therefore, in the present study, it shall be investigated if corvids that do not habitually use tools in the wild still have the cognitive and physical capacities to solve tool-related tasks.

1.5. Aims and Predictions

The present experiment examines if common ravens and carrion crows, two species for which there are no reports of tool use in the wild, innovatively and spontaneously use stone tools in a technical problem solving task. This task involved dropping stones into a tube to collapse a platform to obtain food. As neither rooks nor New Caledonian crows spontaneously dropped stones into an apparatus (Bird & Emery 2009, von Bayern et al. 2009), it was not expected that the ravens or crows would do it.

Nevertheless, ravens, which are play-caching inedible objects in their first years of life, have been observed to playfully insert objects into unrewarded vertical tubes and holes (Auersperg et al. 2015). It may therefore be possible that spontaneous 'tool-use' may initially occur accidentally during playful interaction, e.g. when trying to play-cache the stone inside the tube and being immediately reinforced by an unexpected reward (similar behaviour has been reported in captive kea; Gajdon et al. 2014). Additionally, as carrion crows intentionally drop nuts in the wild (e.g. Nihei & Higuchi 2001), it might be possible that the crows also have a tendency to drop stones, but not necessarily into captivities.

We also tested how different kinds of experience with the functional properties of the apparatus affected the birds' performance. In particular, the experiment should reveal if the bird's abilities to solve a stone dropping task differ when they receive pre-experience with collapsing the platform either from above by pushing it down with their beaks or from below by pulling it down with a string. These kinds of pre-experience were chosen because they did not involve unattached tools and were assumed to require less cognitive effort than dropping stones into the box. It was expected that this facilitation would enhance the birds' performance considerably. If the birds understood the physical properties of the apparatus, they should transfer their knowledge from both conditions to a stone dropping task in which they collapse the platform from above. However, if they had not learned about the collapsibility of the platform itself but only that something has to be applied from above, it is expected that the transfer to dropping stones occurs only after having already pushed the platform down from above (cf. New Caledonian crows: von Bayern et al. 2009) and not when just having pulled the platform down from below.

Another aim of the study was to reveal if ravens and crows can make a transfer from using one tool to using another, namely from stones to sticks. Rooks were successful in making such a transfer (Bird & Emery 2009), which raises the possibility that ravens and crows can do it as well.
Overall, the study addresses the general question whether understanding of causality in the physical domain is a specific evolutionary adaptation of tool using species.

2. Materials and Methods

2.1. Subjects

The subjects of the study were ten common ravens (*Corvus corax;* three females, seven males) and eight carrion crows (*Corvus corone*; five females, three males). All subjects (Table 1) hatched in spring 2012 and were hand raised under identical conditions and by the same people. All birds were individually marked with coloured rings.

Table 1: Study subjects. Siblings are listed in sequence and the different colours mark the boarders between the sibling groups.

Species	Name	Sex	Origin	Type of breeding location
Ravens	Adele	f	Bayerischer Wald	Animal park
	Laggie	m	Bayerischer Wald	Animal park
	Tom	m	Bayerischer Wald	Animal park
	George	m	Sweden	Animal park
	Horst	m	Sweden	Animal park
	Louise	f	Sweden	Animal park
	Nobel	f	Sweden	Animal park
	Max	m	Wels	Animal park
	Paul	m	Wels	Animal park
	Rufus	m	Korneuburg	Private owner
Crows	Corbie	m	Donauinsel	Nest
	Daisy	f	Donauinsel	Nest
	Souki	f	Donauinsel	Nest
	Peppi	f	Donauinsel	Nest
	Rainer	f	Donauinsel	Nest
	Signore	m	Donauinsel	Nest
	Saul	m	Donauinsel	Nest
	Juno	f	Donauinsel	Nest

In their enclosures, the birds were exposed to stones, wooden logs, sticks and other objects for enrichment. It can be assumed that all birds had pre-experience with dropping objects, e.g. by picking things up and releasing them or by observing conspecifics doing so. However, none of the birds had participated in any tool-related experiments before or had had pre-experience with inserting objects into an apparatus in a food-rewarded context.

2.2. Housing Conditions

All birds were housed in outdoor aviaries at Haidlhof Research Station near Bad Vöslau, south of Vienna, Austria. Both, ravens and crows were kept in single species group-housing. The birds were tested in roofed testing compartments that were connected to the main enclosures (Figure 1) and could be freely accessed at times when no experiments were conducted. While closed, all test compartments were visually isolated from the rest of the aviaries. Birds could access the testing compartments voluntarily and were separated from the group for the duration of any individual test sessions. All birds were marked with coloured leg bands for individual identification.

The ground consisted of natural soil covered with differently sized gravel in the main aviaries and of sand in the testing compartments. All enclosures provided numerous perches as well as some natural and artificial objects for enrichment such as wooden sticks, wood chips, bottles or plastic cups. All groups had ad libitum access to fresh drinking and bathing water and were fed twice per day, once in the morning before starting the experiments and once in the evening after finishing the experiments. Food consisted of fruits, curd cheese or yoghurt and bread in the morning and of meat and bread in the evening.

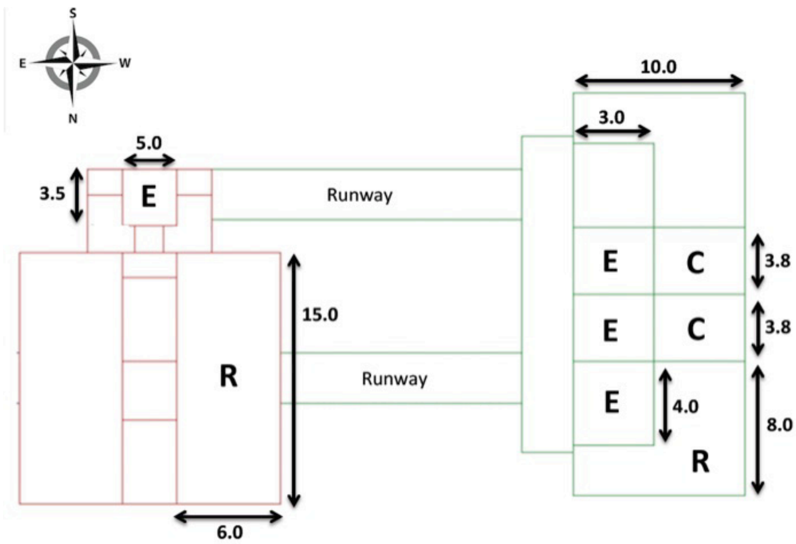

Figure 1: Enclosures of the test subjects at Haidlhof Research Station.
R = raven enclosure, C = crow enclosure, E = experimental compartment.
All length specifications are given in metres.
Illustration by Alex Munteanu, modified by Theresa Matzinger.

