universität wien

DISSERTATION

Titel der Dissertation

Do Kea (*Nestor notabilis*) consider spatial relationships between objects?

Physical cognition in a highly neophilic New Zealand

angestrebter akademischer Grad

Doktor/in der Naturwissenschaften (Dr. rer.nat.)

Verfasserin / Verfasser:	Alice Marie Isabel Auersperg
Dissertationsgebiet (lt. Studienblatt):	A 091 439 Doktorat Zoologie
Betreuerin / Betreuer:	Univ.-Prof. Dr. Ludwig Huber

Wien, im November 2010

Acknowledgements

I foremost want to thank the key figures that made this work at all possible: All the kea that ungrudgingly cooperated and participated as subjects in the following experiments: Hope, Coco, Tammy, Becky, Gino, Capu, Willy, Lilly, Sunny, Rudy, Anu, Plume, Mismo, Kermit, Roku, Bruce, Knut, Luke, Frowin, Zappel, John, Kima, Elvira, Rosie, Berliner, Sepperl and Aurora (Special credit to the kea Linus for volunteering to provide me a personal Punchinello).

I am also grateful to Gyula Gajdon, firstly for his excellent coaching and schooling throughout this thesis and secondly for boosting the kea lab into a new level of scientific organization and animal care taking.

My supervisor, Ludwig Huber for numerous inspiring conversations and many comments on the experimental drafts presented in this thesis.

The WAF for financing my studies, as well the FWF for financing the kea lab during the course of this work.

My family, particularly my parents, brothers and sister as well as my parents in law for supporting my passion for animal behaviour and tolerating many most peculiar pets.

My uncle Franzi for his interest and his support of my work.

My sister Auguste and Alex Kacelnik for their cooperation in a comparative approach of problem solving in the kea and New Caledonian crows.

Irenäus Eibl Eibesfeldt, whose works have encouraged my interests in Zoology.

The members of the Kea Lab for their cooperation and team spirit, in particular our two fantastic care takers Siegrid and Tanja, who make sure that we have well kept, fully enriched and happy subjects to work with every day.

All members of the Department of Cognitive Biology in Vienna who have commented on previous versions of the manuscripts presented in this thesis.

The Konrad Lorenz Institute for Ethology in Vienna and Dustin Penn for hosting our experimental subjects while this study was conduced

The Tiergarten Schönbrunn in Vienna, who have kindly provided the kea Mismo, Elvira, Rosie, Berliner and Aurora.

Last but not least, my husband Lukas who encouraged and supported my interests with endless patience throughout this thesis and who is also responsible for constructing most of the apparatuses presented.

If naturalists go to heaven [about which there is considerable ecclesiastical doubt], I hope that it will be furnished with a troop of kakapo to amuse me in the evening instead of a television."

Gerald Durrell

For my Family (and other animals)

Do Kea (*Nestor notabilis*) consider spatial relationships between objects?

Physical cognition in a highly neophilic New Zealand parrot

Alice Marie Isabel Auersperg

DEPARTMENT OF COGNITIVE BIOLOGY

UNIVERSITÄT WIEN

Author Contributions

Chapter 1. Alice Auersperg

Chapter 2. I designed this study with input from both of my co-authors (Gyula Gajdon and Ludwig Huber) I collected and analyzed the data and wrote a first draft of the paper. Both co-authors were involved in editing and revising the paper.

Chapter 3.

I designed this study with input from both of my co-authors (Gyula Gajdon and Ludwig Huber) I collected and analyzed the data and wrote a first draft of the paper. The co-authors were involved in editing and revising the paper.

Chapter 4.

Two coauthors (A. von Bayern, G. Gajdon) and I designed this study together with equal contribution from each party. I collected and analyzed the data and wrote the first draft of the paper. All authors (Auguste von Bayern, Gyula Gajdon, Alex Kacelnik, Ludwig Huber and myself) were heavily involved in editing and revising the paper.

Chapters 5.

I designed this study with input from both co-authors (Gyula Gajdon and Ludwig Huber) I collected and analyzed the data and wrote the first draft of the paper. All co-authors were involved in editing and revising the paper.

Chapter 6.

Alice Auersperg

Summary

The Technical Intelligence Hypothesis (TIH) helps to explain the evolution of intelligent behaviour in some animals. Complex environmental circumstances as well as unusual niches may cultivate adaptive flexibility as well as an increased innovation rate in the species concerned and may consequently advance investment in higher cognitive abilities. Currently there are a great number of studies investigating how animals perceive their physical environment, whether they can accumulate knowledge about it through experience and observation and whether they can use this knowledge in a goal directed manner.

The kea is a New Zealand mountain parrot, which is exposed to harsh climate conditions and seasonally restricted food resources, but also a lack of predation in its favor. Due to these circumstances, the birds have developed very strong neophilia towards novel objects, which are often manipulated extensively. The kea herewith depicts an adequate avian model for testing the TIH.

The experiments that result from this thesis mainly concentrate on the kea's perception of the spatial relationships of objects within its environment and how it can make use of them to its advantage. Chapter two is concerned with the Gestalt perception between a desired, out of reach item and the appearance of the support that object is resting upon. Chapter three, four and five examine inter alia one of the most complex object relationships in the animal world: The use of objects as tools. We can show that the kea, which is not a natural (or genetical) tool user, is able to produce behaviour in the laboratory that fulfills the requirements of tool use. The kea proved to be competent, not only in inserting compact tools into tubes in order to knock a food reward out of place, but also in learning to use stick-like tools as a functional extension of their beaks. It is however still unclear as to what extent the animals have a causal understanding of the problems concerned or whether most of their actions result from rapid learning in combination with complex motor control over their body movements. The implications of this study as well as future directions will be discussed in the concluding chapter (chapter six).

Zusammenfassung

Die Technische Intelligenz Hypothese (TIH) hilft die Evolution von fortgeschrittenen geistigen Fähigkeiten in einigen Tierarten zu erklären. Eine komplexe Umwelt, sowie eine ungewöhnliche Nischenbetzetung kann eine hohe Annpassungs/Innovationsrate erfordern, was unter den passenden Umständen intelligenzfördernd wirken kann. Es gibt daher inzwischen zahlreiche Untersuchungen die sich damit beschäftgen wie bestimmte Tiere ihre physische Umwelt wahrnehmen, ob sie sich durch Erfahrungen und Beobachtungen diesbezüglich Wissen aneigenen können und ob sie dieses schliesslich zielgerichtet einsetzten können. Der Kea ist ein Neuseeländischer Bergpapagei, der harten Klimabedingungen sowie einem seasonal begrenzten Resourcenangebot aber dafür auch einem Mangel an nartürlichen Raubfeinden ausgesetzt ist. Aufgrund dieser Umstände entwickelte sich eine stark ausgebildete Neophilie gegenüber unbekannten Gegenständen, welche von den Tieren oft lange Zeit manipulativ untersucht werden. Der Kea stellt hiermit eine passende Model Spezies aus der Vogelwelt zur Untersuchung der TIH dar. Die Experimente, welcher aus dieser Arbeit resultieren, konzentrieren sich hauptsächlich darauf, wie der Kea räumliche Beziehungen zwischen Gegenständen in seiner Umgebung wahrnimmt und diese zu seinem Vorteil nutzen kann. In Kapitel zwei geht es um die Gestalt Wahrnehmung zwischen einem begehrtem Objekt und der Beschaffenheit des Untergrundes auf dem sich dieses Objekt befindet. Kapitel drei bis fünf beschäftigen sich unter anderem mit einer der kompliziertesten und sowie am häufigsten diskutierten Objektbeziehung, welche von Tieren erstellt werden kann: der Gebrauch von Gegenständen als Werkzeug. Wir können zeigen, dass der Kea, welcher kein nartürlicher (oder genetischer) Wekzeuggebraucher ist in der Lage ist im Labor Objektrelationen zu erzeugen welche die Bedingungen von Werkzeuggebrauch erfüllen. Die Tiere zeigten sich in der Lage nicht nur kompakte Objekte in Öffungen zu stecken um ein feststeckendes Futter zu befreien, sondern auch stockartige Werkzeuge als funktionale Verlängerung eines Körperteils zu verwenden. Es ist jedoch noch weitgehend unklar inwiefern ein kausales Verständnis über die physikalischen Hintergünde der Aufgabe vorhanden ist oder ob die Handlungen auf schnellem Assoziationlernen sowie komplexer Körperkontrolle basieren. Die Implikationen dieser Studien und künftige Forschungsansätze werden im abschliessenden Kapitel sechs diskutiert.

Table of Contents

Chapter 1 Introduction

1.1 Introduction

Over the last century modern society has becoming increasingly open towards the possibility of complex mental processing in non-human animals. A rising number of of animal traits, previously believed to be solely human (such as tool use, theory of mind, mental time travel, parts of language understanding ectera.; for example in: Bugnyar & Heinrich, 2005; Clayton et al., 2005; Goodall, 1964; Pepperberg, 1999) are feeding our interest in what is going on within an animal's mind and what evolutionary processes are responsible for such apparently intelligent behaviours. The discoveries of such abilities not only satisfys scientific and common interests but can also help meliorate animals' legal keeping conditions and conservational statuses or they may simply cultivate appreciation and facilitate cohabitation.

The kea (*Nestor notabilis*) is a legally protected, generalist New Zealand parrot, which constantly explores its physical environment, progressively broadening its foraging repetoire (Diamond & Bond, 1999). For its lack of neophobia as well as its restless appetite for destroying novel items, this mountain parrot is loved as much as it can sometimes be bothersome to the humans sharing its habitat. The curiosity as well as the dexterity with which it haptically explores conspicuous object properties for functional affordances reminds of human children as well as juvenile primates collecting physical expertise (Gajdon et al. submitted). The current leader of the Vienna kea lab sometimes jokingly referred to the kea being a result of tossing a chicken and a capuchin monkey together into a magic hat. In recent years several studies exposed some of the kea's competences in the physical domain such as an appreciation of physical connectedness, affordance learning and even the use of compact objects as tools (Gajdon et al., submitted; Huber et al., 2001; Werdenich & Huber, 2006). This thesis concentrates on the kea's perception of spatial relationships between objects and will in this context also pick up on investigating the newly found tool use abilities into further detail.

I will use the following introductionary part of this thesis to explain some of the basic principles of physical cognition research as well as present some of the most important studies on physical problem solving in birds. I will thereafter explain details about the kea's ecology as well as a summary of previous kea studies, some of which are relevant to the experimental part of this thesis. Finally I will outline the structure as well as the main aims of my work.

1.2 Physical Cognition

1.2.1 The Technical Intelligence Hypothesis

It can be very hard to unmask the selection pressures responsible for intelligent behaviour since cognitive mechanisms may evolve convergently in different species and may therefore be qualitatively as well as quantitatively different. On a more general basis we could say that high level cognitive processing must evolve in response to cumulated incidences of complexities or novelties.

One of the most challenging situations in terms of complexity seems to be life in a social setting. In order to survive in a large group it may be necessary to learn the idiosyncrasies, the affiliations as well as the rank of other group mates in order to be able to attract, avoid, deceive or manipulate them and consequently gain access to desired resources and mating opportunities (Byrne & Whiten, 1988; Emery et al., 2007; Humphrey ,1976; Jolley, 1966; Whiten & Byrne, 1997).

The British psychologist Nicolas Humphrey (1976) wrote an essay on the evolution of intelligence after spending time in the Virunga mountains with Diane Fossey's gorillas. He argues that technical problems could never be approached through creative or truly innovative thinking. In his opinion they are always a product of simple trial and error learning or imitation of others and that even the most advanced technologies are rather a product of acquired knowledge than imaginative reasoning. He postulated that wild gorillas, for example, which are assumed to be intellectually competent, lead a very simple existence in terms of physical inventions. The complex structure of ape (and human) societies rather then technical competence must be responsible for innovative thinking and a creative intellect. In 1988 Richard Byrne and Andrew Whiten formulated the Social/Machiavellian Intelligence Hypothesis (MIH) which represents the assumption that the driving force behind the evolution of intelligence are foremost the complexities that come with social life rather then other ecological factors.

The Social Intelligence Hypothesis so far does a fantastic job explaining intelligent behavior in many large brained species such as most primates and some birds (Emery, 2004). It is however not always applicable as it fails to explain for example the differences in relative brain size and behavioral complexity between the great apes and remaining monkey clade, which do not live in larger or more complicated social goups (Byrne, 1997). In order to explain this grade shift Richard Byrne (1997) postulated a Technical Intelligence Hypothesis. Firstly their comparably greater body weight requires coordinated motor actions during climbing, thus apes need to be able to simulate their body movement in their mind. He argues that this implies perceiving the own body as an independent

entity. Secondly apes not only heavier than monkeys but also rely mostly on ripe fruit. In order to survive against feeding competitors such as monkeys the apes need to develop a mental representation (cognitive maps) of food locations in an environment that is constantly changing within space and time. Thirdly, all apes build complex beds, which require specific construction skills. A combination of these circumstances may have led to additional representational abilities in the physical domain (Byrne, 1997).

Animal technology, the competency to learn about, use and/or understand the physical principles behind natural object relationships as means to achieve a certain goal is henceforth currently also considered an important source feeding the evolution of intelligent behavior. Environmental complexities such as unusual niches, a seasonality of food availability or extravagant food sources may drive a species to acquire a broad spectrum of foraging techniques that they can flexibly resort to (Shettlewoth, 1998). Such circumstances may also increase the need for physical innovations in order to cope with novelties supposedly by means of reasoning abilities (Bond et al., 2007; Jones, 2005; Shettleworth, 1998; Sol et al., 2002; Tomasello & Call, 1997; Webster & Lefebvre, 2001).

1.2.2 Folk Physics

Presently there are two approaches to investigate physical cognition in animals in the laboratory (Weir, 2005). Firstly the Piagetian approach (Piaget, 1952): this approach investigates the question *whether* an animal is capable of intelligent behaviour (Weir, 2005). Such tasks mostly target the level of final performance a subject can achieve. This approach can be problematic, for example when comparing different species. From paradigms with yes/no solutions we cannot conclude about two species' intellectual differences since there are too many alternative explanations for success or failure that can not be controlled (for example differences in perception, motivation, attention, ecetera).

The second approach is the 'folk physical approach' used by Povinelli (2000) in his studies on chimpanzees and human infants. This approach focuses on the mechanisms that control an animal's behaviour, raising the question of *how* animals approach a problem (Weir, 2005). In order to investigate the underlying processes of innovative problem solving we need to focus on how a subject explores a novel apparatus and what previous experiences it can apply in order evaluate the necessary actions to finally come up with a solution. An understanding of the physical world exists in two forms: the scientific form (of theoretical physics) and the non-scientific form (the physics of ordinary man or 'Folk physics'), which is far more important from a biological point of view since is determines our behavior in many respects (Köhler, 1925). Folk physics is asking *how*

the world works as opposed to scientific physic, which questions *why* it works (Povinelli 2004). This "common sense understanding of how the world works" is likely to predicit environmental responses that occur on a daily basis (Povinelli 2004).

1.2.3 The 'Insight Problem' in Physical Cognition

Most studies in physical cognition research on animals target insightful understanding of technical problems. At present, the most commonly cited definition of insight was proposed by Thorpe (1964) as " the sudden production of a new adaptive response not arrived at by trial and error behaviour or as the solution of a problem by the sudden adaptive reorganization of experience". Performance within the frame of this definition may therefore not be explainable by lower processes such as associative/ trial and error learning.

It is however hugely problematic to control for or to exclude all arbitrary cues or previous experiences within a laboratory setting. There is hardly any experiment to date that can verify insight in animals beyond any doubt. The best way to prove insight would be if a subject responded with the correct solution without any prior ineffective actions to a completely new setup. Such spontaneous performance is however very rare and seldom reflects the true course of events by which understanding is accomplished (Weir, 2005).

In many cases animals are given some controlled experiences, which they thereafter have to transfer into a novel context. Such approaches can also be problematic since they may firstly involve some form of 'shaping'. Shaping is a process by which a complex behaviour is produced as a result of successive behaviours, which are increasingly similar to the target behaviour (Peterson, 2004). This does not exclude insight but after the mental process required to achieve the final behaviour may have been facilitated and may be strongly deviant from a natural situation, it has often become quite elusive. A second problem is that the successful performance may be a product of 'chaining' (the joining of previous acquired behavioural sequences that derive from associative learning; Epstein et al., 1984). Due to a lack of clear definitional outlines, it will also remain a matter of debate when a tranfer response becomes insightful or when it can still be explained by chaining or is reinforced by excessive shaping (Lindt et al., 2009).

Apparently insightful behaviour can often not be confirmed because in contrary to human subjects, we cannot ask an animal what exactly it learned and which experience it used in order to solve the problem (Weir, 2005). Some transfer tests are gradually

changing several properties of the task in order to unfold which properties (functionally relevant versus irrelevant) the animals attend to when solving the problem (for example Hauser et al., 1999; Taylor et al., 2009). Although such tasks are probably a good way of detecting properties used to solve the problem in absence of verbal communication, the subjects may still attend to the functionally relevant features as arbitrary cues even in the absence of understanding (Weir, 2005).

Beside the hardship caused by attempting to prove insightful behaviour, it is often neglected that 'insight' itself is an umbrella term with blurry borders. Once behaviours are observed that seemingly fit Thorpe's (1964) definition, studies often neither investigate what exact aspects of a problem the subjects have grasped nor where this understanding originated from in further detail. Ironically the mere discovery of so-called insightful behaviour, if we are unable to trace back its roots, brings little insight to us. In order for us to progressively understand cognitive processing in animals we need to focus much more on carefully unpeeling the factors influencing as well as the mechanisms underlying problem solving abilities and physical cognition (von Bayern et al., 2009) rather than targeting intelligent behaviour in a more general consensus.