2.3. Apparatus and Experimental Setup

The experiment required the subjects to extract food from an apparatus (Figure 2: A). The apparatus consisted of a transparent Plexiglas box (15.0 x 15.0 x 10.0 cm) with an open vertical tube (inner diameter: 3.0 cm, length: 10.0 cm) on top, similar to the apparatuses used in Bird & Emery (2009) and von Bayern et al. (2009). A collapsible opaque aluminium platform (14.8 x 14.8 x 0.1 cm) was fixed with hinges inside the box and held in a horizontal position by a magnet. A food reward (commercially available dog food pellets, “Frolic”, or cat food pellets, “Clever”) was placed on the platform. The reward was never placed directly underneath the tube opening, but was slightly displaced sideward. The food reward could be obtained by applying force to the platform, which caused the magnet to detach, the platform to collapse and the food reward to roll out through an opening at the lower edge of the box (Figure 2: B).

Force could be applied to the platform in four different ways: firstly, by dropping a stone through the open tube onto the platform, secondly, by pulling a string (length: 15.0 cm) attached to the bottom of the platform and reaching out through the opening at the lower edge of the box, thirdly, by directly pushing the platform with the beak through a shortened tube (length: 4.0 cm) and fourthly by pushing the platform with a stick (diameter: 1.0 cm, length: 15.0 cm) through the long open tube.
In test conditions that essentially required stones or sticks to solve the task, four of the respective tools were provided at approx. 5 cm distance to the box. When stones were necessary to solve the task, one of the four stones was placed at each corner of the box. In conditions that required sticks, two sticks each were positioned at two randomized opposing sides of the box.
Tools that had been used or were removed from their original position were placed back into their original position by the experimenter at the beginning of a new trial. Tools that were lost through caching were replaced with new tools.
Rebaiting of the apparatus occurred out of sight of the birds via the opening at the lower edge of the box.

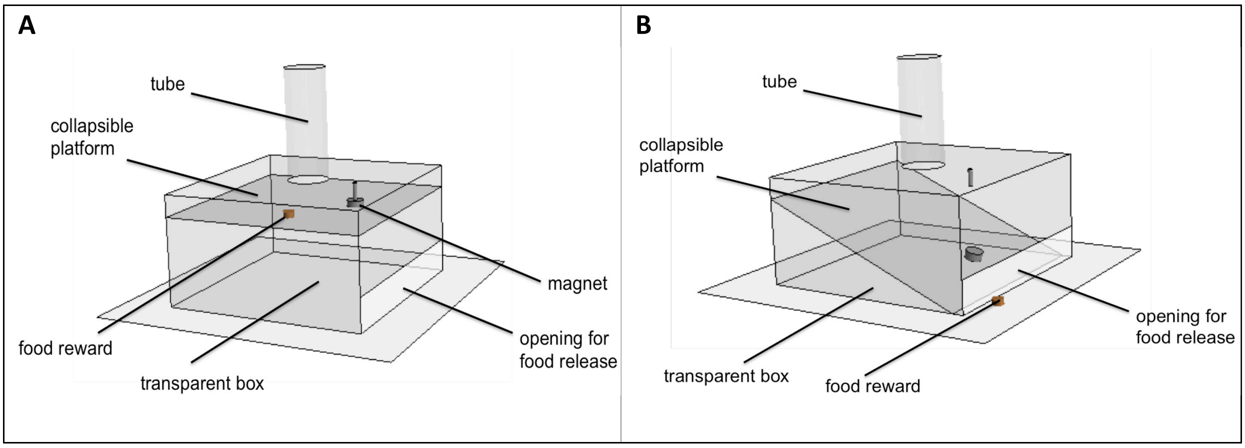

Figure 2: A: Baited apparatus with the platform in its horizontal position.
B: Apparatus with the platform collapsed.

2.4. Habituation

Before the start of the experiment, the birds were habituated to the apparatus with the platform collapsed, i.e. unhinged from the magnet. No food rewards were used during the habituation phase.
At first, the birds were habituated to the box in a group context for two sessions à 10 min each. In this phase the box was left in the main enclosures. During the group-habituation phase, all birds approached and touched the box at least once.
Then, an individual habituation phase followed: it consisted of one session à 10 min, in which subjects were separated in a test compartment with the non-functional box. In this individual habituation phase, five out of ten ravens and three out of eight crows approached and inspected the box from a distance less than one metre from the box. Due to time restrictions, we did not apply the criterion of touching the box in the individual habituation phase.

2.5. Testing Procedure

The testing procedure entailed several consecutive stages (Figure 3). The stages a bird participated in depended on its performance in previous stages.
Depending on the stage, a stage consisted of different numbers of sessions with 10 trials each. If a bird did not complete a trial within 10 min, the session was terminated and testing continued with the next session on the following day. In case a bird dropped the platform in an unintended way, i.e. through strongly pecking on the box or through moving, lifting and dropping the whole apparatus, the respective trial was repeated at the end of the session.
The criterion of mastery for all stages was to successfully complete two consecutive sessions. If the criterion was not achieved within the set number of sessions for the respective stage, it was discontinued. For subjects that successfully completed only the last of the set number of sessions, an additional session was added to give them the chance to still reach the criterion.