1.3 Avian Problem Solving

1.3.1. Introduction

Investigating cognitive mechanisms in animals is a relatively young field of research and being its subjects was for a long time monopolized by primates especially by the great apes. Certain brain regions in birds are used in a similar way as in mammals. The avian High vocal centre and Neostriatum caudolaterale have been found to work in a manner similar to that of the mammalian neocortex (Jarvis et al., 2005). Despite the long divergent evolutionary history of birds and mammals, early avian and primate cognitive development have many convergent features (Emery & Clayton, 2004; Ivaniuk, 2005). Only in the course of the last thirty years has the focus of interest in complex cognition gradually expanded from apes to their feathered counterparts as well. Two avian families are particularly promising model candidates for avian cognition: corvids and psittacines. Their relative forebrain-hindbrain ratios are the largest so far measured in birds (Emery & Clayton; 2004; Emery 2006).

Studies on corvids and parrots are responsible for some of the most surprising discoveries in animal cognition research to date. For example some of the best evidence of

social intelligence and theory of mind derived from studies on food caching corvids. Common ravens as well as some Jays seem to be capable of forming transitive inferences of the thoughts and intentions of other conspecfics. (Bugnyar & Heinrich, 2005; Bugnyar & Kotrschal, 2002; Clayton et al., 2005; Emery & Clayton, 2001; Emery et al., 2004; Paz-y-Mino et al., 2004, Weir, 2005).

Birds also deliver some convincing examples of episodic-like memory: Western scrubjays are capable of traveling mentally into the future. They discriminate in their preference to recover food caches containing perishable but valuable food items towards less valuable but unperishable food items depending on the time that has passed since the items have been cached (Clayton & Dickinson, 1998; Griffith et al., 1999). Similarly, humming birds can remember which feeders have been visited when and can adjust their visits to the frequencies (10 or 20 minutes) that those feeders are refilled (Henderson et al., 2006).

Studies on language and communication on animals have been revolutionized by one bird in particular. Irene Pepperberg's 30 year long A(nimal) L(earning) EX(periment), during which the African Gray Parrot "Alex" was taught certain aspects of the English language entailed many exciting results (Pepperberg, 1999). Alex acquired a vocabulary of about 150 words and learned to label 50 different objects. He was able to answer questions about different properties of the same objects (shape, color, matter) and could count up to seven. He could also answer different questions about categorical groups of objects (for example, on a platter with green and red balls as well as green and red cubes, he could count up not only all balls and not only all green objects but also just the green balls). He also had basic concepts of size (bigger and smaller) as well as which properties of two objects were same and different (same color, different shape).

Many intriguing findings have been made in physical cognition from studies on avian problem solving. Birds have proved competent in many physical problems such as Piagetian object permanence, form and Gestalt perception, means-end relationships, causal reasoning or tool use and manufacture (Bird & Emery, 2009; Funk, 2002; Pepperberg et al., 1997; Salviczek et al., 2009; Seed et al., 2007; Weir et al., 2002). In the following parts of this chapter, I will attempt to summarize some of the most important findings of the last couple of years.

1.3.2 Means to an end: the vertical string-pulling paradigm

A commonly used tool for testing means-end comprehension in birds is the vertical string pulling paradigm, as it requires complex motor control over concerted actions of different body parts (Heinrich, 1995). In this task the subject is pulling a string up a perch in multiple and repeated foot and beak actions: the bird pulls a piece of string up with its beak, steps on a loop and pulls the remaining string again until it reaches a food reward attached to the end. Simple versions of the string pulling paradigm were initially used to test different species of finches as well as canaries. Vince (1958) found that juveniles generally performed better then adult individuals of these species. More complex versions in which subjects had to generalize their string pulling skills to novel situations have been successfully accomplished by some corvids and psitttacines: common ravens not only succeeded in pulling a string up a perch but the same animals were in succession to this also successful in pulling a string downwards toward them in another setup, while other birds, without pre-experience failed to do so (Bugnyar & Heinrich, 2005).

Schmuck-Paim et al. (2009) tested several Neotropical parrots and found that two species of macaws remained successful even when the spatial relationship between the strings, the presence of a reward or the physical contact between the string and reward was varied.

It is however still unclear whether the animals understand the physical connection of the reward to the string or whether their pulling actions are simply reinforced by the 'mental reward' of the food moving closer. Taylor et al. (2010) devised an experimental setup which included visually restrictions to the string pulling paradigm (see Figure 1). They found that experienced New Caldonian crows reduced their performance and increased their errors but their success recovered when a mirror was added to provide visual feedback. These findings suggest that string pulling in this species may not be based on insight but on operant conditioning mediated by a perceptual-motor feedback cycle.

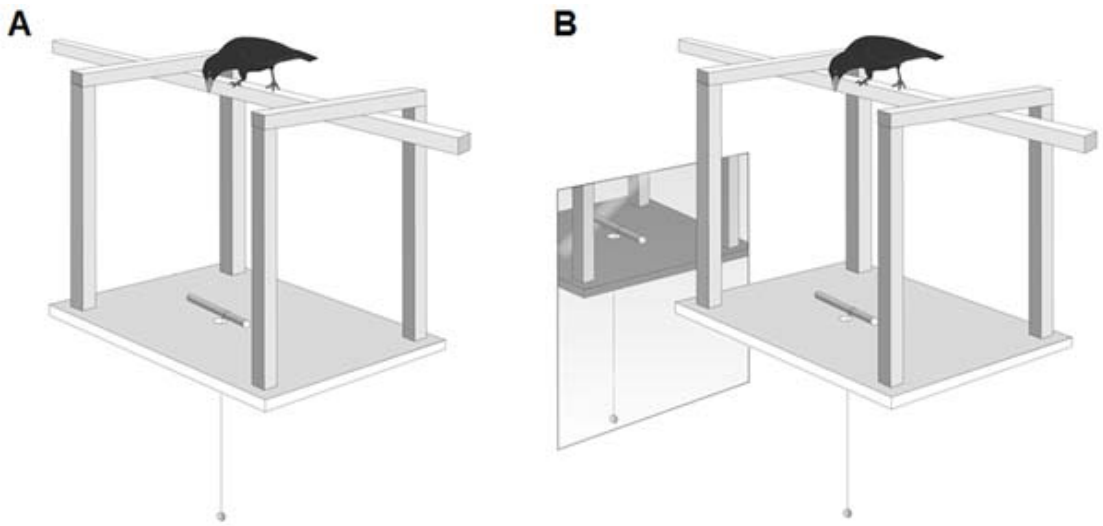


Figure 1.(A) The visually-restricted apparatus (B) a mirror provides visual feedback during pulling by Taylor et al. 2007 in PLOS ONE

3.1.3 Causal reasoning – The trap tube paradigm

One of the most important tools used for physical problem solving is an understanding of causality (one event, the effect happens consequential to another, the cause). Huber & Gajdon (2006) suggest that a fully developed human capacity for causal reasoning may be identified in terms of the construction of representations of event sequences in which one event is understood to bring about another event, and that these event sequences can be predicted and/or controlled.

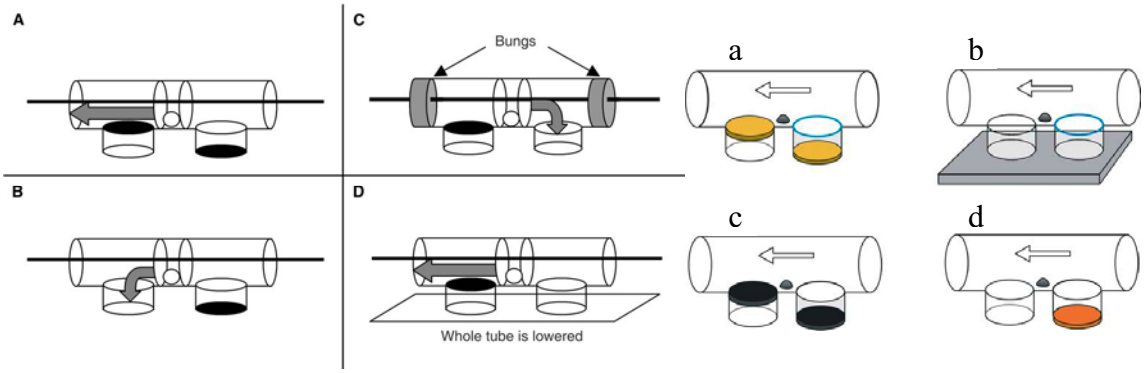
The laboratory test most frequently used to test an understanding of causality in the physical domain is the trap tube paradigm. The task was designed by Limongelli & Visalberghi (1994), who tested whether captive capuchin monkeys could push a food item trough a horizontal Plexiglas tube with a stick, avoiding a trap (a small container) on the tube floor. After 140 trials, one of four individuals performed above chance level. Further investigations in which the trap was inverted (and therefore non-functional) however, demonstrated that it had merely learned a rule: insert the stick into the opening farthest from the reward. One year later Limongelli et al. (1995) tested adult chimpanzees with a similar setup. Two of five individuals learned to work the apparatus. To further investigate whether the animals were using a distance-based associative rule, they conducted further testing using a second tube where the trap was closer to one end. The reward was placed next to the trap (and was therefore displaced from the centre of the tube). If the stick was now inserted at the end farthest away from the reward, the food would end up inside the trap. After 60 trials, both subjects performed high above chance level. They did however not use the critical inverted trap condition as used in the original experiment. Povinelli &

Reaux (2000) criticised the former since they could indeed exclude a procedural rule to insert the tool into the opening farthest from the reward but not an associative rule to always push the reward away from the general direction of the trap, even when it was inverted. Only one individual (the female Megan) succeeded in learning the standard problem (the chimps were younger than the ones used by Limongelli et al., 1995). In the inverted trap condition Megan behaved as if the trap was still able to affect the reward by consistently pushing the food away from the trap. Mulcahy & Call (2006) argued that pushing food away from the body is difficult for chimpanzees and being required to do so may intervene with their performance. They presented three ape species on a modified trap tube task that allowed subjects to push or rake the reward towards them with the tool. They found that all but one of the subjects preferred to rake the food towards themselves. Three subjects avoided the trap only when it was not inverted. The authors conclude that apes showed some causal knowledge about the task once they were allowed to use their preferred tool actions. Other studies by the same research group, in which subjects were given more opportunities to use their preferred behavioural strategies (push versus rake; trap tube versus trap platform; with or without tool use) further emphasize the necessity to offer tasks that that are carefully adapted to the species specific characteristics (Martin-Odas et al., 2008; Martin-Odas et al., 2009; Seed et al., 2009).

Surprisingly, the first avian candidate tested on this task was neither a parrot nor a corvid. Tebbich & Bshary (2004) tested the Galapagos woodpecker finch, which uses cactus spines and small twigs to probe for grubs in the bark of trees. One out of six subjects was successful in avoiding the trap, but only after the previously transparent tube was exchanged with an opaque one maximizing the contrast between the tube and the trap. This subject was also consistently raking the reward towards herself instead of pushing it away. Interestingly, and contrary to the capuchin monkey (Limongelli & Visahlberghi, 1994), the performance of the same subject switched back to random once the trap was inverted. The authors still suggest that the animal lacked a mental representation of the physics involved but rather observed the effect of multiple tool manipulations on the reward: the bird often switched tube sides and inserted the tool at both openings before actively pushing the reward into a direction.

More studies testing for a mental representation of the causal properties of the trap tube task in birds derive from corvids. Seed et al. (2006) redesigned the trap tube task so it could be handled without a tool: the animals could acquire the reward by pulling a stick,

which was attached to two discs situated on each side of the reward (see Figure 2). They offered two traps, one functional, and one non-functional and the birds had to decide in which direction to pull. All birds learned to pull the food either over a non-functional trap that was closed at the top with a black disc (see Figure 2, condition A) or into a non-functional trap that had an open base (so the reward could fall out; see Figure 2, condition B) rather then into a functional trap, which had a black disc at the base. They were able to transfer from one condition to the other on their first trial. During the previous tests, the functional trap always had a black disc covering the base. Since the birds may simply have learned to always pull away from this feature the authors devised two further transfer tests featuring the two previously non-functional traps; the tube was however manipulated in such a way that these would now trap the food. Remarkably, one of the seven subjects immediately passed both of these conditions (see Figure 2, condition C and D) suggesting that his behavior cannot be explained by simple procedural rule learning. It is however still unclear which cognitive mechanisms underlie its performance. Tebbich et al. (2007) tested three rooks and found that all individuals failed two similar transfer tasks. They imply that the successful individual in Seed et al. (2006) may have abstracted a rule based on various observable features, such as surface continuity and the inability of objects to pass through barriers, without necessarily understanding the causal properties of the task



Experimental conditions of the trap tube problem by Seed et al. 2007 (left) in CURRENT BIOLOGY and by Taylor et al 2008. (right) respectively, in PROCEEDING OF THE ROYAL SOCIETY B

In 2008 Taylor et al. presented a similar setup to the tool using New Caledonian crows. Their apparatus was similar to the one in Seed et al. (2006) but stick tools were used instead of discs and they removed different features from several transfer tests in a stepwise manner in order to identify which features were used by the crows to avoid the trap. Three out of six crows learned to solve a task in which they had to pull the reward over a non-functional trap (with a disc on top; see Figure 2; condition a; right) while avoiding a functional trap (disc at the base) that was marked with a blue rim. The first transfer still featured the blue rim, but the discs were removed (b), the second transfer

included the two discs but not the blue rim (c), and the third transfer was similar to a condition in the rook study which included a functional trap as well as a non-functional trap without a trap base, through which the food could fall out. The three crows were successful in all transfer tests except for the third transfer during which they often moved the reward between the two holes without pulling it into either. The authors suggested a reluctance in the birds to pull the food into the holes. All three successful crows also spontaneously solved a trap table task, which is a visually distinct (color, material, shape) but causally similar problem. The authors thereafter conclude that the crows are aware of the causal relations in the problem. I do, however believe that the lack of performance in the third transfer renders it still possible that subjects learned a rule of thumb to avoid surface disruptions of any kind and seem to have a more limited causal representation of the path the food will follow as a response to their action than one of the rooks did.

1.3.4. Problem solving and avian tool use

New Caledonian Crows as well as rooks were also the main source of excitement in reference to avian tool use in the past years: New Caledonian crows (NCC) are likely to be the most proficient non-human tool users: they manufacture a surprisingly wide variety of stick like tools in different shapes from different materials in order to obtain wood boring beetle larvae from the bark of trees (Hunt, 1996). The animals break twigs off trees and remove redundant leaves to use them as probing tools. They also produce two types of hook tools, shaped twig hooks or pandanus leaf tools (Hunt, 1996). The Pandanus leaf is a thick, hard leaf type with small barbs at the edge from which the crows tear off long pieces (see Figure 3). The crows manufacture three different types of tools from Pandanus leaves: narrow, wide and step-cut tools. Step-cut tools are pointed by cutting up to five steps into the leaf gradually decreasing its width (Hunt & Gray, 2003). The thinner part is used as the working end and the leaf barbs are facing backwards during foraging. This way the target is not only pierced but also hooked onto the barbs (Hunt, 1996).

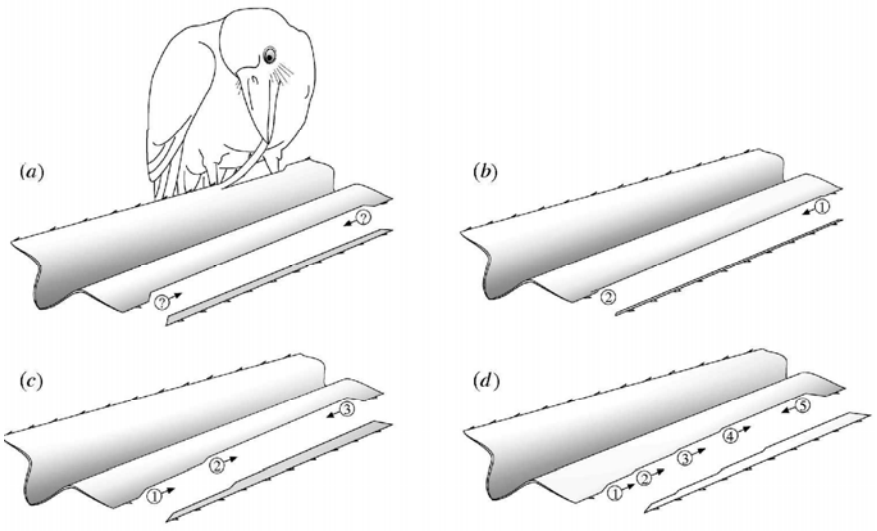


Figure 3.
Manufacture of Different types of Pandanus leaves
a) wide
b) narrow
c) 3 step
d) 5 step
by Hunt&Gray 2003 in PROC. ROYAL SOC. B.

The crows never hold the tool at the working end after manufacturing the tools themselves. They do not, however pay attention to the orientation of the barbs if a completed tool is offered to them on a table, but they instead flip the tool if it is not working properly. The animals seem to be using a procedural rule during tool making that allows the working end of the tool to always automatically end up in the appropriate orientation (Holzhaider et al., 2008). NCCs are genetical tool users but their tool using (and making) skills improve over the course of their lifes (Kenward et al., 2005). There is a social aspect to the development of tool related skills in juveniles and even evidence of cumulative technological evolution of tool use between different regions on the island of New Caledonia (Hunt & Gray, 2003; Kenward et al., 2006).

NCCs also demonstrated interesting innovative performances when tested in more unnatural settings in the laboratory. Famously, the captive female Betty was tested in an experimental setup in which she had to choose between a straight and a hook shaped wire to obtain a piece of meat within a bucket from a vertical pipe. After she failed to find the hook tool, she spontaneously stepped on the straight wire and used her beak to bend it into a hook shape (Weir et al., 2002).