The first test stage, the ***Spontaneous Stone Use Test***, tested whether the subjects would spontaneously drop stones into the box without any pre-experience. This stage consisted of 10 sessions.
Birds that did not reach the criterion within the Spontaneous Stone Use Test continued with ***Training 1***. In Training 1, subjects could apply force to the platform directly instead of having to combine a tool with the apparatus. Direct handling of the platform could occur in two different ways: either by pulling a string attached to its bottom *('Pull String' Group*), or by directly pushing it with the beak through a shortened tube *('Push Platform' Group).* For the training, both the ravens and the crows were semi-randomly assigned to one of the two groups ('Pull String' Group and 'Push Platform' Group). The training stage also consisted of 10 sessions.
After having finished Training 1, all birds – independently of their performance in Training 1 – proceeded to ***Stone Use Test 1***, in which they were retested with the same setup as in the Spontaneous Stone Use Test.
Subjects that have not reached the criterion in Stone Use Test 1 continued with ***Training 2***, a second training stage à 5 sessions in the same groups as in Training 1. This was followed by one more session of another stone dropping task, ***Stone Use Test 2***.
Birds that had successfully completed one of the stone use tests (i.e. the Spontaneous Stone Use Test, Stone Use Test 1 or Stone Use Test 2), were tested in the ***Stick Transfer Test*** if they were able to push down the platform with a stick instead of dropping a stone. The Stick Transfer Test consisted of 5 sessions.
After having participated in the Stick Transfer Test, birds took part in a ***Stone Use Retest*** to check if they continued using the stones. The Stone Use Retest had the same setup as the Spontaneous Stone Use Test, but consisted of just one session.
In the ***Stick Control Test***, birds that had successfully completed neither one of the stone use tests nor one of the training tasks were tested in 5 sessions if they nevertheless were able to use sticks to push down the platform.
All stages of the experiment were videotaped and coded from the videos.

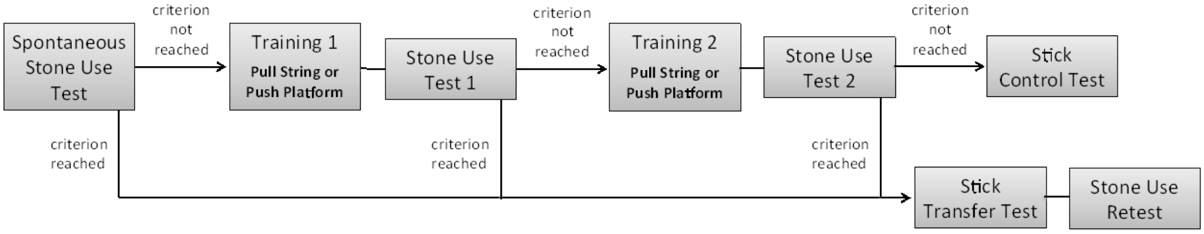

Figure 3: Stages of the testing procedure.

2.6. Data Analysis

All videos were analysed with Solomon Coder (András Péter, Version beta 12.09.04), a program for behaviour coding. 20 % of the data was double rated by a second rater for interobserver reliability. Interobserver reliability was adequate (Cohen's kappa: k = 0.92).

Data was exported to Microsoft Excel 2011 and analysed with the statistical software IBM SPSS Statistics, Version 20.

The subjects' motivation to participate in the respective conditions was evaluated by analysing how frequently the birds manipulated the box itself and the appropriate objects that had to be handled to solve the task, i.e. stones, sticks, the string or the platform. For these analyses, only unsuccessful trials, i.e. trials in which the subjects did not collapse the platform, were considered. The extent of box and tool manipulation in these unsuccessful trials was measured by computing the mean percentage of unsuccessful trials in which at least one peck was directed against the box and the mean percentage of unsuccessful trials in which the appropriate objects were touched at least once. First, the percentages were calculated for each subject (which failed at least in one trial in the respective test) and then the mean was computed.

Binary GLMMs with a logit link function were calculated to assess the effect of species, experimental condition, session number, trial number within a session and total trial number on whether an individual directed at least one peck against the box or touched the appropriate object at least once. In these models, the pecks or the touches were the response variable, whereas species, experimental condition, session number, trial number within a session and total trial number were entered as fixed variables. Moreover, to represent the nested structure of the study's repeated data, the data was structured to be nested in each individual. Consequently, subject identity was entered as random variable to the models. All models were run including all main effects and two-way interactions of experimental condition and species. Additionally, several reduced models were run and the best fitting model was selected with the corrected Akaike Information Criteria (cAIC). Here, only the best fitting models are reported.

The reported p-values are two tailed and effects were considered as statistically significant when the respective p-values were less than 0.05. Where appropriate, *post hoc* analyses were run using Mann-Whitney U-tests.

3. Results

3.1. Success in Collapsing the Platform

3.1.1. Spontaneous Stone Use Test

Unexpectedly, 5 out of 18 subjects, including members of both species, spontaneously inserted stones into the tube and thus collapsed the platform. 1 out of 10 ravens succeeded in spontaneously dropping stones into the tube, whereas 4 out of 8 crows reached the criterion.

The stone dropping raven and the stone dropping crows needed similarly long to reach the criterion of mastery. The only successful raven needed 7 sessions and the four crows needed 6.5 ± SE 0.9 sessions to complete the task (Figure 4: black bars). However, after having solved their first trial, i.e. after having dropped the stone into the tube for the first time, the birds reached the criterion almost instantaneously. When counting from the sessions in which the birds used the stones successfully for the first time, the one raven needed 2 sessions, which is the minimum number of sessions required, and the four crows needed 2.8 ± SE 0.5 sessions to finish the test (Figure 4: grey bars).