Tool making, acting on the tool before using it, as in NCCs is rarely seen in animals. Taking it a step further would entail using a tool to act on an inedible object, for example using a tool on another tool (Wimpenny et al., 2009). Such so-called Meta-tool use has been investigated in NCCs by Taylor et al. (2007) as well as by Wimpenny et al. (2009). Taylor at al. (2007) confronted seven crows with an apparatus featuring a tool-box containing a food reward and at a small distance two other tool-boxes, one containing a long stick tool the other a small stone. A short stick tool (too short to reach the food reward but long enough to reach the long tool or the stone) was offered on the table. All seven NCCs learned to use the short tool to extract a longer tool with which the reward

could be obtained. Four of them successfully obtained the food on the first trial. The authors assume the observed behaviour to be a product of analogical reasoning. Wimpenny et al. (2009) were concerned that the behaviour may however also be underpinned by a range of different cognitive mechanisms, which have not yet been explicitly identified. It is for example possible that the crows recovered the longer stick (and not the stone) because sticks have become secondary reinforcers due to previous experience. In order to investigate the extent to which crows understand the physical interactions underlying their performance, they tested seven NCCs with multiple inaccessible tools, which differed in functionality dependant on the trial. If tools are extracted because they are secondary reinforcers, then they will be extracted independently of their functionality rather then selected according to the situation. They offered several conditions with varying difficulty, one requiring Tertiary tool use: using a short tool to retrieve a longer tool, which could then be used to retrieve a third tool which was finally long enough to reach the food reward.

Five out of seven subjects used the tool sequentially; four of them repeatedly mastered the tertiary condition. Although the animals did not use a random probing strategy, the authors still did not confirm finding sufficient evidence of analogical reasoning since simpler processes such as chaining may be sufficient to explain sequential tool use.

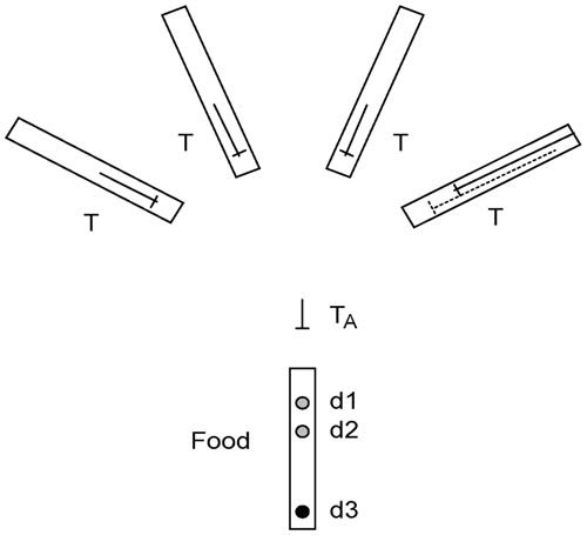


Figure 4
The food is located in the central tube and can be at any of three depths (d1, d2 or d3). Tools are located in four tool tubes. Three tool-tubes (T) contain 10 cm tools and one is 20 cm. They are not accessible by beak alone. There is a 6 cm tool on the tabletop, which is long enough to reach the 10 cm tools but not the 20 cm tool, which is shifted backwards in some trials. In order to reach d3 the subject has to use T_A to retrieve a 10 cm tool and hereafter use the 10 cm T to retrieve a 20 cm T, which can finally be used to retrieve the reward

In Wimpenny et al. 2009; in PLOS ONE

NCCs also successfully used compact objects as tools in a task that required dropping stones into vertical tubes in order to free a food reward on a collapsible platform inside the tube (von Bayern et al., 2009). The crows mastered the task after they had pre-experience trials in which they could collapse the platform by pressing it down with a

stick. The results indicate that the crows were able to master the task after learning about specific functional properties of the apparatus (collapsibility in response to tool contact).

Most astonishing flexibility in tools use was reported from a corvid, which is not a natural tool user in the wild, the rook. The flexibility with which this bird innovatively applied various tools in several different tasks in an experimental series by Bird & Emery (2009_2) surprised even the researchers themselves.

The subjects received a pre-training which taught them that a platform inside a vertical Plexiglas tube containing a reward was collapsible by accidentally nudging a stone into the tube (which was placed on rim of the tube) or by observing other rooks drop a stone into the opening. Four subjects thereafter picked up a stone from the base of the tube and dropped it into the opening. Offered a choice of several different stone sizes, they preferred the largest stones. When the diameter of the tube however, was reduced (see Figure 5, a) the animals switched to using small stones (three of four subjects in the first trial) indicating that they attended to tool size as a functionally relevant property. When the stones were not in sight, all subjects left the experimental compartment and went into the outdoors area, returning with the appropriate tool.

Confronted with a choice between a round stone and a long thin stone they all chose the latter regardless of tube size. To fit the long stone into the thin tube they rotated it into the appropriate orientation more often then when inserting it into the wide tube. The stones were thereafter removed to investigate whether the animals could transfer their knowledge to using a stick tool. When provided with a thick stick, the animals simply dropped it into the tube as previously. When provided with a thin stick, they kept holding the tool end and applied pressure to it until the platform collapsed. In a two choice test featuring the thin tube, the subjects could choose between either a long stick (+) and a large stone (-) or a short stick (-) and a small stone (+). The large stone was too big to fit into the opening and the short stick was to light to collapse the platform. All subjects chose the functional tool regardless of tool type. The authors do however, point out that we cannot eliminate the possibility that the animals may have a preference for long sticks. The successful subjects were now tested in a meta-tool task in which they had to insert a large stone into a wide tube containing a small stone (rather a second wide tube, containing another large stone) in order to reach the reward inside a thin tube (See Figure 5, b). Even this task, was readily addressed by all subjects on the first trial. The first step to tool manufacture is tool modification, which is not even found in all animals that are natural tool users in the wild. Subjects were therefore provided with the small tube as well as a twig with some side branches that had to be broken off to make the tool functional.

The subjects succeeded in most of the trials, but the majority of modifications were conducted while the twig was already partially inserted into the tube. The final set of experiments was based on previous hook use experiments on New Caledonian crows (Weir et al.2002). Here the animals had to use the functional (hooked) end of a stick like hook tool in order to retrieve a baited bucket from a vertical tube (see Figure 5,c). All subjects inserted the hooked end more often then the straight end. Three out of four subjects were successful on the first trial. When finally offered only a straight piece of wire to extract the bucket, all four animals successfully manufactured a hook on the first trial as reported before from Betty, the New Caledonian crow (Weir et al., 2002). The findings of Bird & Emery (2009_1) contradict previous assumptions that natural tool use is the major driving force required for advanced levels of technical intelligence and indicate that tool use in corvids is more a domain general than a domain specific trait.

Such findings open the possibility of finding the capacity of tool use in other non tool using bird species depending on their ecological background (Bird & Emery 2009).

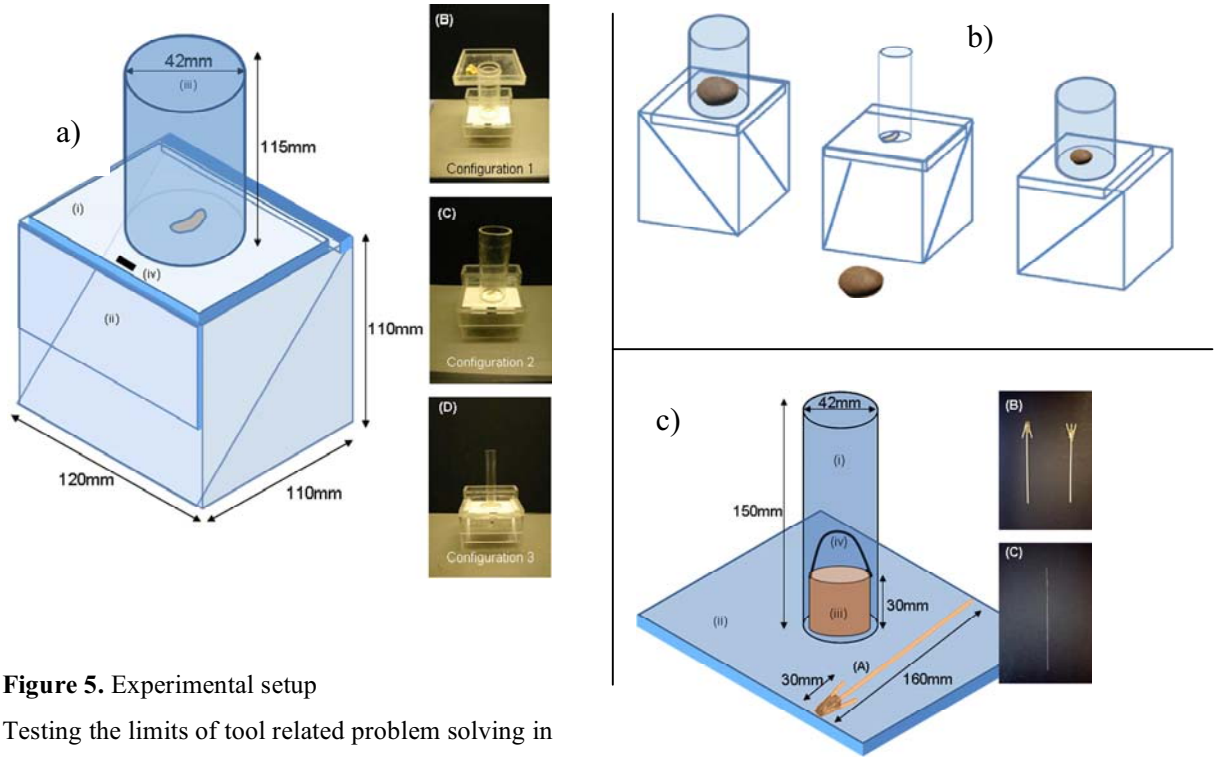


Figure 5. Experimental setup
Testing the limits of tool related problem solving in rooks. a) basic apparatus with out of reach waxworm resting on a collapsible platform (thin and wide tubes respectively). b) Setup for metatool task.
c) setup for hooktool task (bucket containing food can be pulled up using a hook)
by Bird & Emery 2009_1 in PNAS

In 2007 Mendes et al. investigated whether orangutans could use water as a tool to reach a peanut in its shell lying loosely on the base of a vertical transparent tube. Within the first trial, all five apes collected water from a drinker, carried it inside their mouth

cavity and spat it into the tube, raising the water level until they could reach the peanut by hand. A similar problem was presented to rooks by Bird & Emery (2009_2): the animals readily inserted stones into a partly filled tube, raising the water level and moving a floating worm into reach. Three of the four subjects thereby quickly learned (second trial) to use large rather than small stones and to insert stones into tubes filled with water rather than sawdust. Regarding possible higher cognitive processes underlying the animals' performance it is however problematic that the subjects had pre-experience with dropping stones into tubes from previous tasks (Bird & Emery, 2009_1). For each stone that was dropped into a tube containing water in this experiment, their action was immediately positively reinforced (mentally rewarded) by the reward moving closer within their reach. The resulting behaviour can be explained by a fast win-stay acquisition.

There are relatively few studies of tool use in parrots (despite ongoing kea studies which will be discussed in 1.5 of this Chapter, as well as Chapters 3, 4 and 5) as well as a few observations in other species. Most such tool actions are either self-directed or part of a display (Borsari & Ottoni, 2005; Overington et al,. 2009; Wood, 1984). Black Palm cockatoos use thick sticks as drumming tools for mating displays. The males drum against hollow tree cavities to announce possible nesting spots to the female (Wood, 1984). Hyacinth macaws use pieces of wood as a wedge to prevent nuts from slipping out of their firm grip (Borsari & Ottoni 2009).

It has been debated whether tool use in birds can be explained by higher level mental processing since similarly complicated object relationships are already routinely established during nest building. Tool related avian behaviour may therefore simply develop as a way to avoid costly morphological adaptions (Hansell, 2000; Hansell & Ruxton 2008). Psittacine studies on tool use promise to be particularly interesting in this matter because many large parrot species do not use complex nest construction techniques and are therefore lacking the ecological advantages that other birds such as corvids may have.

1.4 Mountain Clown and Feathered Wolf, the Ecology of the Kea

"The keas were certainly uncooperative to say the least. They always made quite sure that they were in the worst possible position for filming. While some stayed to annoy me, the rest concentrated on attacking and dismantling a pile of boxes behind the hotel"
Gerald Durrell

About 85 million years ago, during the cretaceous, New Zealand separated from the primordial landmass that is now Antarctica and Australia. Since then its bizarre flora and fauna have developed independently from other continents. A unique avian kingdom arose lacking any mammalian predators except for two species of bats (Fleming, 1979). The inhabitants of this kingdom quickly filled many mammalian niches, producing various notable creatures such as the giant moa, a massive wingless ostrich like bird that weighed as much as 230 kg; the Haast eagle, with the largest wingspan that ever existed; the long billed kiwi which lays eggs a quarter of its body mass, or the kakapo, a flightless parrot which produces deep booming noises during its lekking season (Fleming, 1979; Higgins, 1999).

One of the islands' most conspicuous inhabitants is the kea (*Nestor notabilis*), one of the six native parrot species. The kea is endemic to the alpine regions of the South Island such as Arthur's pass and Mount Cook National Park at about 700-2000 m altitude and is the world's only mountain parrot (Breejart, 1988; Campbell, 1976; Forshaw, 1989). It also is one of the few big parrot species that lives in social groups that are hierarchically organized (Breejart, 1988; Campbell, 1976; Jackson, 1960; Diamond & Bond, 1999).

Its peculiar nature, its extreme curiosity, its complete lack of neophobia and its endless appetite for demolition has stirred interest and attention as well as anger and incomprehension in the people of New Zealand for a long time.

The kea was separated from its common ancestor to its closest relative, the kaka (*Nestor meridionalis*) during the glacial periods in the early Pleistocene (Fleming, 1979). Habitat fragmentation, as well as geographic barriers, led to the division of the primordial Nestor parrot into two new species: the kaka, exploiting the milder climates of the northern forests and the kea, which was exposed to the harsh conditions above the forest line of the mountains (Fleming, 1979). It was here, in that grim and unforgiving habitat the kea developed many complex behavioural strategies that fuelled the evolution of its intelligence (Diamond & Bond 1999). An unpredictability as well as seasonality of food availability may drive a species inhabiting complex environments to acquire a broad spectrum of foraging techniques that they can flexibly resort to (Shettlewoth 1998). Such environments also increase the need for innovation in order to cope with novelties supposedly by means of their reasoning abilities (Bond et al., 2007; Jones, 2005; Tomasello & Call, 1997; Shettleworth, 1998; Sol et al., 2002; Webster & Lefebvre, 2001).

Due to its minimalist surroundings the kea evolved as a true generalist: Its niche includes a vast array of food sources. It feeds on more than 100 plant species as well as fruit, foliage, nectar, nuts, berries, flowers, various roots, eggs, small animals and carrion (Diamond & Bond, 1999).

The mountain parrot's complex niche requires a broad spectrum of behavioural activities as well as a set of all purpose foraging tools: its long, narrow and pointed beak can be used for various procedures such as tearing, pushing, pulling and probing. They additionally use their tongue for exploration and palpating and their feet for supporting objects that are currently under rostral manipulation (Diamond & Bond, 1999). The alpine territory is strongly confined by seasonal resources that are often unreliable (Diamond & Bond, 1999). In spring the birds catch grubs, grasshoppers and other insects and dig up the roots of mountain daisies. Some communities even locate the nests of shearwater birds and dig up and kill chicks that weigh several pounds and are easily the same size as themselves or bigger (Lindsay & Morris, 2000). In the summer they additionally feed on fruit and berries and lap up the nectar of flowers. In the autumn they resort to the beech forests harvesting its fruits and collecting young leaves and shoots. During the winter the animals often struggle to survive and they opportunistically kill small animals and tear open carcasses (Aspinall, 1990; Diamond and Bond, 1999; Jackson 1960; Myers 1924). In the late 19th century the wool industry started to bloom in New Zealand and great amounts

of merino sheep were introduced into the kea's territory. The kea supposedly started to feed solely on the resulting carrion at the time but quickly moved on to sit on live sheep's back, opening out skin patches in order to reach the rich fat layers (Jackson 1962). The affected livestock often died of exhaustion, infections or blood loss. Consequently the government introduced a bounty scheme offering as much as three shillings on a kea's head (Diamond & Bond 1999). This triggered a wave of persecution leading to the slaughter of more then 150.000 kea until 1986 when a conservation law came into force. Kea are presently classified as a second priority threatened species (Molloy & Davis 1994), with an estimated wild population of between 1000 and 5000 birds (Anderson 1986), although younger studies argue that the populations may have recovered to 15000 heads (Diamond &Bond, 1992). Although the combined pressures of excessive hunting, the deforestation of large land masses and introduction of mammalian predators annihilated over a third of New Zealands original landbirds, the kea still persists at low population level in its alpine habitats (Diamond & Bond, 1999).

Kea are frequently observed foraging in social groups in places where food is abundant (Clark, 1970). Large feeding aggregations carry many benefits especially for young animals, which may acquire social information about the location of food resources, which food items are edible, new feeding methods as well as opportunities for social interaction (Brejaart, 1988; Campbell, 1976; Clayton, 1978; Diamond & Bond, 1991; Turner, 1965).

The mountain parrots have an unusually long period of post fledging care by both parents as well as other group males (Diamond and Bond 1991; Jackson, 1962b; 1963). Jackson (1963) and Diamond & Bond (1991) observed incidents of male kea allofeeding fledglings for five or six weeks after they left the nests. In our captive group we observed juveniles triggering feeding responses in unrelated adult males over their entire first summer.