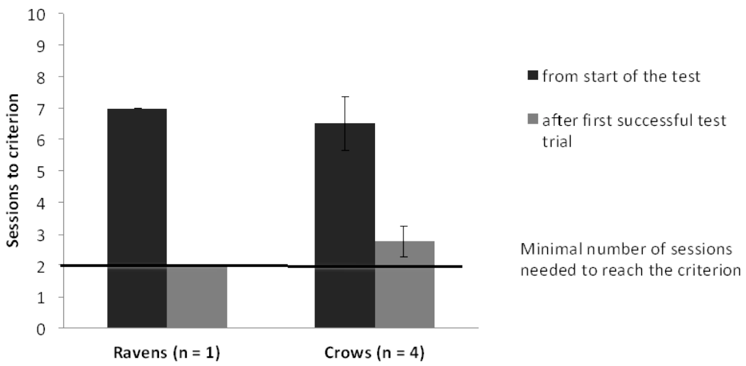

Figure 4: Mean number of sessions that the successful birds needed to reach the criterion of mastery in the Spontaneous Stone Use Test. Black: number of sessions counted from the start of the test. Grey: number of sessions counted from the session in which the birds have solved one test trial correctly for the first time, i.e. after the birds have 'discovered' the solution. Whiskers indicate the standard error of the mean.

3.1.2. Training 1

All birds that did not reach the criterion in the Spontaneous Stone Use Test, namely nine ravens and four crows, proceeded to the first training stage, Training 1. None of the ravens solved the training task, neither in the string pulling condition (n = 5), nor in the platform pushing condition (n = 4). In contrast, one crow in the 'Pull String' Group (n = 2) and both crows in the 'Push Platform' Group (n = 2) reached the criterion of mastery in Training 1.
Although they did not reach the criterion of mastery, 4 out of 5 ravens in the 'Pull String' Group and 1 out of 4 ravens in the 'Push Platform' Group solved the respective tasks at least once, i.e. in at least one trial (for exact numbers see Table 2).

Table 2: Total number of correctly solved trials of the ravens in Training 1.

	Individuals	Total number of correctly solved trials in Training 1
'Pull String' Group	Adele	2
	Horst	1
	Max	0
	Nobel	8
	Tom	3
'Push Platform' Group	George	11
	Laggie	0
	Louise	0
	Rufus	0

3.1.3. Stone Use Test 1

The crow that had successfully completed Training 1 in the 'Pull String' Group and one of the crows that had successfully mastered Training 1 in the 'Push Platform' Group also reached the criterion for dropping stones into the tube in Stone Use Test 1. The subject from the 'Pull String' Group reached the criterion immediately, i.e. within two sessions, and the subject from the 'Push Platform' Group needed seven sessions to do so, starting to drop stones in session 6.

Additionally, one raven that has solved two trials in the string pulling condition of Training 1 reached the criterion of mastery for stone dropping in Stone Use Test 1. This subject started dropping stones in session 8 and completed the task in session 10.

3.1.4. Training 2

Training 2 was just carried out with the eight remaining ravens that had been unsuccessful both in the Spontaneous Stone Use Test and in Stone Use Test 1. In Training 2, one raven in the 'Pull String' Group reached the criterion of mastery. However, all other subjects remained unsuccessful.
Out of logistical reasons, Training 2 could not be carried out with the one remaining crow that had not solved any of the previous tasks. This crow proceeded to the Stick Control Test immediately.

3.1.5. Stone Use Test 2

In Stone Use Test 2 neither the ravens that were unsuccessful in Training 2, nor the one raven that was successful in sting pulling in Training 2 solved the stone dropping task.

3.1.6. Overall Stone Use Performance

When pooling the results of all Stone Use Tests, i.e. the Spontaneous Stone Use Test, Stone Use Test 1 and Stone Use Test 2, in total 20 % of the ravens (2 out of 10 subjects) and 75 % of the crows (6 out of 8 subjects) were proficient in using stone tools and have reached the criterion for one of the stone dropping tasks (Figure 5).

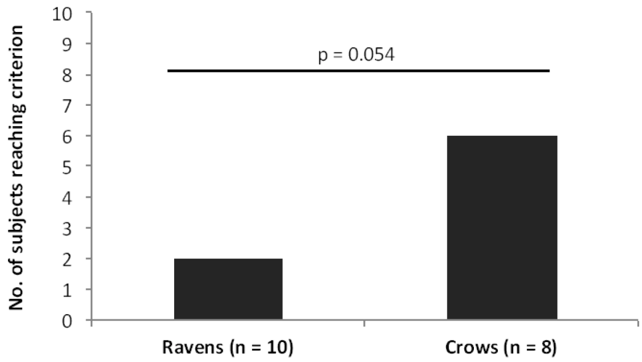

Figure 5: Absolute number of subjects reaching the criterion of mastery in one of the Stone Use Tests, i.e. in the Spontaneous Stone Use Test, in Stone Use Test 1 or in Stone Use Test 2; p = 0.054: Fisher's exact test.

3.1.7. Stick Transfer Test

The Stick Transfer Test was carried out with all subjects that had successfully completed one of the Stone Use Tests, i.e. the Spontaneous Stone Use Test, Stone Use Test 1 or Stone Use Test 2. These were 2 ravens and 6 crows. All subjects that have reached the criterion for the stone dropping task in one of the previous tests also made attempts to use the sticks by touching the tube of the box with a stick. One raven and three crows were successful in collapsing the platform with the stick at least once. However, just one crow reached the criterion in the Stick Transfer Test. This crow needed six sessions to complete the task.
Further, two crows used stones from the aviaries, which were not presented within the experimental setup in close proximity to the box, to drop them onto the platform (Figure 6).

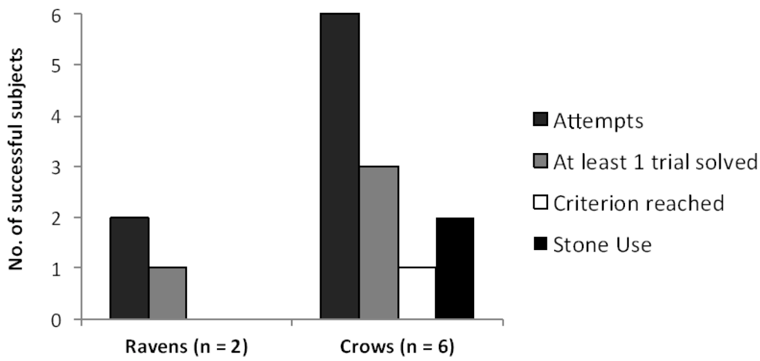

Figure 6: Number of subjects making attempts to use sticks (dark grey), solving at least one trial with a stick (light grey), reaching the criterion of mastery by using sticks (white) and using stones from the aviaries to collapse the platform (black).