Kea fledglings are poor foragers and spent most of their time manipulating and examining inedible objects. They show little evidence of an ability to distinguish between edible and inedible items (Diamond & Bond, 1991).

Once they reach the juvenile phase, although they are not as frequently fed by others they are still granted special treatment: juvenile kea use a baby-defense/appeasement display called "hunching" in which they fluff up their head and neck plumage and spread their wings a little. This allows them to conquer resources that are already occupied by older birds (Diamond & Bond, 1991, Diamond & Bond, 1999; Tinbergen, 1960). Juvenile birds are more likely to take over new food from others and

less likely to be displaced from obtained food (Diamond & Bond, 1991; Elliot & Kemp, 1999). The hunching advantage vanishes with the characteristic appearance of a juvenile after two or three years (yellow coloring around the eye and beak area) henceforth subadults are less successful in obtaining and protecting resources and move on to pilfering occupied food sites (Diamond & Bond, 1991). As the kea reach maturity (after about four or five years; Higgins 1999) they again become focused on object exploration as during their fledgling phase. They have, however, massively improved their skill of identifying edible items and waste little time on objects that turn out to be unprofitable resources. They henceforth become increasingly efficient in discovering and exploiting new food sources.

Young kea have been described as 'open program animals': due to their initial inability to discriminate edible from inedible items, they display a remarkably open minded attitude towards objects in their environment and spent hours mauling and dismantling them (Diamond & Bond, 1999). During their extended youth they also exhibit the most elaborate and time consuming play behaviour of any other bird species known (Diamond & Bond. 1999, Diamond et al., 2006; Keller, 1975). Not only do they play with other individuals in the group but also with a wide range of different objects with interesting properties, much like human toddlers (Gajdon et al., submitted; Diamond & Bond, 1999). The play of even its closest relatives, the kaka (*Nestor meridionalis*) and the kakapo (*Strigops habroptilus*) lack the intensity, diversity, duration, and structure of the kea's play (Diamond & Bond, 2004; Diamond et al., 2006). Kea are also more likely to engage in social, joint object manipulation and that occasionally includes members of other age groups (Diamond & Bond, 2004).

Play behaviour in birds may be predicted from developmental patters and parental association. A model by Diamond and Bond (2003) suggests that play behaviour can be cultivated by (1) belonging to a large brained, altricial order, (2) living in complex, stable social groups, and (3) slow maturation and maintenance of an extended post-fledging association between juveniles and adults (Ortega & Bekoff, 1987; Skutch, 1987; Collar, 1997; Heinrich & Smolker, 1998; Power, 2000; Diamond & Bond, 2003). Kea have longer and more intense post fledging relationships to adult birds, have more complex social structures and reach sexual maturity later than kaka and kakapo (Diamond et al., 2006).

Diamond & Bond (1999) suspect the primary profit of elaborate object play in the kea to lie within the affordances of an object, which are "its intrinsic and contextual properties that determine the number of ways it can be used." The more complex

affordances an object is offering, the more intense the play will be. This way the animal can opportunistically broaden its behavioral repertoire and achieve a "neurological readiness" for novel situations by developing generalized skills it can flexibly resort to when facing unknown problems (Diamond & Bond, 1999).

Its ability to store and apply information about its physical environment has made the kea an important avian model for studying technical cognition, which I will discuss in the following part of this chapter.

1.5 A brief history of previous kea studies

Despite the kea's conspicous demeanour as well as its high profile in tourism and mounteneering, New Zealanders have attempted few investigations of the mechanims behind the peculiar behaviour of this potentially very intelligent bird. New Zealand's resarch on the kea has mainly been limited to population ecology and conservation purposes. One of the first people attracted to studying the kea in the wild was a Mount Cook park ranger at Arthur's pass National Park. Robert Jackson developed a distinct fascination for these birds and during the 1960's dedicated a decade to observing and banding several hundreds kea. He spend a lot of time hiking in the mountains and lurking in dumpsites to observe their behaviour. His findings were the foundations for our present day knowledge of most of the kea's population dynamics and wildlife ecology until, unfortunately, he dissapeared on a camping trip (Diamond & Bond 1999; Jackson 1960; 1962; 1953; 1969).

Judy Diamond and Alan Bond from the University of Nebraska later used the same site for their three year long conquest to investigate the kea's social behaviour and learning abilities, which have so far been largely neclected (Diamond & Bond, 1999). Their field observations on a banded group of 38 kea resulted in numerous records of foraging and social behavior. From these derived what we know today about the kea's complex social structures as well as their elaborate object play as described in the previous part of this chapter (Diamond & Bond 1991; 1999, 2003; 2004; Bond & Diamond 2005; Diamond et al. 2006).

During the last decade, members of the department of Cognitive Biology from the University of Vienna, became increasingly interested in studying the kea not only in the field, around Mount Cook National Park, but also under more controlled circumstances in captivity. Most laboratory studies were conducted either with zoo animals in cooperation with the Tiergarten Schönbrunn in Vienna or with subjects housed at the Konrad Lorenz Institute for Comparative Ethology (KLIVV).

All experiments that derive from this thesis are solely focused on kea, housed at the KLIVV in a large, outdoor group aviary (15 x 10 m and 4 m high) At the time, the aviary was split into a large group area (10 x10 m) as well as a smaller experimental compartment (10 x 5m) that could be visually isolated from the remaining aviary using opaque sliding doors. At the time I started to work at the KLIVV the aviary, contained 24 birds: 12 adults, one of them female, as well as 12 juveniles, eight of which were female and four male. In the course of this thesis, some individuals died but three juveniles were born and we were entrusted with some individuals from the Vienna zoo.[*] To date, the Vienna Kea Lab is still supervising the largest group of captive kea in Europe in a giant new group aviary of 500 m^2 at the recently funded research station Haidlhof in Lower Austria and is still the sole team in the world investigating the intelligence of the kea in the Laboratory.

Over the years the kea lab assessed several aspects of the kea's behaviour such as: physical cognition, social learning, social intelligence, cooperation and the interrelation between these topics.

One of the first published lab studies on the kea in Vienna was conducted by Tebbich et al. (1996). They investigated whether the animals would cooperate in an instrumental task which involved a seesaw-like apparatus: if a lever was pushed down at one side, it lifted a cap closing a food container. The birds could not feed and lift the lever at the same time and therefore relied on the cooperation of other individuals to press down

[*] see Appendix 1 & 2 for Information on the present kea stock and the dimensions of the KLIVV aviary

the lever for them. The researchers were targeting tit for tat behavior, which would entail the feeder and the helper taking turns. They found however that the distribution of the two roles was closely related to the animals' hierarchy, with the more dominant individuals being fed by their submissive partners.

Huber et al. (2001) conducted a social learning experiment featuring an Artificial Fruit box, which was locked using several different devices. Dismantling the devices required three different action patters: poking out a bolt, pulling a splint pin and twisting out a screw. Some observer subjects received demonstrations from experienced individuals. Although observers did not manage to open the box, they were more successful at opening the locking devices then their naïve conspecifics. Huber et al. (2001) assume that these results arise as a consequence of affordance learning. The animals are apparently paying less attention to the actions of the demonstrator than to the movement of the object's affordances. They may thereafter use this acquired knowledge to remove the locking devices while applying their own individual behavioural strategy. The authors suspect that since the subjects seem to learn something about the functionalities of the affordances, their improved performance cannot be a result of simple stimulus enhancement.

In order to expand social learning experiments on the kea to the field, Gajdon et al. (2004) devised a novel Tube Removal paradigm. The task required pushing a small tube over the top of a longish vertical pole in order to reach the butter inside that tube. While pushing the tube with their bills, the animals had to simultaneously climb the pole, which complicated the task (see Figure 1). After training a demonstrator, only two of 15 observers mastered the problem. Although the task seemed to be within the animals' cognitive and physical capacities, their skills did not distinctively improve after watching more demonstrations. This may be explained by a dissociation between social transmission of foraging techniques in the wild versus social learning potential in the lab. Further studies on captive kea in Vienna support these assumptions since laboratory subjects quickly mastered the original version of the task either individually or after only a few demonstrations (Gajdo, Wolf & Huber; unpublished data). Their continuous exposure to experimental procedures and apparatuses may progressively upgrade the problem solving capacities in laboratory subjects versus wild animals.

.

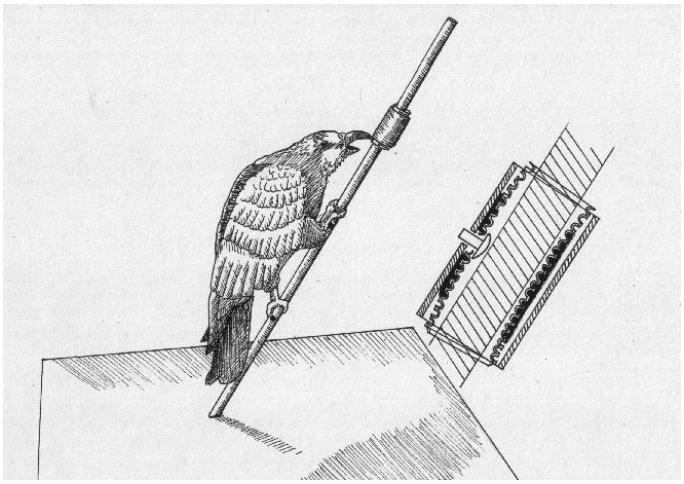


Figure 1. Tube Removal, basic apparatus. The bird has to walk up the pole while simultaneously pushing a tube, baited with butter. By Gajdon et al. 2004, in LEARNING & BEHAVIOUR

Social transmission of feeding innovations in the field was also limited in a local population of kea at the study site in Mount Cook, from which some individuals were reported to open large rubbish bins using a sophisticated technique. Gajdon et al. (2006) took the opportunity to investigate how this self initiated innovation would spread across the population. Only five of 36 male animals acquired the appropriate behavioural sequence: Open the lid and keep holding it while walking backwards in order to flip it over. The successful individuals took a very log time to become efficient in this behaviour and only nine percent of the opening attempts were successful. The amount of individual experience with the lids rather than social cues or an insightful understanding of the physical properties involved seem to be responsible for their successful performance.

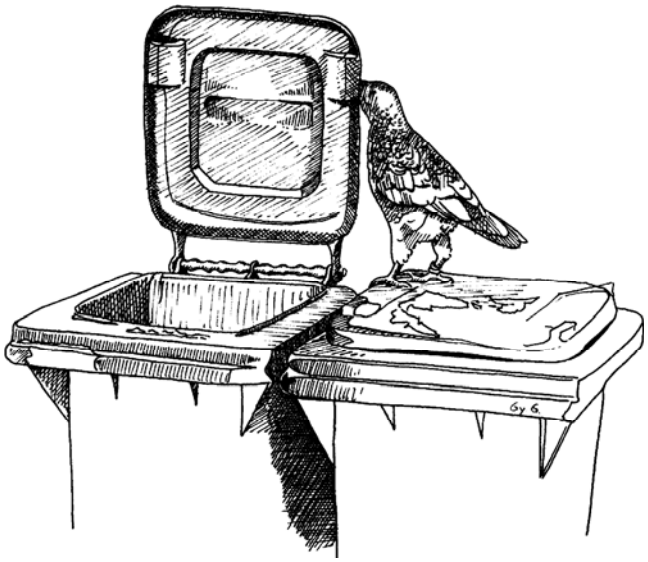


Figure 2. Bin opening by wild kea in Mount Cook. By Gajdon et al. 2006, in ANIMAL COGNITION

In the meantime, interest arose in studying the kea's physical abilities outside the social context such as cooperation and social learning. Huber & Gajdon (2006) argued that studies on high cognitive abilities in the physical domain have long been concentrated mainly on tool using species but should also be expanded to animals showing high levels of curiosity, object manipulation, exploration and extractive foraging such as the kea. They suggested the kea as a non-tool using model species, perfectly fitted to test aspects of the Technical Intelligence Hypothesis as proposed by Byrne (1997). In the course of her doctoral thesis, Dagmar Werdenich (Werdenich & Huber, 2004, unpublished data) exposed the kea to two classic tasks targeting higher cognitive abilities in the physical domain, the trap tube and the string pulling paradigm (which were discussed in part 1.3 of this chapter). During a initial training phase, the six subjects quickly learned that pulling one of two plungers with discs attached (as in Seed et al., 2006) would bring a food reward inside a horizontal Plexiglas tube within their reach. When a trap (small Plexiglas container) was added to the apparatus, the keas did not learn to pull the reward away from the trap and still randomly chose sites after 100 trials. Even after developing another apparatus in which the reward could be directly moved with the bill through a narrow groove inside the tube, the performance remained at chance level indicating that the animals did not attend to the functionally relevant features of this particular task. In a similar setup by Liedtke et al. (2010) all but one individual solved this task by lifting the food over the trap. They did however fail again when the lifting was prevented.

Before studies in the lab in Vienna, the string pulling paradigm had been attempted on wild kea by Johnston (1999) in the wild. During these investigations, only six out of 19 subjects mastered the task on their first trial. When Werdenich & Huber (2006) continued the study on captive subjects, all seven subjects flew directly up to the perch. In contrast to the field results, all of them (except for one fledgling) succeeded in pulling up a 70 cm single string on their first trial within a few seconds using efficient foot beak coordination. They thereafter presented the birds with two strings, one baited with food, one with a piece of wood. All but two subjects chose the correct string on the first trial. The subjects reached an overall performance of 86% correct within the first ten trials, clearly indicating that their manipulations of the string were goal directed. After the two strings were crossed, most birds were incorrect on the first trial but four birds quickly adjusted to the problem with very few incorrect choices. In another test the two strings were offered in a slanted position (bent off to the same side), positioning the food reward underneath the spot where the unbaited string was attached to the perch. All but one bird were successful

on the first trial and were able to maintain their performance. To test whether the animals' choices were influenced by weight as a relevant physical object property, the subjects were now offered a choice between a light food container and a two kilo stone, which was baited with lots of butter. Four out of seven subjects correctly chose the small container on their first trial, the overall performance was however 81% within the first ten trials, indicating some unsuccessful attempts which were quickly corrected. In a final task, the subjects were confronted with a reward suspended from a string that was long enough for a kea to easily pick the reward up from the ground. Only one of the seven subjects changed its behavioural strategy from pulling the reward up the perch to simply plucking it off from the ground. The results of this study indicate that although the animals do not seem to possess a fully established understanding of all physical properties involved in this task, they can still flexibly and rapidly adapt to various versions of the task seemingly showing some understanding of the string as a functional connection to the reward. Further controls, restricting the visual connection of the reward during pulling (see Taylor et al., 2010) are presently under investigation.

Observing object play in captive kea is constantly fueling new ideas for experimental setups. We often find toys such as stone pepples, sticks, sea shells and painted wooden bricks sunk into cavities such as holes in the aviary floor, the guide rail for the our sliding doors, or even also in fitted into small cups and vessels. Gyula Gajdon became interested in investigating the whereabouts of this behaviour in more detail. Gajdon et al. (submitted) discovered that their subjects inserted various sorts of objects into vertically arranged tubes, although there was no food reward involved. The insertion happened intentionally: when open and closed tubes were offered simultaneously, the kea carried the objects ten times more often to the open tubes. They also grabbed elongated toys at one end (as opposed to the middle) to facilitate insertion into the tube opening. Actively producing spatial relationships between objects can often be regarded as a precursor of tool use (Fragazy et al., 2004). Subjects, which had inserted objects into tubes outside the feeding context also succeeded in a means end tool use task featuring two vertically slanted tubes, inside which a peanut was affixed using cream cheese. One of the tubes was open, one was closed (using a wire mesh) at the top. In order to reach the peanut, the animals had to drop the smaller of two differently sized objects into the open tube end. The animals combined the objects significantly more often an ineffective manner than would be expected by chance before they succeeded for the first time in retrieving the reward. The kea seem to explore the apparatus's affordances much like

human toddlers in a playful way not necessarily in an immediately goal directed manner. The study highlights fundamental differences in selective actions during tool related behaviour in the neophilic kea in contrary to more neophobic species such as corvids. The authors suggest that technical competence in large brained birds such as corvids and parrots is likely to develop in interaction between the species' cognitive potential and the strength of their explorative drive that in succession or in parallel opens up the possibility for development of tool related behaviour.

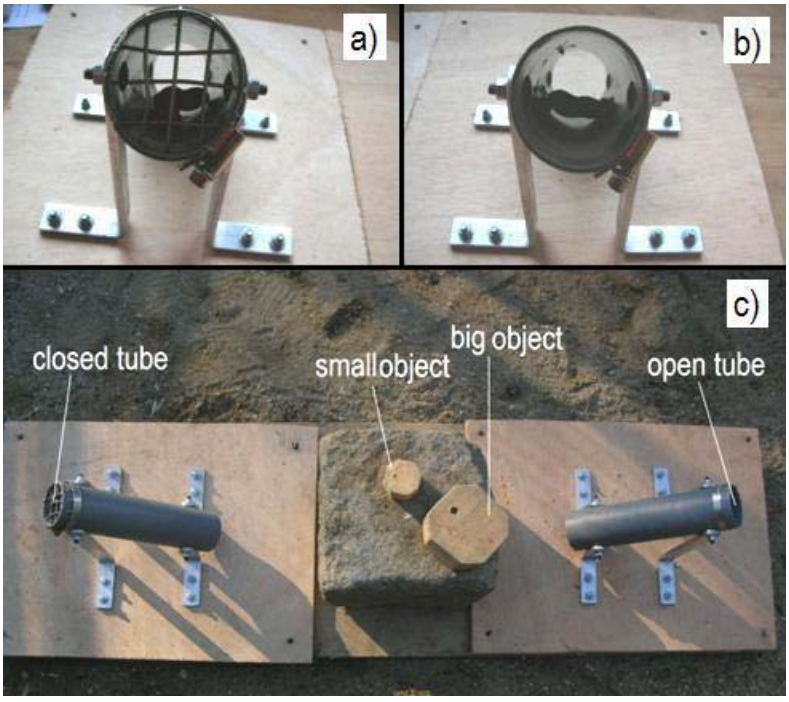


Figure 3. Experimental setup for the inserting as means paradigm: Two opaque tubes fixed in a vertically slanted position. One tube has a wire mesh on the top end one is open; both contain a food reward. Two differently sized (small correct; big incorrect) are offered alongside the tubes. By Gajdon et al. *Submitted*

Finding advanced competent performances in the physical tasks in kea invites us to make a direct comparison to the corvid family, as an obvious candidate for similar traits.

Schloegl et al. (2009) tested kea as well as common ravens in an experimental choice by exclusion task in which animals had to determine which of two differently shaped opaque tubes contained a food reward. The tubes were bent in different ways providing partial information to the location of the food (for example if no reward is visible in both tubes but one tube is straight and one is bent, the food has to be in the latter). Although the kea chose the baited tube more often then the ravens, the ravens seemed to choose by exclusion more frequently then the kea. The differences in exploration technique seem for a large extend to be responsible for these outcomes implying that many of their cognitive abilities are derived under different selection

pressures.

Previous kea studies have not only played a significant role in the study of avian problem solving but have also provided the first approaches to explain the peculiar behaviour of this remarkable bird, increasing an appreciation of this animal in its natural habitat. They have however, brought up countless new research questions, some of which will be addressed in the course of this thesis.

1.6 Aims and Structure of this thesis

This thesis focuses in particular on the kea's perception of spatial relationships between objects as well as on the extent consideration payed to such physical relationships during problem solving.

Chapter two investigates the kea's performance in various versions of the classical physical support problem, a means-end task which was originally developed by Piaget (1952) to test sensory developement in human infants. The task features an out of reach object, which can be acquired by pulling the support the object rests upon. Various versions of the problem, in which the perceptual properties of the support as well as the position of the desired object where being alternated have previously been presented to primates such as cotton top tamarin monkeys as well as chimpanzees (Hauser et al., 1999; Hermann et al. 2008; Povinelli; 2001). The problem has also been adressed in two other parrot species (Mendonça-Furtado & Ottoni, 2008; Funk, 2002).

Previous studies have discovered the kea's capacity to use compact objects as tools by inserting them into tubes stabilized in a vertically slanted position (Gajdon et al. submitted). In order to investigate how the animals can generalize their experience to tasks involving more complex object relationships, chapter three proceeds with an aberration of this paradigm in which all functional relationships have to be established by the animals themselves. In order to retrieve a food reward, a correctly sized object has to be actively carried to a tube lying loosely on the ground. After inserting the object, the tube has to be lifted on the same side. This will result in the object breaking a spaghetti inside the tube, releasing a food reward, which was transfixed on the spaghetti. The object relationships established here fulfill the requirements for second order tool use according to Frangazy et al. (2004): to act with an object A (tube) in relation to an object B (ball) following a placement of object B in relation to a third object C (reward). We also investigate how the animals react to interruptions (blockages) that will influence the path of the reward depending on where the tube is lifted.

One of the most competent problem solvers of the corvid family is the New

Caledonian crow (Taylor et al. 2007; Taylor et al. 2009; von Bayern et al. 2009; Weir et al, 2002). Finding the capacity for tool use in the kea makes a comparison of problem solving abilities in the two species possible. In chapter four a novel paradigm, the Multi Access box for comparing problem solving abilities in extractive foragers is introduced.

After finding innovative stick tool use in one kea in the previous experiment it was still unclear whether the animal was using the tool as a functional extension of its beak or whether he was manoeuvring it randomly until the reward appeared. In chapter five we therefore used the same bird to train other individuals and thereafter confront them with a two choice paradigm in which they have to use the tool to hit the correct out of two baited boxes.

In chapter six I depict the implications as well as possible future directions resulting from the experiments described in this thesis.

1.7 References

Anderson R. (1986) Keas for keeps. *Forest and Bird* **17**(1):2-5

Aspinall, J.C. (1967) Some observations on keas. *New Zealand Tussock and Grassland Revue* **12**:14-17

Beck, B. B. (1980). *Animal tool behavior: the use and manufacture of tools by animals*. New York; London, Garland STPM Pres

Bird, CD & Emery, NJ. $(2009)_1$. Insightful problem solving and creative tool modification by captive rooks. *Proceedings of the National Academy of Sciences,* **106**, 10370-10375

Bird, C.D. & Emery, N.J. $(2009)_2$. Rooks use stones to raise the water level to reach a floating worm. *Current Biology*, **19**, 1410-1414.

Bond, A.B. & Diamond, J. (1992) Population estimates of kea in Arthur's Pass National Park. *Notornis* **39**: 151-160.

Bond, A.B., Wilson, K.J. & Diamond, J. (1991) Sexual dimorphism in the kea *(Nestor notabilis). Emu* **91**: 12-19.

Borsari, E., Ottoni, E.B. (2005) Preliminary observations of tool use in captive hyacinth

macaws (*Anodorhynchus hyacinthinus*). *Animal Cognition* **8**(1), 48-52

Brejaart, R. (1988) Diet and Feeding Behaviour of the Kea (*Nestor notabilis*). M.S. Thesis. Lincoln University, Canterbury (N. Z.)

Bugnyar, T. & Kotrschal, K. (2002) Observational learning and the raiding of food caches in ravens, *Corvus corax*: Is it "tactical deception"? *Animal Behaviour* **64**, 185-195

Bugnyar, T. & Heinrich, B. (2005) Food-storing ravens differentiate between knowlegeable and ignorant competitors. *Proceedings Royal Society London Series B* **272**, 1641-1646

Bugnyar, T., Stoewe, M., Heinrich, B. (2007) The ontogeny of caching in ravens, *Corvus corax*. *Animal Behaviour,* **74**, 757e767

Byrne RW (1997) The technical intelligence hypothesis: an additionalevolutionary stimulus to intelligence? In: Whiten A, Byrne RW(eds) Machiavellian intelligence. vol II: extensions and evaluations. Cambridge University Press, Cambridge, pp 289–211

Byrne RW, Whiten A (1988) Machiavellian intelligence. Social expertise and the evolution of the intellect in monkeys, apes, and humans. Clarendon Press, Oxford

Campbell, B. A. (1976) Feeding habits of the kea in the Routeburn basin. M.S. thesis. University of Otago, Dunedin

Clayton, D.A.(1978) Socially facilitated behaviour. *Quarterly Review of Biology* **53**(4):373-392

Clayton, N.S. & Dickinson, A. (1998). "Episodic-like memory during cache recovery by scrub jays". *Nature* **395** (6699): 272–4

Clark, A.H. (1970) *The invasion of New Zealand by people, plants and animals.* Westpoort Con.: Greenwood Press

Collar, N.J. (1997). *Family Psittacidae (Parrots).* In: Handbook of birds of the world, Vol. 4: Sandgrouse to Cuckoos (del Hoyo, J., Elliott, A. & Sargatal, J., eds). Lynx Edicions, Barcelona, p. 280-477.

de Mendonça-Furtado O, Ottoni E B (2008) Learning generalization in problem solving by a blue-fronted parrot (*Amazona aestiva*). *Animal Cognition* **11**:719-725

Diamond, J., Eason, D., Reid, C. & Bond, A.B. (2006) Social play in kakapo (*Strigops habroptilus*) with comparisons to kea (*Nestor notabilis*) and kaka (*Nestor meridionalis*). *Behaviour* **143**: 1397-1423.

Diamond, J. & Bond, A.B. (2004) Social play in kaka (*Nestor meridionalis*) with comparisons to kea (*Nestor notabilis*). *Behaviour* **141**: 777-799.

Diamond, J & Bond, A.B. (2003) A comparative analysis of social play in birds. *Behaviour* **140**: 1091-1115

Diamond, J. & Bond, A.B. (1999) *Kea, Bird of Paradox: The Evolution and Behavior of a New Zealand Parrot*. Berkeley, CA: U. of California Press.

Diamond, J. & Bond, A.B. (1991) Social behavior and the ontogeny of foraging in the Kea *(Nestor notabilis). Ethology* **88**: 128-144.

Elliott, G. & Kemp, J. (2004). Effect of hunting and predation on kea, and a method of monitoring kea populations: Results of kea research on the St Arnaud Range. Department of Conservation, Wellington, New Zealand.

Emery, NJ. (2004). The evolution of social cognition. In: Easton, A & Emery, NJ. (Eds.), Cognitive Neuroscience of Social Behaviour. Psychology Press.

Emery, N.J.& Clayton, N.S.(2004) The mentality of crows: Convergent evolution of intelligence in corvids and apes, *Science* **306**,1903–1907

Emery, N. J. (2006) Cognitive ornithology: the evolution of avian intelligence. *Phil. Trans. R. Soc. B* **361**, 23–43

Emery, N.J., Clayton, N.S., Frith, C.D. (2007*)* Introduction. Social intelligence: from brain to culture. *Phil. Trans. R. Soc. B.* **362,** 485-488

Epstein, R., Kirshnit, C.E., Lanza, R.P., & Rubin, L.C. (1984). Insight in the pigeon: antecedents and determinants of an intelligent performance. *Nature* **308**: 61-62.

Fleming, C.A.(1979) *The geological history of New Zealand and its life.* Auckland: Auckland University Press

Forshaw, J. M. 1989. *Parrots of the world.* 3rd ed. Australia: Lansdowner

Frangazy, D.M., Visahlberghi, E., Fedigan, L.M. (2004) *The Complete Capuchin.* Cambridge University Press

Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E. B., de Oliveira M. G. (2004). Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology,* **64**(4), 359-366

Funk, M. (2002) Problem solving skills in young yellow crowned parakeets (*Cyanoramphus auriceps*) *Animal Cognition.* **5**(3), 167-176

Gajdon, G. K., Fijn, N.,Huber, L. (2004) Testing social learning in a wild mountain parrot, the kea (Nestor notabilis). *Learning & Behavior* **32**, 62-71.

Gajdon, G. K., Fijn, N., Huber, L. (2006) Limited spread of innovation in a wild parrot, the kea (Nestor notabilis). *Animal Cognition* **9**, 173-181.

Gajdon, G.K., Lichtnegger, M., Huber, L. Toddler like object exploration 1 helps captive mountain parrots to innovate tool use behaviour. Submitted

Griffiths D, Dickinson A, Clayton N (1999). "Episodic memory: what can animals remember about their past?".*Trends in cognitive sciences* **3** (2): 74–80

Goodall, J. (1964). Tool using and aimed throwing in a community of free-living chimpanzees. *Nature, London,* **201**, 1264-1266.

Hansell, M. & Ruxton, G. (2008). Setting tool use within the context of animal construction behaviour. Trends in Ecology and Evolution, **23**,73–78

Hauser M D, Kralik J D & Botto-Mahan C (1999) Problem solving and functional design features: experiments on cotton-top tamarins, *Saguinus Oedipus oedipus*. *Animal Behaviour* **57**:565 – 582

Heinrich, B. & Bugnyar, T. (2005) Testing problem solving in ravens: String-pulling to reach food. *Ethology.* **111**, 962-976

Heinrich, B. & Smolker, R. (1998). *Play in common ravens (Corvus corax). In: Animal play: Evolutionary, comparative and ecological perspectives* (Bekoff, M. & Byers, J.A., eds). Cambridge University Press, Cambridge, p. 27-44

Henderson, J., Anrew Hurley, T., Bateson, M., Healy, S.D. (2006) Timing in Free-Living Rufous Hummingbirds, *Selasphorus rufus*. *Current Biology* **7,**16, 5, 512-515

Hauser M D, Kralik J D & Botto-Mahan C (1999) Problem solving and functional design features: experiments on cotton-top tamarins, *Saguinus Oedipus oedipus*. *Animal Behaviour* **57**:565 – 582

Herrmann, E, Wobber, V & Call, J (2008) Great Apes' (Pan troglodytes, Pan paniscus, Gorilla gorilla, Pongo pygmaeus) Understanding of Tool Functional Properties After Limited Experience. *Journal of Comparative Psychology* **122**: 220-230.

Higgins, P. J. (Ed.) (1999). *Handbook of Australian, New Zealand & Antarctic birds (Volume 4).* Oxford University Press, Melbourne, Australia

Holzhaider, J.C., Hunt, G.R., Campbell, V.M. and Gray, R.D. (2008). Do wild New Caledonian crows (*Corvus moneduloides*) attend to the functional properties of their tools? *Animal Cognition* **11**, 243-254.

Huber, L., Rechberger, S., Taborski (2001) Social learning affects object exploration and manipulation in keas, *Nestor notabilis* . *Animal Behaviour*, **62**, 945-954.

Huber, L. & Gajdon, G. (2006). Technical intelligence in animals: the kea model. *Animal Cognition* **9,** 295–305.

Huber, L. (2007) Emulation Learning: The Integration of Technical and Social Cognition. In: *Imitation and Social Learning in Robots, Humans and Animals: Behavioural, Social and Communicative Dimensions* (Ed. by Dautenhahn, K. & Nehaniv, C. L.), pp. 427–439. Cambridge, UK: Cambridge University Press.

Humphrey, N. K. (1976) The social function of intellect. In Growing points in ethology (eds P. P. G. Bateson & R. A.Hinde), pp. 303–317. Cambridge, UK: Cambridge University Press.

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

Hunt, G.R. and Gray, R.D. (2004). The crafting of hook tools by wild New Caledonian crows. *Proceedings of the Royal Society, London* B (suppl.) **271**, S88-S90

Hunt, G.R. and Gray, R.D. (2003). Diversification and cumulative evolution in tool manufacture by New Caledonian crows. *Proceedings of the Royal Society, London* B **270**, 867-874

Iwaniuk, A. N., Dean, K. M. & Nelson, J. E. (2005). Interspecific allometry of the brain and brain regions in parrots (*Psittaciformes*): comparisons with other birds and primates. *Brain, Behaviour and Evolution*, **65**, 40–59.

Jackson, J.R.(1960) Keas at Arthur's Pass. *Notornis* **9**:39-59

Jackson, J.R. (1662)a. Do kea attack sheep. *Notornis* **10:** 33-38

Jackson, J.R. (1962)b. Life of the kea. *Cantebury Mountaineer*.**31**:120-123

Jackson, J.R. (1963) The nesting of keas. *Notornis* **10**:319-326

Jarvis, E. D. & Consortium, A. B. N. **(**2005). Avain brains and a new understanding of vertebrate brain evolution. *Nature Reviews Neuroscience*,

Johnston, R. 1999. The Kea (*Nestor notabilis*): A New Zealand problem or problem solver? Master thesis. Christchurch: University of Canterbury

Jolly, A. (1966). Lemur social behavior and primate intelligence. *Science*, **153**, 501–506.

Jones, C. B. (2005). *Behavioral flexibility in primates: Causes and consequences*. New York: Springer-Verlag

Jones T.B & Kamil, A.C. (1973) Tool-making and tool-using in the Northern blue jay, *Science* **180** 1076–1078

Kacelnik, A. 2009. Tools for thoughts or thoughts for tools? *Proceedings of the National Academy of Sciences of the United States of America **106***, 10071-10072.

Keller, R. (1975) Das Spielverhalten der Kea (*Nestor notabilis* Gould) des Züricher Zoos. *Zeitschrift für Tierpsychology* **38**:393-408

Kenward, B., Weir, A.A.S., Rutz, C., & Kacelnik, A. (2005). Tool manufacture by naive juvenile crows. *Nature* **433:** 121.

Kenward, B., Rutz, C., Weir, A.A.S., & Kacelnik, A. (2006). Development of tool use in New Caledonian crows: inherited action patterns and social influence. *Animal Behaviour* **72**: 1329-1343.

Köhler, W. (1925). *The mentality of apes.* London: Harcourt Brace.

Limongelli L, Boysen ST, Visalberghi E (1995) Comprehension ofcause–effect relations in a tool-using task by chimpanzees (*Pantroglodytes*). Journal of Comparative Psychology 109:18–26

Lind, J., Ghirlanda, S., Enquist, M. (2009) Insight learning or shaping? PNAS **106** (28) E77; *published online*

Martin-Ordas, G., Call, J**.** & Colmenares, F. (2008). Tubes, tables and traps: great apes solve two functionally-equivalent trap tasks but show no evidence of transfer across tasks. *Animal Cognition,* **11***,* 423-430.

Martin-Ordas, G. & Call, J**.** (2009). Assessing generalization within and between trap tasks in the great apes. *International Journal of Comparative Psychology,* **22**, 43-60.

Mendes, N., Hanus, D., Call, J. (2007) Raising the water level: Orangutans use water as a tool. *Biology Letters* **3**(5): 453-455

Molloy, J., Davis, A. 1994. *Setting priorities for the conservation of New Zealand's threatened plants and animals.* Wellington: Department of Conservation

A.C. Moura and P.C. Lee, Capuchin stone tool use in Caatinga dry forest, *Science* **306** (2004), p. 1909

Mulcahy, N.J. & Call, J. (2006). How great apes perform on a modified trap-tube task. *Animal Cognition,* **9***,* 193-199.

Myers, J.G.(1924) The relation of bird to agriculture in New Zealand, X: The kea or mountain parrot*. New Zealand Journal of Agriculture* **29**:25

Ortega, J.C. & Bekoff, M. (1987). Avian play: Comparative evolutionary and developmental trends. *Auk* **104**: 338-341

Reader, S. M., Laland, K. N. (2002) Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences of the United States of America*, **99**(7), 4436-4441

Paz-y-Miño, G, Bond, A.B., Kamil, A.C., & Balda, R.P. (2004). Pinyon jays use transitive inference to predict social dominance. *Nature*. **430**:778-782.