The crow that successfully completed Training 1 in the platform pushing group, but did not succeed in the stone dropping tasks, combined the stick with the tube nine times in total. However, the subject did not succeed in a single trial to collapse the platform with the stick.
In contrast, the raven that reached the criterion in Training 2 in the string pulling group, but did not drop stones, also did not attempt to use the sticks.

3.1.8. Stick Control Test

All individuals that had reached the criterion in none of the previous Stone Use Tests (Spontaneous Stone Use Test, Stone Use Test 1, Stone Use Test 2), and none of the training conditions (Training 1, Training 2), namely 7 ravens and 1 crow participated in the stick control test.
None of these birds touched the tube with the stick even once.

3.1.9. Stone Use Retest

All birds that have successfully passed the criterion for one of the Stone Use Tests continued using the stones after the Stick Transfer Test. All of these individuals passed the criterion of mastery in the Stone Use Retest immediately.

3.2. Box and Tool Manipulation in Unsuccessful Trials: Pecks and Touches

The generalized linear mixed models (GLMMs) on the extent of pecks against the box and touches of the appropriate objects (i.e. stones, string, platform, sticks, resp.) revealed that the birds' behaviour differed between the test conditions. It also showed that in certain test conditions the pecking and touching behaviour differed between the two species. The nature of these differences however varied between the test conditions.
The models revealed significant effects of test condition on both the pecks against the box ($F = 2.710$, $df1 = 5$, $df2 = 409$, $p = 0.02$) and the touches of appropriate objects ($F = 3.307$, $df1 = 5$, $df2 = 408$, $p = 0.006$). The models also showed an interaction effect between species and test condition for the pecks against the box (GLMM: interaction species x test condition: $F = 4.406$, $df1 = 6$, $df2 = 409$, $p = 0.000$) and the touches of the appropriate objects (GLMM: interaction species x test condition: $F = 7.962$, $df1 = 6$, $df2 = 408$, $p = 0.000$), suggesting that in the respective test conditions the ravens' and the crows' pecking and touching behaviour differed. Post hoc analyses indeed revealed that the differences in behaviour between the ravens and the crows had different directions in the different test conditions.
In unsuccessful trials in the Spontaneous Stone Use Test, the percentage of trials in which at least one peck was directed against the box was higher for the crows than for the ravens (Mann-Whitney U test, $p \leq 0.05$, ravens: 16.11 ± SE 6.17 %, crows: 59.58 ± SE 10.81 %) . In contrast, in unsuccessful trials of Stone Use Test 1, the percentage of trials in which at least one peck was directed against the box was almost the same for the ravens and the crows (ravens: 36.67 ± SE 7.99 %, crows: 36.67 ± SE 21.86 %; Figure 7). Further, in unsuccessful trials of the Stick Transfer Test, the ravens pecked at the box at a significantly higher percentage of trials than the crows (Mann-Whitney U test, $p \leq 0.05$, ravens 90.00 ± SE 10.0 %, crows 43.89 ± SE 9.75 %).

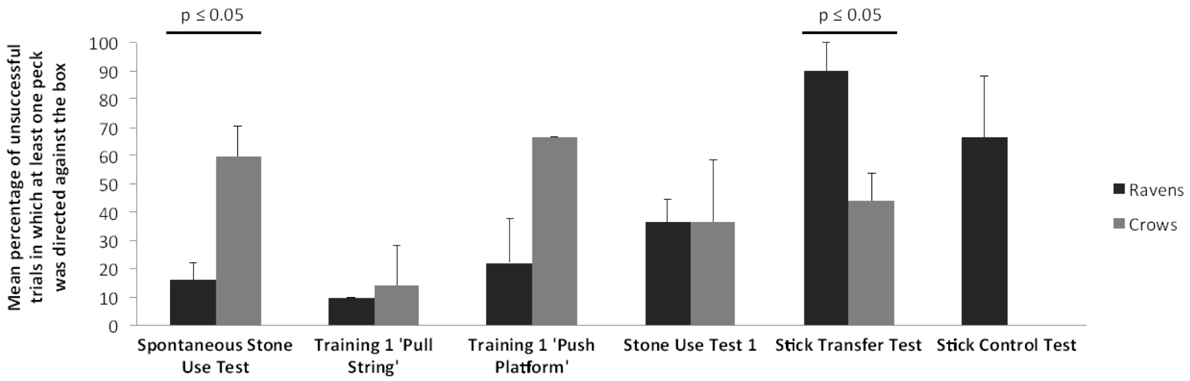

Figure 7: Mean percentage of unsuccessful trials in which at least one peck was directed against the box in the Spontaneous Stone Use Test, in Training 1 ‘Pull String’, in Training 1 ‘Push Platform’, in Stone Use Test 1, in the Stick Transfer Test and the Stick Control Test. Whiskers indicate the standard error of the mean. For the sample size of each condition see Appendix Table A1.

Similarly, in unsuccessful trials of the Spontaneous Stone Use Test and in the string pulling condition of Training 1, the crows touched the appropriate objects (stones, string, platform, stick, resp.) at a higher percentage of trials than the ravens (Spontaneous Stone Use Test: Mann-Whitney U test, $p \leq 0.05$, ravens 14.11 ± SE 3.99 %, crows 71.67 ± SE 9.02 %; Training 1 ‘Pull String’ Group: Mann-Whitney U test, $p \leq 0.05$, ravens 2.00 ± SE 2.0 0 %, crows 29.29 ± SE 0.71 %). In Stone Use Test 1 and in the Stick Transfer Test, however, the mean percentages of trials in which the ravens and the crows touched the appropriate objects were comparable (Stone Use Test 1: ravens: 43.33 ± SE 3.33 %, crows: 53.33 ± SE 17.64 %; Stick Transfer Test: ravens: 100.00 ± SE 0.00 %, crows: 91.67 ± SE 5.27 %; Figure 8).

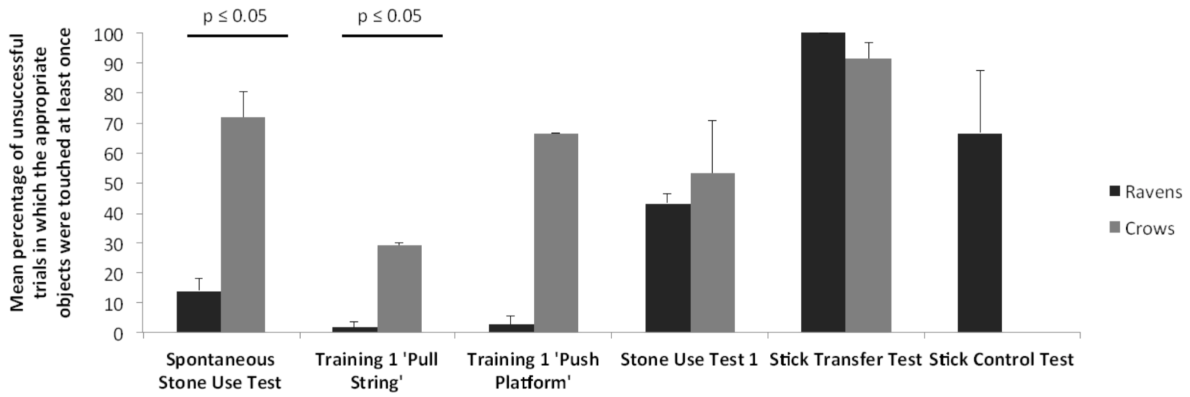

Figure 8: Mean percentage of unsuccessful trials in which the respective appropriate objects (stones, string, platform, stick) were touched with the beak at least once in the Spontaneous Stone Use Test, in Training 1 ‘Pull String’, in Training 1 ‘Push Platform’, in Stone Use Test 1, in the Stick Transfer Test and in the Stick Control Test. Whiskers indicate the standard error of the mean. For the sample size of each condition see Appendix Table A1.

In the Stick Transfer Test, in some cases, when the birds were not successful with the sticks, they solved the task incorrectly by pecking on the box with so much force that the platform fell down

because of the impact of the peck. This happened 45 times in one of the two ravens, and 3, 5 and 7 times respectively in three of the six crows.
In the Stick Transfer Test, the six crows directed 3.96 ± SE 1.00 pecks per trial against the box and made 3.46 ± SE 0.57 attempts per trial to solve the task with the sticks. In contrast, the two ravens pecked the box 11.00 ± SE 6.20 times per trial and attempted to solve the task with the sticks 4.10 ± SE 1.51 times per trial (successful, unsuccessful and incorrectly solved trials considered).

4. Discussion

4.1. Spontaneous Stone Tool Use

The first main finding of the present study was that, astonishingly, members of both species dropped stones into the box spontaneously and without prior experience with the functional characteristics of the apparatus. This is remarkable insofar as there are no reports of tool use for both ravens and carrion crows in the wild. Furthermore, adult New Caledonian crows, a corvid species that uses tools in the wild, did not drop stones spontaneously into baited tubes in previous studies (von Bayern et al. 2009; Taylor et al. 2011). The failure of New Caledonian crows might be attributed to the fact that their tool use is highly domain-specific. As extractive foragers they usually use stick tools, but not stones (Taylor et al. 2011). In contrast, ravens and crows cache their food (Bugnyar et al. 2007) and therefore manipulate gravel frequently. Interestingly, in a study on object play, both young New Caledonian crows and ravens playfully inserted objects into tubes and holes in a non-foraging context. In contrast to present findings, the rate of such insertions was much higher in New Caledonian crows than in ravens (Auersperg et al. 2015). In New Caledonian crows, this playful inserting behaviour was limited to birds that were subadult at the time of testing, which may explain the lack of similar recordings in the studies with baited tubes (von Bayern et al. 2009; Taylor et al. 2011). Since ravens inserted objects playfully into tubes (Auersperg et al. 2015) and since this has not been previously studied in carrion crows, the first successful insertions without any pre-experience with the functional properties of the apparatus might not have been goal directed actions, but may rather have resulted from playful combinations of the tools with different parts of the apparatus followed by fast reinforcement after the latter proved to be rewarding. Similar behaviour has been shown in captive kea (Gajdon et al. 2014).

Overall, there was a trend of the crows outperforming the ravens in the dropping tasks. An observation that might help to explain this result is that wild crows were recorded to drop nuts on the ground to crack them open (Nihei & Higuchi 2001) and can therefore be presumed to also drop other objects such as stones. Alternatively, the ravens, which received the same amount of habituation as the crows, may simply be more neophobic towards the apparatus than the crows and be more reluctant to interact with its affordances (see 4.4 below; ravens' neophobia in the feeding context: e.g. Heinrich 1988; Heinrich et al. 1995; Kijne & Kotrschal 2002; neophobia towards experimenters in test settings: e.g. Cibulski et al. 2014: no differences in neophobia between ravens and carrion crows recorded, but: ravens tended to approach experimenters more often than crows).

4.2. Evidence for Understanding the Mechanism of the Box

The second important implication of the study is that ravens and crows may at least possess some appreciation of the causalities of the task. This can be assumed for several reasons.

Firstly, successful crows from both training conditions subsequently also dropped stones into the apparatus. This suggests that they have transferred the information that they had gained in the training to other tasks, irrespective of having collapsed the platform in the training from below or above. Hence, they might have some understanding of the causal mechanisms of the task. In this respect it was particularly interesting to find that the bird with the string pulling experience solved the task immediately and remained successful in Stone Use Test 1. It spontaneously dropped objects from above through the tube onto the platform although its experience was limited to collapsing the platform with the string from below. Nevertheless, the successful subject with the experience of platform pushing required 7 sessions in Stone Use Test 1. Subsequently, here it cannot be excluded that the accumulating experience with the original apparatus rather than a transfer from pre-experience was responsible for success.