Pepperberg, I. (1999) *the Alex studies.* Harvard U niversity Press

Pepperberg, I., Willner, M.R., Gravitz , L.B. (1997) Development of Piagetian Object Permanence in a Grey Parrot *(Psittacus erithacus)* Jownal of Comparative Psychology Vol. Ill, No. 1,63-75

Peterson GB (2004) A day of great illumination: B. F. Skinner's discovery of shaping. J Exp Anal Behav 82:317–328.

Piaget, J. (1952). *The origins of intelligence in children.* New York, NY: International Universities Press.

Povinelli DJ (2000) *Folk physics for apes: a chimpanzee's theory of how the world works.* Oxford University Press, Oxford

Power, T.G. (2000). *Play and exploration in children and animals*. Lawrence Erlbaum Assoc. Pubs., Mahwah, NJ

Salwiczek LH, Emery NJ, Schlinger B, Clayton NS (2009) The development of caching and object permanence in Western scrub-jays (Aphelocoma californica): which emerges first? *Journal of Comparative Psychology.***123**(3):295-303.

Schloegl, C., Dierks, A., Gajdon, G. K., Huber, L., Kotrschal, K. & Bugnyar, T. 2009. What You See Is What You Get? Exclusion Performances in Ravens and Keas. *PLoS ONE*, **4**, e6368.

Schmuck-Paim, C., Borsari, A., Ottoni, E.B. (2009) Means to an end: Neotropical parrots manage to pull strings to meet their goals. *Animal Cognition* **12/2,** 287-301

Shettleworth, S. J. (1998). *Cognition, evolution, and behavior*. Oxford, England: Oxford University Press.

Seed AM, Tebbich S, Emery NJ, Clayton NS (2006) Investigating physical cognition in rooks, *Corvus frugilegus*. *Current Biology* **16:**697–701

Seed, A.M., Call, J., Emery, N.J. & Clayton, N.S. (2009). Chimpanzees solve the trap problem when the confound of tool-use is removed. *Journal of Experimental Psychology: Animal Behavior Processes, 35*, 23-34.

Seed, A. M., Emery, N. J. & Clayton, N. S. (2009). Intelligence in corvids and apes: a case of convergent evolution? *Ethology* **115**, 401-420

Skutch, A.F. (1987). *Helpers at birds' nests*. University of Iowa Press, Iowa City, IA.

Sol, D., Timmermans, S., Lefebvre, L. (2002). Behavioural flexibility and invasion success in birds. *Animal Behaviour* **63**: 495-502.

Taylor, A.H., Hunt, G.R., Holzhaider, J.C. and Gray, R.D. (2007). Spontaneous metatool use in New Caledonian Crows. *Current Biology* **17**, 1504-1507.

Taylor, A.H., Hunt, G.R., Medina, F.S. and Gray, R.D. (2009). Do New Caledonian crows solve physical problems through causal reasoning? *Proceedings of the Royal Society, London* B **276**, 247-254

Taylor, A.H., Medina, F., Holzhaider, J.C., Hearne, L., Hunt, G.R. and Gray, R.D. (2010). An investigation into the cognition behind spontaneous string pulling in New Caledonian crows. *PLoS One* **5**, e9345.

Tebbich, S., Taborsky, M., Winkler, H. (1996) Social manipulation causes cooperation in keas. *Animal Behaviour*, **52,** 1–10

Tebbich S, Bshary R (2004) Cognitive abilities related to tool use in the woodpecker finch, *Cactospiza pallida*. *Animal Behaviour* **67**:689–697

Tennie, C., Call, J., Tomasello, M.(2010) Evidence for Emulation in chimpanzees in Social Settings using the Floating Peanut Task. *Plos One.* **5**(5) e10544

Thorpe WH (1964) Learning and Instinct in Animals (Methuen, London).

Tinbergen, N. (1960) *The hering gulls world.* New York. Basic Books.

Tomasello, M., & Call, J. (1997). *Primate cognition*. Oxford, England: Oxford University Press

Turner, E.R.A.(1965) Social feeding in birds. *Behaviour* **24**:1-46

Visalberghi E, Limongelli L (1994) Lack of comprehension of cause–effect relations in tool-using capuchin monkeys (*Cebus apella*). Journal of Comparative Psychology 108:15–22

Vince, M. A. 1958. "String-pulling" in birds. (2) differences related to age in greenfinches, chaffinches and canaries. *Animal Behaviour*, **6,** 53-59.

von Bayern, A. M. F., Heathcote, R. J. P., Rutz, C., Kacelnik, A .(2009)The role of experience in problem solving and innovative tool use in crows. *Current Biology*, **19**(22),1965-8

Webster, S. J. & Lefebvre, L. (2001) Problem solving and neophobia in a columbiform–passeriform assemblage in Barbados. *Animal Behaviour*, **62**, 23–32.

Weir, A. A. S. (2005) *Cognitive Psychology of Tool Use in New Caledonian Crows*. Phd Thesis. Magdalen College and Department of Zoology; University of Oxford

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

Werdenich D, Huber L (2006) A case of quick problem solving in birds: string-pulling in keas (Nestor notabilis). *Animal Behaviour* **71**:855-863

Wimpenny, J. H., Weir, A. A. S., Clayton, L., Rutz, C., Kacelnik A. (2009) Cognitive Processes Associated with Sequential Tool Use in New Caledonian Crows. *PLoS ONE,* **4**(8), e6471. doi:10.13

Wood, G.A.(1984) Tool Use by the Palm Cockatoo *Probosciger aterrimus* During Display. *Corella.* **8**(4) 94.95

Chapter 2

Published in

Royal Society Publishing
Informing the science of the future

biology letters

Kea (*Nestor notabilis*) consider spatial relationships between objects in the support problem*

Alice M I. Auersperg, Gyula K. Gajdon and Ludwig Huber

August 2009
Vol 5(4) pp.455-458

* for supplementary material see Appendix III

Kea (*Nestor notabilis*) consider spatial relationships between objects in the support problem

Alice MI Auersperg*, Gyula K Gajdon, and Ludwig Huber

Department of Neurobiology and Cognition Research, Althanstrasse14, 1090 Vienna
Konrad Lorenz Institute for Ethology, Savoyenstrasse1a, 1160 Vienna
** Author for correspondence (Email: alice_bayern@hotmail.com)*

The 'Support Problem' is a benchmark test for investigating the understanding of spatial relationships between objects. We tested the kea parrots' performance in a paradigm that has previously been studied in primates. Kea perform comparably well to tamarins when they are confronted with a choice between two support devices, one of which has a reward resting on it and the other slightly next to it, or when given a choice between a continuous and a disrupted support. Kea did better than chimpanzees in some tasks in which the perceptual connection of the food to the support was altered. The results indicate that kea are capable of assessing the spatial means-end relationships of this problem spontaneously and in a way that is comparable with primates.

Keywords: Physical cognition • means-end task • support problem • aves

1. INTRODUCTION

Knowledge about complex object relations can increase foraging efficiency and may be an important factor contributing to the evolution of intelligence (Byrne 1997). So far, cognitive abilities in the physical domain have been investigated most extensively in primates. Recent studies however suggest that some avian species have evolved higher cognitive abilities convergent to primates (Emery & Clayton 2004). Particularly corvids and psittacines have achieved great accomplishments in physical tasks such as understanding cause-effect relationships, tool use and manufacture (Hunt & Gray 1996, Pepperberg 2004).

The 'Physical Support Problem', first formulated by Piaget (1952) is a classical means-end problem in which the subject has to pull a support as a 'means' to reach a desired 'end'. In an study by Funk (2002) young kakarikis succeeded in pulling a piece of cloth in order to reach the seeds resting upon it. Hauser et al. (1999) also used this design to test learning generalization in cotton-top tamarins. During their first task, the 'On Problem', the subjects had to choose between pulling a cloth with a food pellet on it versus pulling another cloth with the same reward closely next to it. In the 'Connected Problem', subjects had to choose between a pellet resting on an intact piece of cloth versus another reward resting on a cloth that was cut in two pieces, hence, separated by a small gap. Herrmann et al. (2008) later tested the three great ape species on the On- and the Connected Task, which mastered the two problems outstandingly. When Schmidt & Cook (2006) presented pigeons with the Connected Problem however, the subjects required more then 100 trials to succeed. Hauser et al. (1999)'s experiment was replicated by de Mendonça-Furtado & Ottoni (2008) using a single blue-fronted amazon. The individual was tested in the 'On Problem' only and took much longer to learn the task than the tamarins did.

To test whether subjects choose on the coherent form perception of the support around the food reward instead of the physical connection, Povinelli (2000) confronted chimpanzees with tasks where the food in incorrect options was more perceptually contained within the optical field of the support whereas less contained in correct options. Chimpanzees performed at chance in these tasks suggesting that they used the perceptual features rather than a concept of physical connection during choice making.

The kea, a New Zealand parrot, proved to be competent in a vertical pulling task, which involved some understanding of the physical 'connectedness' of objects (Werdenich & Huber 2006). The kea might likewise be an adequate model for addressing a horizontal pulling task. The following study attempts to assess the performance of the kea, as an avian example, in several of the previous variations of the 'Physical Support Problem'.

2. MATERIALS AND METHODS

Six juveniles between 13 and 15 months of age, two of which were males, and two subadult males at four years of age participated in this study. They were all kept in one big outdoor aviary at the Konrad Lorenz Institute for Ethology, Vienna (see electronic supplements for a more detailed description of the methodology).

The apparatus consisted of a wooden box (60cm x 30cm x 30cm) with a Perspex-front that left a 4 cm gap at the bottom. Two red wooden slats, (25cm x 5.5cm x 0.4 cm) were arranged in parallel (20 cm apart) underneath the Plexiglas partition (Figure 1). A reward (peanut) could only be obtained by pulling the baited slat at its end (Figure 1). If there was only one correct slat in the following test series, its side was determined randomly.

All subjects received a basic training followed by five transfer tests (Hauser et al. 1999; Povinelli 2000). During the training sessions, one (two trials), both or neither (one trial each) slat was baited in random order.

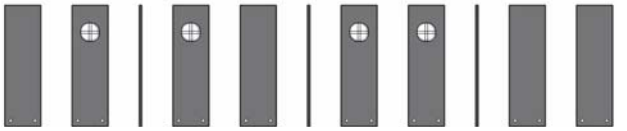
Immediately before each of the following testing sessions subjects had to successfully complete a given number of trials from the previous set up as a precondition to continue (Table 1). This ensured that the subjects were well motivated and attentive. If they failed the precondition, the procedure started again on the next day.

In the following '*On Problem'*, (three test trials per session), two equal rewards were used; one was placed onto the end of one slat and the other was placed one centimetre next to the end of the other slat. In the proceeding '*Connected Problem*' both slats were baited, but one was interrupted by a 2cm gap (six trials per session).

In the final problems for *Control of Perceptual Containment* (six trials per session), four wooden slats, the ends of which were cut into four distinct shapes were used (Figure 1). In the first task 'Combination A′ the reward appeared less contained by the perceptual field of the correct slat (option 1) than of the incorrect option (2). In the next task 'Combination B', the incorrect option (4) seemed perceptually very similar to the correct option (3). In the final task, the birds were offered a combination of the previous options.

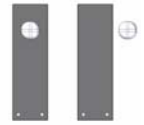
All subjects were tested in visual isolation from other group members. A trial was completed if a subject touched one of the slats; each subject was given one testing session per day and a maximum of ten sessions for each problem. The number of trials per session and the criteria required for a subject to advance to the next task are depicted in Table 1.

Training 1x per session



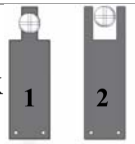
Basic Apparatus

On 3x

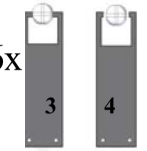


Connected 6x

Combin. **A** 6x



Combin. ***B*** 6x



Mixed Combinations 1x

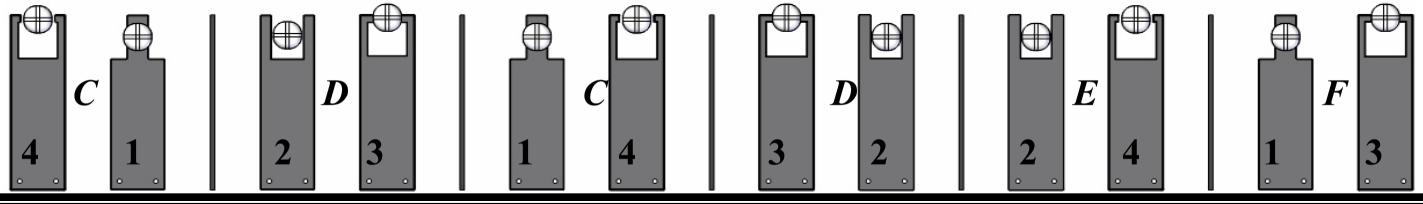


Figure 1. Paired slat combinations as offered in the various tasks. In the On and the Connected task as well as in Combinations A-B the correct slat is semi-randomly allocated (3x right; 3x left)

3. RESULTS

During training, the birds pulled the correct slat 92.5% in the first ten trials. In the 'neither slat baited' condition they stopped pulling altogether in the fifth session Subjects did not show a side preference in trials where both slats were baited (45% left; 55% right choices after five sessions).

In the On Problem six out of eight birds chose correctly in their first trial and five reached significance within the first ten trials. The youngest females Lilly and Willy however, both regressed to begging behaviour when faced with the apparatus in the course of this task and had to be excluded from further testing. In the Connected Problem, no kea except the juvenile male Anu, was above chance level within ten trials (Table1). Gino did not meet the requirement for passing into the next stage after ten sessions.

Four kea mastered combination A. and three subjects Combination B within ten trials (Table 1); After this condition Plume and Anu had to be excluded from testing due to severe motivational difficulties. The three remaining subjects solved the last condition (Combination C&D) within ten trials (Table 1). None of the birds could restrain themselves from pulling slats on the 'none-baited' condition of this task (Combination E).

Table 1. Summary of the results for the different conditions for each subject

Condition	*Subject*	*Criterion*	*Pre-condition*	*Trials / session*	*1st trial correct*	*% correct 1st 10 trials*	*p-values Binominal Test n=10*
Training	Zappel†	8 consecutive correct choices		4	Yes	100*	*0.001*
	Linus†				Yes	90*	*0.001*
	Gino				Yes	100*	*0.001*
	Anu				Yes	100*	*0.001*
	Hope				Yes	90*	*0.001*
	Plume				Yes	80*	*0.044*
	Willy				Yes	80*	*0.044*
	Lilly				Yes	90*	*0.001*
On	Zappel†	2 sessions correct	1 training session	3	Yes	100*	0.001
	Linus†				Yes	100*	0.001
	Gino				No	70	0.117
	Anu				Yes	90*	0.001
	Hope				Yes	90*	0.001
	Plume				Yes	80*	0.044
	Willy				No	70	0.117
	Lilly				Yes	60	0.205
Connected	Zappel†	5 consecutive correct choices / session	3 On Trials	6	No	60	0.205
	Linus†				No	50	0.246
	Gino				Yes	70	0.117
	Anu				Yes	100*	0.001
	Hope				No	60	0.205
	Plume				Yes	60	0.205
A	Zappel†	5 consecutive correct choices / session	3 Connected Trials	6	Yes	90*	0.001
	Linus†				Yes	100*	0.001
	Anu				Yes	80*	0.044
	Hope				No	70	0.117
	Plume				Yes	100*	0.001
B	Zappel†	5 consecutive correct choices / session	3 A-Trials	6	No	80*	0.044
	Linus†				Yes	90*	0.001
	Anu				No	70*	0.117
	Hope				Yes	100*	0.001
	Plume				Yes	80*	0.044
C-D	Zappel†	5 consecutive correct choices / session	2 A-Trials	8	Yes	100*	0.001
	Linus†				No	80*	0.044
	Hope		2 B-Trials		Yes	100*	0.001

• values significantly above chance † subadult males

4. DISCUSSION

Although our test subjects included six juveniles (kea reach maturity at four years of age), all birds expeditiously accomplished the 'On Problem'. This is remarkable given that in a similar situation where two infant (19-month old) chimpanzees had to choose between 2 pieces of cloth, one of which carried a reward, only one subject was capable of solving the problem (Spinozzi & Potí 1993). Similarly to the kea, adult tamarins mastered 78% correct choices on the first trials of the 'On Problem' (Hauser 1999). The amazon tested by de Mendonça-Furtado & Ottoni (2008) in contrary, took over 600 trials to reach its criterion in the 'On Problem'. This neo-tropical parrot had presumably learned to memorise the fused food-reward perceptual form as the correct option.

The kea displayed initial difficulties with the 'Connected Problem'. They chose correctly in 42 % of the first two trials but reached 75% in trials 3 and 4. This renders it unlikely that the subjects perceived the disrupted condition as two separate pieces as opposed to a single piece disrupted by a gap as put forward by Povinelli (2000).

Three kea mastered all perceptual containment tasks surprisingly fast and accurately and did not decrease in performance after the combinations were intermixed. In contrast, the chimpanzees tested by Povinelli (2000) were not capable of solving any similar combinations spontaneously above chance level. It should be considered at this point that the visual acuity of birds is about two to three times better than that of primates (Lythgoe 1979), which might have facilitated their choices.

Nevertheless it is difficult to determine to what degree the kea were capable of recognizing a sophisticated concept behind the problem. The 'Connected Problem' should generally rule out that the animals had learned simply to choose any options in which the reward is placed on the support material ignoring the connection of the same material to their reach. All kea tested on the 'Connected Problem' apart from Anu did not master this challenge immediately, but succeeded eventually after very few sessions. It is therefore possible that most of them initially applied the previous rule before accommodating to the new task. The results of the perceptual containment combinations however render it unlikely that they made their choices based on the fusion of form between the reward and the support.