A second finding that points towards a causal understanding of the task is that after having completed their first trial successfully, the birds reached the criterion of mastery almost instantaneously. However, it might also be possible that their behaviour was the result of rather fast associative learning or even one-trial learning.

Although some of the results look promising at this point, due to the limited sample size of birds passing the pre-experiences further testing (possibly including shaping unsuccessful subjects with the respective pre-experiences) will be required to make firm assumptions.

4.3. Stick Tool Use

All birds that had successfully inserted stones into the tube also attempted to use sticks to release the platform. As just those birds that were proficient in stone tool use, but not those in the control group made attempts to use sticks, it can be assumed that the birds were possibly able to make a transfer between the tools and understood that something has to be added to the box from above to obtain a reward. However, an alternative explanation for this behaviour might be that the birds that had been successful with inserting the stones into the tube just continued performing a similar behaviour than the one that had previously been rewarding without having an understanding of the affordances of the apparatus. It is unlikely that the birds from the control group were just neophobic because in the Stick Control Test these birds were highly motivated and both touched the sticks and pecked at the box frequently.

The finding that although all stone dropping birds made attempts to use the sticks, just one crow reached the criterion for actually inserting the sticks into the tube might be explained by anatomical constraints (cf. Troscianko et al. 2012). Although ravens and carrion crows construct nests out of twigs and branches, which requires at least some handling skills for elongated objects like sticks (Hansell & Ruxton 2008), they do not employ sticks with the same proficiency as for example New Caledonian crows. New Caledonian crows' proficiency in using and crafting stick tools is mainly due to their extreme binocular vision and an unusually straight bill that other corvid species do not possess. These adaptations allow an accurate visual guidance and a secure grip during stick tool deployment (Troscianko et al. 2012). The results of the present experiment underline the suggestion of Troscianko et al. (2012) that despite their high cognitive abilities corvid species which do not have these morphological features cannot be as proficient in stick tool use as New Caledonian crows.

Another factor that might play an important role for the successful insertion of sticks into narrow holes is tool orientation. It could be observed that all test subjects held the sticks almost perpendicular to the bill axis, whereas New Caledonian crows commonly have a straight or just slightly angled grip when inserting sticks into small holes (cf. Troscianko et al. 2012).

After not being successful with the sticks, two crows switched to using stones from the aviary ground to collapse the platform. The setting of the test compartments did not allow testing the birds fully avoiding the presence of stones. However, if the use of stones in the Stick Transfer Task could have been prevented, these birds may have continued using the sticks and might eventually have solved the task. Still, it is remarkable that the birds actively transported new stone tools to the box. However, other than rooks in Bird & Emery (2009) the subjects also selected inappropriate, i.e. too large or too light tools. Also, in one anecdotal incidence in the Stick Transfer Test, one crow, Corbie, manipulated a piece of bark and divided it into two parts. One of these parts was functional and could be inserted into the tube, whereas the other one was too large to be inserted. Before collapsing the platform with the functional part, Corbie first attempted to insert the non-functional tool into the tube. In addition, some birds threw sand into the tube when they were not successful with any other tool. Therefore it remains unlikely that subjects have a concept of the functional properties a tool must have to be suitable for the task. However, it could also be possible that their knowledge about the suitability of particular objects as tools was overridden by a strong desire to perform an action or motor pattern that had been rewarded before.

4.4. Training and Motivation

It was surprising that the overall training performance of the ravens was so poor and that none of the ravens was successful in the first training stage. It was assumed that directly pushing down the platform with the beak may be less demanding than actively combining a tool with the apparatus. Similarly, it was expected that pulling the platform down with a string would be a task that could be accomplished easily because ravens have already been shown to master vertical string-pulling tasks (Heinrich 1995; Heinrich 2000). Further, the close evolutionary relationship between crows and ravens makes it unlikely that their abilities to solve the tasks are that divergent.

Therefore, it is likely that the ravens' poor overall performance in the training is the result of reasons unrelated to their technical problem solving skills. For example, the ravens might have been less motivated or more neophobic than the crows, which is reflected by the low mean percentage of unsuccessful trials in which the respective appropriate objects were touched at least once in the early stages of the experiment. As the ravens were not as manipulative as the crows, they had fewer opportunities to accidentally collapse the platform during undirected manipulations of the apparatus. Therefore, they also had fewer chances to learn about the box's mechanism. Consequently, their failure in the training cannot be taken as evidence that the ravens do not have the cognitive capacities for solving these tasks, but rather as an indication for the subjects' neophobia or lack of motivation.

In the second training stage, the motivation of the ravens to peck the box or touch the appropriate objects changed only marginally. However, in Stone Use Test 2, the ravens touched the tools and pecked on the box more than in earlier stages, which further indicates that they were only gradually loosing their neophobia towards the apparatus.

It is yet unclear why one raven that solved just a few trials in the first training stage succeeded in the stone dropping task in Stone Use Test 1. This particular raven did not have more pre-experience than any of the other ravens. A possible explanation could be that this raven overcame its neophobia, started manipulating the box and then began dropping stones. This would indicate that this raven was also able to spontaneously use stone tools without any experience from the training.

Another control that would shed light on the effects of the training, but was not possible due to the limited number of birds available, would be to add another group of birds that after the Spontaneous Stone Use Test immediately proceeds to Stone Use Test 1 without any further training.