Kea at this age class have an extraordinarily intense and complex play behaviour (Diamond & Bond. 2004). In contrast to the blue-fronted parrot (de Mendonça-Furtado & Ottoni 2008) kea typically spend a lot of time during the day playing with objects on the ground as many primates do (Diamond & Bond 2004). The juveniles and subadults in our aviary are frequently seen carrying objects, putting them on top of each other and even carrying an object with another one placed on top of it. Through experience they might have developed an intuitive assessment of the effect the movement of an underlying object may have on another one resting on top of it and vice versa. An acquired knowledge/intuitive understanding can be applied when confronted with the Support Problem without requiring a more abstract folk physics i.e. that it is the weight of the top object that is establishing the physical connection to the support (Povinelli 2000).

Our findings demonstrate that the ability to spontaneously consider means end relationships in the support problem is not monopolized by primates. To investigate to what degree this decision making process underlies a causal inference is still a quest of future research.

This study was supported by the Austrian science fund (FWF). We would like to thank Lukas Auersperg and Auguste von Bayern for useful comments on earlier versions of the manuscript

References

Byrne RW (1997) The technical intelligence hypothesis: an additional evolutionary stimulus to intelligence? In: Whiten A, Byrne RW (eds) Machiavellian intelligence. vol II: extensions and evaluations. Cambridge University Press, Cambridge, pp 289–211

Hauser M D, Kralik J D & Botto-Mahan C (1999) Problem solving and functional design features: experiments on cotton-top tamarins, *Saguinus Oedipus oedipus*. *Animal Behaviour* **57**:565 – 582

Herrmann, E, Wobber, V & Call, J (2008) Great Apes' (Pan troglodytes, Pan paniscus, Gorilla gorilla, Pongo pygmaeus) Understanding of Tool Functional Properties After Limited Experience. *Journal of Comparative Psychology* **122**: 220-230.

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

Diamond J, Bond A B (2004) Social play in kaka (*Nestor meridionalis*) in comparison to kea (*Nestor notabilis*) *Behaviour* **141**: 777-798

Emery N J, Clayton N S (2004) The mentality of crows: convergent evolution of *intelligence in corvids and apes. Science **306**:1903–1907*

Funk, M (2002) Problem solving skills in young yellow-crowned parakeets (Cyanoramphus auriceps). *Animal Cognition* **5:** 167-76

Lythgoe, J N (1979) *The Ecology of Vision.* Oxford: Clarendon Press, 180–183.

de Mendonça-Furtado O, Ottoni E B (2008) Learning generalization in problem solving by a blue-fronted parrot (*Amazona aestiva*). *Animal Cognition* **11**:719-725

Pepperberg I M (2004) 'Insightful' string-pulling in grey parrots (Psittacus erithacus) is affected by vocal competence. Animal Cognition, **7**: 263–266.

Piaget J (1952). *The origins of intelligence in children.* New York: International Universities Press.

Povinelli D J (2000) *Folk Physics for Apes. The Chimpanzee's Theory of How the World Works*. Oxford University Press.

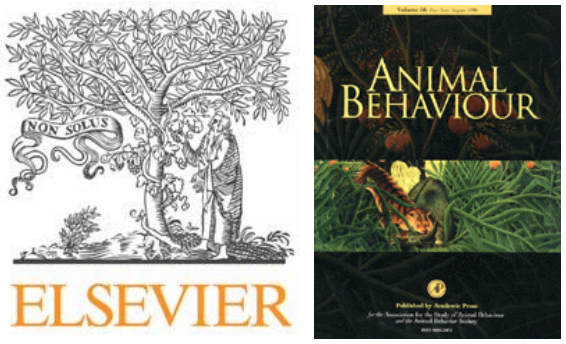
Schmidt, G F & Cook, R G (2006) Mind the Gap: Means-End Discrimination by Pigeons. *Animal Behaviour* **71**: 599-608.

Spinozzi G & Potı́ P (1993) Piagetian Stage 5 in Two Infant Chimpanzees (*Pan troglodytes*): The Development of Permanence of Objects and the Spatialization of Causality. *International Journal of Primatology* **14**: 905-917

Werdenich D, Huber L (2006) A case of quick problem solving in birds: string pulling in keas, *Nestor notabilis. Animal Behaviour* **71**: 855-863

Chapter 3

Published in



Kea (*Nestor notabilis*) produce dynamic relationships between objects in a second order tool use task

A.M.I. Auersperg, G.K. Gajdon, L. Huber

Published online September 2010

Kea (*Nestor notabilis*) produce dynamic relationships between objects in a second order tool use task

Alice MI Auersperg[1, 2]*, Gyula K Gajdon[1, 2], and Ludwig Huber[1]

[1]*Department of Cognitive Biology, Althanstrasse14, 1090 Vienna*

[2] *Konrad Lorenz Institute for Ethology, Savoyenstrasse1a, 1160 Vienna*

**Author for* correspondence *(Email: alice_bayern@hotmail.com)*

Summary

Studies on advanced forms of tool use in birds have mainly been concentrated on corvids as yet. In this study captive kea, a neophilic New Zealand parrot species produce different orders of spatial object relationships in a Tube Lifting/Object Inserting Paradigm. Here we can show, that the kea, which are neither natural tool users nor nest builders readily solve a second order tool use task. They also learn to produce highly complicated means-means end sequences in a short period of time.

Keywords

birds · physical cognition · means-end · tool use

Introduction

Creating sophisticated object relationships to achieve a goal has been considered to be one of the defining features of intelligent species (Schaik, Deaner & Merrill 1999, Reader &Laland 2002).

The more complicated object relationships created by animals often involve the use of tools as means to reach a desired item. Tool use is defined by Ben Beck (1980) as "the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool." Tool use competences can be categorized in terms of levels

of complexity: Fragazy , Visalberghi & Fedigan (2004_1) describe the relationships produced when a subject acts on an object and an action on a second object occurs by default as zero order relations as for example pulling a piece of cloth with a food reward resting upon it (Auersperg, Gajdon & Huber 2009). Acting with object A in relation to object B (for example pounding a nut with a stone) is classified as a first order relation. Finally, acting with object A in relation to object B following a placement of object B in relation to a third object C would be entitled second order relationships. Wimpenny, Weir, Clayton, Rutz & Kacelnik (2009) also describe 'secondary tool use' as 'using one tool on another object to access it or modify it for the use as a tool'.

Secondary tool use has rarely been observed in non-human animals other than primates. There is however increasing evidence of elaborate consideration of object relationships in two corvid species. The New Caldonian crow (*Corvus moneduloides)*, which routinely uses tools within its natural environment, has recently shown secondary tool manipulation in the laboratory in the form of meta-tool use (Taylor, Hunt, Holzhaider & Gray 2007; Wimpeny et al. 2009). There is also evidence that these birds have some causal understanding about the effects that objects may have on one another (von Bayern, Heathcote, Rutz, Kacelnik 2009; Taylor, Hunt, Medina & Gray 2009).

Recently, there have also even been impressive demonstrations of first and second order tool use in a non-tool using corvid, the rook (*Corvus frugilegus*) (Bird & Emery 2009). To our present knowledge there has been no investigation of secondary tool use in any bird species other than corvids.

There is currently debate on whether tool use stimulated the evolution of intelligence in tool using species or whether it is more likely to be a by-product of general purpose intelligence (Bird & Emery 2009).

It has also been argued that most birds are routinely establishing more complicated object relationships during nest building than during tool use and that tool use might merely have evolved to replace morphological adaptations (Hansell & Ruxton 2008; Kacelnik 2009). It would therefore be interesting to test complex levels of tool use in species that lack sophisticated nest construction.

The kea is a parrot, resident in the mountain region of New Zealand. This species is

not known to build complex nest cups but to breed in simple burrows (Jackson 1963). As a consequence of a scarcity of predators and a seasonality of food availability, the kea are highly neophilic. Similar to other destructive foragers, like the New World capuchin monkeys that are using tools in the laboratory as well as in the wild (Fragaszy, Izar, Visalberghi, Ottoni, de Oliviera 2004_2, Fragaszy et al 2004_1), kea display an extremely strong urge to manipulate and dismember novel objects (Diamond and Bond 1999, Diamond & Bond 2004). This 'haptic neophilia' may expose the animals to functional object characteristics that are unavailable to more neophobic species. It is likely that such behaviour enhances innovativeness and facilitates learning.

Observations of kea in the laboratory have shown remarkable learning capacities about their physical environment (Werdenich & Huber 2006). They also show intense combinatorial activity during object play, in particular when inserting objects into hollow spaces (Gajdon, Lichtenegger & Huber submitted). Since combinatorial actions may allow access to otherwise inaccessible resources and require an ability to coordinate objects relative to each other, they can be considered as precursors of tool use in non-tool using species (Fragaszy et al. 2004).

In order to examine the keas' sensitivity to different orders of object relationships we devised an experimental setup in which subjects had to establish increasingly complicated levels of spatial relationships between objects by themselves. Our subjects had previously participated in an Inserting as Means Paradigm (Gajdon et al. submitted), in which they had learned to drop the smaller of two differently sized cubes into an opaque tube. The opaque tube was firmly fixed in a vertically slanted position and contained a reward, which was pasted onto the middle of the tube floor using cream cheese. When an object was inserted into the upper end of the tube it would knock against the reward and cause it to fall out at the lower end of the tube. For the following experiment, we used a similar design but the tubes were lying on the ground without fixation.

In the first 'Tube Lifting' paradigm, the reward was lying freely on the tube floor and the tube had to be lifted at one end in order to release the reward. The object relations produced here are Zero order relations (Fragaszy et al. 2004_1).

The following 'Spaghetti Breaking' paradigm, investigated whether the animals could

combine their tool size expertise (Gajdon et al. submitted) with their new experience from the Tube Lifting paradigm to master a second order tool use task. Here, reward was pinned inside the tube using an uncooked spaghetti and could only be attained by inserting the appropriate object and thereafter lifting the tube at the side the object was inserted in order to break the spaghetti and release the reward. The object relationships produced in this case are second order relationships (act with an object A (tube) in relation to an object B (ball) following a placement of object B in relation to a third object C (reward); see Fragazy et al 2004_1).

Subjects

Ten kea participated in the experiment: Three juvenile females (Coco, Plume and Rudy), two juvenile males (Gino & Tammy) as well as five adult males (Mismo, Luke, Frowin, Knut & Kermit). They were all bred in captivity. The juveniles as well as the adult Kermit were hand raised. All subjects were kept together in a large outdoor aviary (15m x10 m x 4 m) at the Konrad Lorenz Institute for Ethology in Vienna. The aviary was equipped with breeding cabins, wooden shelters, foraging tables, a pond, a climbing wall as well as heavy branches that were suspended from the ceiling. Additional environmental enrichment was provided daily (leafy branches, halved coconuts, cardboard boxes and other). The floor of the aviary was covered with sand.

Food was spread every day at noon and at five pm and consisted of a mixture of seeds vitamin supplement, various fruits and vegetables as well as a daily protein source (boiled eggs, cottage cheese with yogurt, corn or minced beef). The amount of food was balanced weekly to keep the birds at their free feeding weights. Fresh drinking water was available *ad libitum.* The subjects were visually isolated from their group mates within an experimental compartment (5m x 10m) during testing using an opaque sliding wall. We confirm that all subjects that participated in the described experiments were housed in accordance with the Austrian Federal Act on the Protection of Animals (Animal Protection Act – TSchG, BGBI. I Nr. 118/2004). Furthermore, as all kea studies are strictly non-invasive and based purely on behavioural tests, they are classified as non-animal experiments in accordance with the Austrian Animal Experiments Act (§ 2, Federal Law Gazette No. 501/1989).

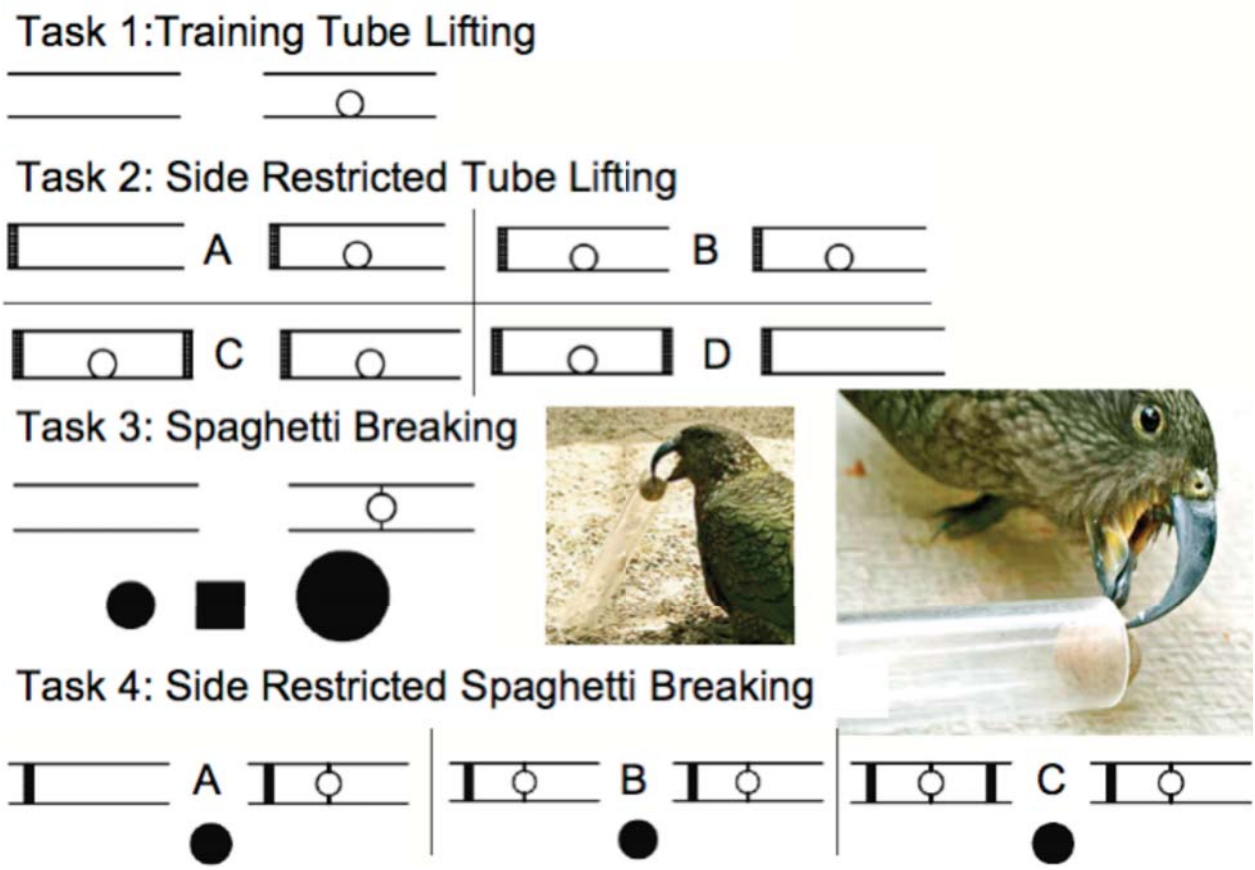


Figure 1. Constellation examples for the four different tasks: the horizontal represent the tubes, the bold vertical lines the stoppers and the small circles the food reward. In Task 3 the three black images represent the three objects offered. The thin vertical lines Task 4 represent the spaghetti, the reward is pierced upon.

Table 1: The Experimental conditions: Tube Lifting (TL), Side restricted Tube Lifting (TLA-D), Spaghetti Breaking (SB) and Side Restricted Spaghetti Breaking (SBA-C); P=hypothesized mean; Trial No./Ses =Number of trials per session; Session No. = Number of session; No. of stoppers=the total number of stoppers on both of the two tubes; Reward Pierced= the state of the reward (pierced upon a spaghetti or free inside the tube)

Cond.	*Correct sequence of action*	*P*	*Trials No./Ses*	*Session No.*	*No. of stoppers*	*Reward pierced*
TL	Choose correct tube	0.5	4	5	0	No
TLA	Choose correct tube; Choose correct end	0.5	2	15	2	No
TLB	Choose correct end	0.5	2	15	2	No
TLC	Choose correct tube; Choose correct end	0.25	2	15	3	No
TLD	Do not touch tubes	-	2	15	3	No
SB	Select correct object; Insert into correct tube; Lift at the same side the object was inserted at	0.5	8	5	0	Yes
SBA	Choose Correct tube; Insert at correct end; Lift same end; Lift opposite end	0.5	2	15	2	Yes
SBB	Insert at correct end; Lift same and Lift opposite end	0.5	2	15	2	Yes
SBC	Choose correct tube. Insert at correct end; Lift same end; Lift opposite end	0.25	2	15	3	Yes

Task 1: Tube Lifting

Methods

A consolidation phase was designed to control whether the animals were motivated by the reward rather then by a more general interest in playing with the apparatus. Two transparent Plexiglas tubes (outer diameter: 4 cm, inner diameter 3 ca 3,8 cm; length 22 cm) were arranged next to one another in line at a distance of about 20-25 cm (see TL,Table 1, Figure 1). One, both or neither of the tubes was baited with a peanut. The animals were not allowed to observe the baiting of the tubes. A trial started as soon as the subject entered the

experimental compartment and ended as soon as the food was retrieved. The reward could be attained by lifting the baited tube and hence, causing the peanut to fall out at the other end. Subjects had to walk approximately 1.5 m towards the apparatus. The birds received five sessions of four trials (left tube baited, right tube baited, both tubes baited and no tube baited) in random order.