4.5. Further Strategies of Ravens and Crows

In addition to the overall motivational differences between the ravens and the crows, the present experiment hints towards the fact that the ravens might rather have tried to use force to solve the tasks instead of applying the tools. This becomes evident in the Stick Transfer Test, in which some of the birds collapsed the platform by strongly pecking the box. The one raven that did so succeeded with this strategy for 45 times, whereas the three crows that did so, succeeded less often, probably because their pecks had less force than those of the ravens. The one crow that finally reached the criterion in the Stick Transfer Test never collapsed the platform through pecking on the box, which could be the reason why it might have focussed on using the stick tools. Additionally, in the Stick Transfer Test the ravens directed more pecks per trial towards the box than the crows, whereas the mean number of attempts per trial was almost the same for both species. It can therefore be suggested that the ravens, which have greater physical strength than the crows, might have preferred solving physical tasks with force, whereas the crows might rather have solved the same tasks with innovative behaviours such as tool use. However, if the platform had been fixed in a way that the ravens could not have pecked it down, their behaviour might have switched to using tools more frequently.

4.6. Comparison of tool use in various species

The study showed that ravens and crows can use both stone and stick tools and therefore adds to evidence that also species that do not habitually use tools in the wild have the cognitive capacities to do so in experimental settings. Similar tool use abilities for supposedly non tool using species have been reported for example for kea (Auersperg et al. 2011), rooks (Bird & Emery 2009; Tebbich et al. 2007), cotton top tamarins (Santos et al. 2006), vervet monkeys (Santos et al. 2006), lemurs (Santos et al. 2005) and marmosets (Spaulding & Hauser 2005). However, there is a great variation in the species' performances, and methods and tools having been used in these studies differ considerably.
Although there is a growing body of work addressing tool use and causal understanding in species that do not use tools in the wild, to date major parts of the literature still focus on tool use and causal understanding in species that also employ tools in the wild (e.g. Santos et al. 2006). These are primarily three ape species (chimpanzees, bonobos and orang-utans), capuchin monkeys and New Caledonian crows (e.g. Bluff et al. 2007; Ottoni & Izar 2008; Seed & Byrne 2010; Visalberghi et al. 1995). These species use a variety of tools in a number of different situations and are to a certain extent also capable of manufacturing tools (Seed & Byrne 2010). Still, experiments on for example chimpanzees and capuchins suggest that despite their natural propensities to use tools in the wild and in captivity, their understanding of tools seems to be limited to features that are perceptually salient in contrast to hidden causal-functional properties (e.g. Emery & Clayton 2009; Santos et al. 2006; Visalberghi & Tomasello 1998; see Povinelli 2000 for a review). Also for New Caledonian Crows there is no clear evidence that they understand physical causalities (Bluff et al. 2007; Taylor et al. 2014; but see: von Bayern et al. 2009).

To shed light on ravens' and crows' physical cognition in a broader context, there is the need to interpret their tool use behaviour in relation to other species' skills. However, for a solid comparison of the performances of ravens and crows with those of other species, a comparative study that investigates causal understanding in several species, including tool users and non tool users, would be needed. To pinpoint the cognitive capacities and limits of these species, such a study would need an identical setup for all species investigated. One exemplary study comparing tool users and non tool users on the same task has been conducted with kea that are highly manipulative and neophilic, but do not use tools in the wild, and New Caledonian crows that readily use and manufacture tools (Auersperg et al. 2011). In this study, the subjects could obtain food from a transparent box with four different techniques, two of which involved the use of tools and two of which did not. After a certain technique had been applied successfully, this task was blocked and subjects could switch to another technique. Subsequently, the birds' choices of techniques and their performances were compared. Testing ravens and crows with an identical setup could help to explain their tool use abilities in a broader phylogenetic context. This study could also be extended to both tool using and non tool using apes and monkeys to compare technical problem solving skills between different taxa.

4.7. Conclusion

To conclude, the results indicate that both ravens and crows are able to spontaneously use stone tools. This throws a new light on technical problem solving abilities and tool use capacities of bird species that do not use tools in the wild. Also, the fact that different kinds of experience with the properties of the box increased performance, supports the assumption that the birds have at least some folk physical apprehension of the functional mechanisms underlying this task, to which degree is however yet unclear. Additionally, a transfer between different tools could be made. Furthermore, the study shows that ravens seem to behave more neophobic towards the apparatus than the crows and that they rather try to solve technical problems with physical force than with tools.
Overall, the results indicate that also birds that do not use tools in the wild have the cognitive capacities to apply tools in experimental settings and are to some degree able to approximate an understanding of the causalities behind the tasks. This hints towards the assumption that tool use abilities might be the result of domain-general rather than domain-specific cognitive capacities.

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List of Figures and Tables

Appendix

Table A1: Mean percentages of unsuccessful trials in which at least one peck was directed against the box ("Pecks") and mean percentages of unsuccessful trials in which a provided stone, the string, the platform or a stick (according to the respective condition) was touched at least once ("Touches"). Only subjects that have done at least one trial in the respective condition (= Sample Size) were considered for calculating the mean percentages and standard errors. R = ravens, C = crows.

		Pecks		Touches		
	Species	**Mean Percentage [%]**	**Standard Error [%]**	**Mean Percentage [%]**	**Standard Error [%]**	**Sample Size**
Spontaneous Stone Use Test	**R**	16.11	6.17	14.11	3.99	10
	C	59.58	10.81	71.67	9.02	8
Training 1 'Pull String' Group	**R**	10.00	0.00	2.00	2.00	5
	C	14.29	14.29	29.29	0.71	2
Training 1 'Push Platform' Group	**R**	22.22	15.71	2.78	2.78	4
	C	66.67	-	66.67	-	1
Stone Use Test 1	**R**	36.67	7.99	43.33	3.33	9
	C	36.67	21.86	53.33	17.64	3
Training 2 'Pull String' Group	**R**	10.00	10.00	0.00	0.00	4
Training 2 'Push Platform' Group	**R**	5.00	5.00	0.00	0.00	4
Stone Use Test 2	**R**	50.00	18.90	75.00	16.37	8
Stick Transfer Test	**R**	90.00	10.00	100.00	0.00	2
	C	43.89	9.75	91.67	5.27	6
Stick Control Test	**R**	66.67	21.08	66.67	21.08	6
	C	0.00	-	0.00	-	1
Stone Use Retest	**R**	-	-	-	-	0
	C	-	-	-	-	0

Curriculum Vitae

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