Results

All data investigated followed a normal distribution (K-S test). No subject made more than two incorrect choices within the ten trials in which just one of the two tubes was baited (Binominal Test, $p=0.044$). All subjects except Frowin stopped lifting tubes in the 'None' condition after five sessions.

Task 2: Side Restricted Tube Lifting

Methods

Two transparent tubes were arranged as in Task 1. The tubes were fitted with wooden stoppers at one or both ends. The four possible testing conditions A-D (TLA-D) are detailed in Figure 1 and Table 1. In all conditions except condition D and C, in which one of the tubes had stoppers at both ends, the peanut was available by lifting a reward-baited tube at the end sealed with a stopper so the food would roll out at the open end. Subjects received 15 sessions of eight trials. Each session comprised each condition twice, and thus, each subject received a total of 30 trials of each condition. The side of the correct tube in conditions A, B and C as well as side of the baited tube in condition D was pseudo-randomized. The arrangement of the stoppers (pointing left or right) was randomized. A trial was scored as correct if the subject directly lifted the side of the tube that would lead it to a reward. Condition D was only considered as correct if the subjects did not lift either tube within the experimental time. A trial lasted two minutes or until the reward was recovered.

Results

Upon the first trial (independent of condition), eight out of ten subjects chose to lift a tube end without a stopper and therefore incorrectly (Binominal Test, p=0.044).

The subjects developed three different techniques during testing: Most subjects lifted the tube directly at the stopper end. Gino grabbed the middle of the tube, lifted it up in a horizontal position and finally poured its content out at one side. Frowin grabbed the lower rim of the open end of a baited tube and lifted it very high above his head until the food fell out towards his bill. His technique became consistent after his fifth session.

In Condition D the kea always tried to open the baited tube with the unavailable reward with their beak and never stopped doing so, as was expected due to their extreme curiosity and their unrestrainable play instinct (Diamond and Bond 1999). We divided the remaining results into three session blocks (session1-5; session 6-10; session 11-15). Within each session block, a subject conducted ten trials of each condition (A, B, C and D). We set the hypothesized mean at 0.5 in Condition A and B and at 0.25 in Condition C. The data followed a normal distribution (K-S test). Performance improved throughout the first two session blocks: We found a significant difference between block one and two (Mixed Model Analysis, mean=-2.67, SE= 0.53, $p<0.001$) but no difference between block two and three (Mixed Model Analysis, mean=-0.77, SE= 0.52, p=0.14). Furthermore, we performed One-sample T-tests for each session block for each condition. The group mastered each of the conditions A, B and C in the second session block (T_A= 2.844, p=0.02; T_B=4.65, p=0.002; T_C=4.009, p=0.004). Kermit and Gino were very successful in all trials of block 2&3 (82% and 78%, respectively) and Mismo even reached 93% correct choices by that time (for individual data see Table 2)

Table 2: Individual performance in the Side Restricted Tube Lifting (TLA-C). Number correct out of 10 trials for each condition (TLA), TLB, TLC) during session 1-5 (TL1), 6-10 (TL2) and 11-15 (TL3)
* statistical significance (Binominal test; hypothesized mean for TLA&B =0,5; for TLC =0,25)

Ind	*TLA1*	*TLB1*	*TLC1*	*TLA2*	*TLB2*	*TLC2*	*TLA3*	*TLB3*	*TLC3*
Co	2	7	4	8*	5	3	10*	9*	4
Gi	6	2	1	9*	7	6*	9*	8*	8*
Ke	6	6	4	10*	7	6*	8*	9*	9*
Kn	8*	7	4	8*	9*	4	9*	5	5
Lu	6	6	4	7	10*	5/	8*	9*	4
Mi	4	8*	1	9*	10*	8*	10*	10*	9*
Pl	2	4	1	8*	5	5	6	10*	4
Ry	4	5	2	7	10*	4	5	6	4
Ta	2	3	2	5	9*	2	7	9*	6*

Discussion Tube lifting

The consolidation phase demonstrated that the reward was clearly visible as well as the primary motivation for the birds.

The group succeeded in all conditions of Task 2 in the second session block. On their very first trial subjects lifted the tube at the open end, causing the reward to fall towards the stopper at the opposite end. This could result from a transferred preference to lift the tubes at the rim, which was rewarding in Task 1. There are possible associative rules that could relate features of the tubes to the food reward: For example, birds may always lift a rewarded tube at the stopper end in condition A and B, or always lift a rewarded tube that only has one stopper at the stopper end in case of condition C. Interestingly some animals accomplished either condition A or B at the same time as condition C. It would be more plausible to first learn to lift at the stopper end and only later attend to number of stoppers at a tube. An alternative explanation would therefore be that they developed an apprehension about the nature of the stoppers (blockage). This will be the subject to future studies.

Frowin used the simplest possible solution to the task: since he consistently grabbed the tubes at the open end and poured the content toward his face he did not have to attend to the number of stoppers in Condition C. Gino always lifted the tube in the middle and poured the

content out. Therefore after choosing a rewarded tube with only one stopper he simultaneously had to attend to the position of the stopper and to the direction of his pouring.

Task 3: Spaghetti Breaking

Methods:

The same nine subjects as in Task 1 and 2 (Gino had died) participated in a short preference test on three unfamiliar wooden objects: a big ball (2r=8cm), a small ball (2r= 3,5cm) and a small cube (4x4cm). Each bird was allowed to explore the objects for five minutes individually while being visually isolated from its group mates.

The following day, the same objects were placed in a triangular arrangement (ca. 1m side length) around two transparent Plexiglas tubes that were aligned next to each other as in Task 1 and 2 (see Task 3; Figure 1). The big ball and the small cube (because of its shape) did not fit into the tube opening. The small ball matched the diameter of the tube opening and could carefully be inserted. One of the tubes was baited with a reward (a piece of rice waffle); the other tube was empty. The reward was pierced upon a piece of uncooked spaghetti (Barilla No.1), which was inserted through a small hole in the middle of the tube. The surplus spaghetti was broken off at the upper surface of the tube and transparent adhesive tape was put over the small hole. If an appropriately sized object was inserted into the tube and if the tube was subsequently lifted at the same end, the object would dash against the spaghetti, break it and release the reward at the opposite end (see Video suppl. mat.).

Subjects received five sessions of eight trials in this task. The baiting was pseudo-randomized (four right and four left baited trials). Trials ended when the reward was recovered or after five minutes. To investigate whether subjects used the most efficient order of actions, a trial was scored as correct if the subject (1) carried the correct object (small ball) to the correct tube, (2) inserted it into the tube and (3) then lifted at the same end. Trials including attempts to lift the tubes before inserting or attempts to insert the wrong objects were scored as incorrect.

Results

Results Object Preference

In the initial exploratory phase (in which only the three objects and no tubes were available to the subjects), the data for the frequencies of manipulations were normally distributed for each object (K-S test). There were no traceable differences in the frequency of the manipulation between the big ball (bb) and the small ball (sb) (Mixed Model Analysis; Mean $Diff._{freqency}$=-0.33, SE=0.56, p=0.56). Both ball objects were however touched more often than the small cube (sc) (Mixed Model Analysis; Mean $Diff_{sb-sc}$=1.55, SE=0.56, p=0.013; Mean $Diff._{bb-sc}$=1.22,SE=0.56, p=0.04).

Results Spaghetti Breaking

Seven out of nine subjects inserted objects into the tubes within the first trial. Two juvenile females, Plume and Ry (Pl and Ry) were excluded from testing after not inserting any object over three sessions. All remaining subjects except Knut stopped lifting the tubes before fetching an object within the first session. Mismo only lifted a tube once in the first trial and then immediately fetched the correct object (sb) and consistently used the correct sequence of action in order to retrieve the reward.

In session one, the mean frequency of lifting tubes before the tool was fetched in the first four trials was 2.95 and in the last four trials 0.2. The Group data within each session was normally distributed (K-S test).

The choices were consistently correct after the second session i.e. after 16 trials (T=3.05, N=7, p=0.023) and the performance kept improving throughout sessions (Mixed Model Analysis; block 1-2, Mean Diff=-39.78, SE= 6.2, $p<0.001$; block 2-3 Mean Diff.=-22.67, SE=6.2, $p<0.001$).

Results Object Preference during Testing

The mean frequency the small ball was touched was 50 times (8.2 times in the first session). The cube was only touched 9.5 times on average, (7.2 of in the first session). The big ball, which was as popular as the small ball in the preference test, was only touched 0.8 times on average (all in the first session). The mean frequency of inserting the correct object into the

incorrect tube was 0.27 across the experiment.

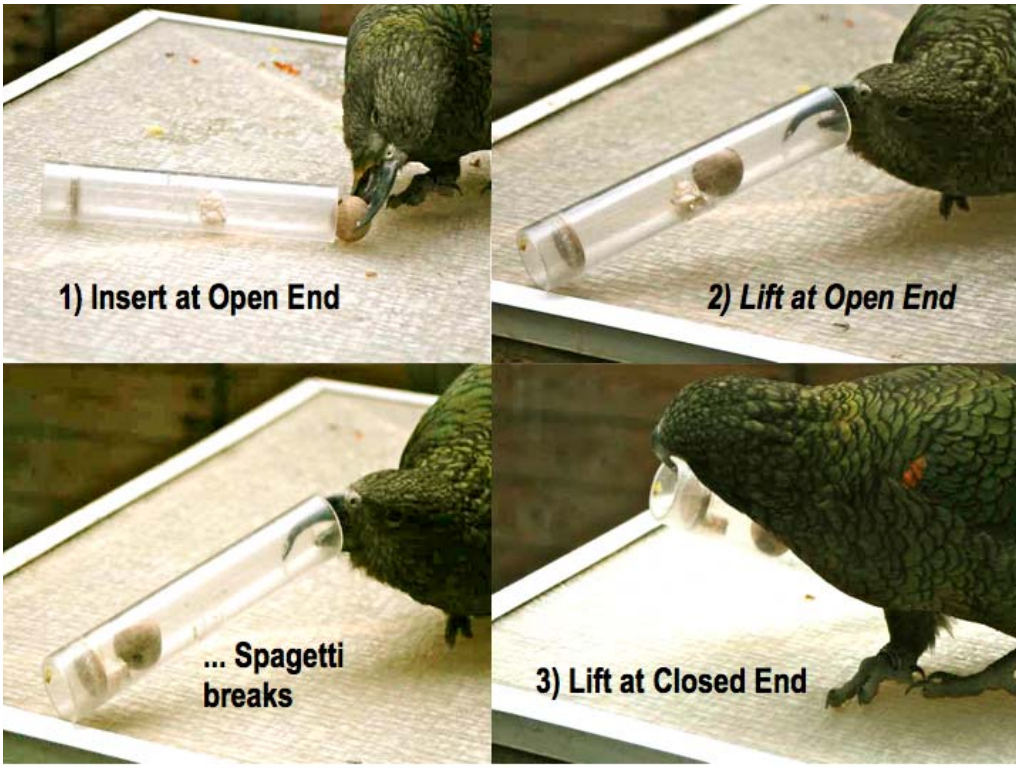
Task 4: Side restricted Spaghetti Breaking

Methods

The reward was pinned onto a Barilla No.1 spaghetti inside the tube, as previously, but the tubes contained wooden stoppers. The stoppers were shifted inside the tubes at ca 1.5 cm distance from the tubes' end. It was still possible to insert an object into a stopper end, but the movement of the object would eventually be blocked. The arrangement of the stoppers was the same as in condition A, B and C in Task 2 (see task 4; Figure 1). The tubes were arranged as previously and only one object (small ball) was placed in between them at a distance of about 30 cm towards the entry of the subject. Subjects received 15 sessions of eight trials. Each session comprised each condition twice, and thus, each subject received a total of 30 trials of each condition. The sequence of actions was regarded as correct if the subject (1) carried the object to the correct tube directly (without previous lifting of the tubes), (2) inserted it at the open end, lifted at the open end and (3) lifted at the closed end causing the reward (and the ball) to fall out. Any derivation from this sequence of action was scored as incorrect (see Figure 2, Video suppl. mat.).

It frequently occurred that although the correct sequence of actions had been conducted the reward was still not available. There were two possible reasons: (1) the tube was not lifted up high enough or too slowly so the object did not break the spaghetti and the reward was still stuck inside the tube (Pierced). (2) The spaghetti broke but only the ball was poured out of the tube and the reward was still lying loosely inside the tube (Loose). We recorded the next action of the subject after such an occurrence. There were four different possibilities. Reinsert the ball at the open end, insert the object at the stopper end, lift the open end or lift the stopper end. The correct action if the reward was still pierced was to reinsert the object at the open end; the correct action if the reward was loose inside the tube was to lift the stopper end. The events were divided into the three session blocks (1-5, 6-10, 11-15) as previously.

Figure 2. Correct sequence of actions in the Side Restricted Spaghetti Breaking: Insert the object at the open end of a baited tube, lift at the same end. The objects hits the spaghetti and releases the reward from is anchorage. Lift at the closed end in order to pour the reward (and the object) out of the tube.



Results Side restricted Spaghetti Breaking

We set the probability of performing correctly by chance (P) conservatively at 0.5 in Condition A and B and at 0.25 in Condition C like in Task 2. Within one block, each subject conducted ten trials of each condition. The data within each block followed a normal distribution (K-S test). Knut (Kn) lost motivation during the second block due to poor health condition.

The subjects did not solve Condition A in the most efficient order (T_{A3}=1.55, p=0.19), but they did master conditions B and C after the second session block i.e. after 10 trials per condition (T_{B3}=2.75, p=0.05, T_{C3}= 7.086, p=0.002). In 79,4% of the incorrect trials of the first session block, the ball was first inserted at the stopper end. The performance improved throughout blocks (Mixed Model Analysis, block 1-2, Mean Diff. =-39.78, SE=6.19, p<0.001, block 2-3 Mean Diff.=-22.67, SE=6.19, p<0.001). The adult male Luke mastered conditions B

and C already after the first session Block, Kermit and Tammy solved the task after the second session block (see Table 3).

Additionally we evaluated events in which the reward was not available after the correct sequence of actions. If ten or more events occurred within one session block of an individual, we conducted a binominal test with the hypothesized mean set at 0.25 (four possible responses). Knut, Luke and Kermit accomplished correct reactions to the 'Pierced' event in the first block, but Knut later decreased in performance due to his health problems. Most subjects reacted accurately to the 'Loose' event after the second session block (see Table 4). Luke solved the problem in the first session block. We do not have enough data from Tammy in the first session block but he had a tendency to react correctly straightaway (see Table 4

Table 3: Individual performance in the Side Restricted Spaghetti Breaking (SBA-C). Number correct out of 10 trials for each condition (SBA, SBB, SBC) during session 1-5 (SB1), 6-10 (SB2) and 11-15 (SB3).*statistical significance (Binominal test; hypothesized mean for SBA&B=0,5; for SBC=0,25)

Ind	*SBA1*	*SBB1*	*SBC1*	*SBA2*	*SBB2*	*SBC2*	*SBA3*	*SBB3*	*SBC3*
Co	2	1	1	5	7	3	4	5	5
Ke	3	3	1	7	9*	4	8*	10*	8*
Kn	2	1	0	2	3	1			
Lu	4	2	0	7	8*	7*	8*	9*	8*
Mi	2	0	0	2	3	3	7	7	7*
Ta	2	2	2	3	4	4	9*	8*	7*

Table 4. Correct/total number of first next actions in regard of the food's current status. 'Pierced'or 'Loose'. (*Above chance according to Binominal test with hypothesized mean at 0,25)

Ind.	*Loose Sess.bl. 1-5*	*Loose 6-10*	*Loose 11-15*	*Pierced 1-5*	*Pierced 6-10*	*Pierced 11-15*
Co	3/7	9/14*	9/11*	4/7	19/23*	4/6
Ke	6/15	13/19*	8/10*	13/19*	21/23*	8/8
Kn	1/6	9/10*	-	11/16*	3/3	-
Mi	3/7	4/5	5/6	1/1	5/9	12/15*
Lu	8/10 *	12/13*	7/7	8/10*	9/10*	3/3
Ta	6/7	14/18*	0/0	2/3	1/2	3/3

Discussion Spaghetti Breaking

In Task 3 seven out of nine subjects obtained the reward on the first trial within the time given. This illustrates that with pre-experience non-tool using kea can rapidly generate complex levels of object relationships like second order tool use. Initially the tubes were lifted before searching for a suitable object, which is a plausible outcome given their experience in Task 1 and 2. The lifting ceased after only one session, in Mismo's case even after the first trial, and subjects went scanning the surroundings for the appropriate object. Hence the animals were able to quickly infer that a tool was needed.

In contrast to the Inserting as Means Paradigm (as described in the introduction; Gajdon et al. submitted), tubes were lying freely on the ground and the diameter of the tubes was much smaller. Subjects could not just drop the correct object as before but it had to be carefully fitted into the tube entrance, which was complicated by the tube lying horizontally and being movable. Once the object was inserted, the tube had to be lifted with the enough power in to create sufficient force in the ball object to break the anchorage of the reward. Additionally subjects had to search for the correct object (the position of which was changed for each trial) at a distance and carry it to the correct tube. This also complicated the task since it required basic planning mechanisms (Visalberghi et al. 2009). Subjects were similarly interested in both ball objects during the preference trial. During the actual test they immediately preferred the small ball, which indicates that they were able to instantaneously transfer their tool size expertise from the Inserting as Means Paradigm (as described in the introduction; Gajdon et al. submitted) to the novel context and objects.

The most efficient action sequence in Task 3 was to find the correct object, carry it to a baited tube, insert it and lift the tube at the same end. The adult male Mismo produced this order immediately and continuously, which indicates that he was able to spontaneously combine both his tool size expertise from the Inserting as Means Paradigm as well as his Tube Lifting experience in this context. The rest of the group accomplished consistency of this order after only 16 trials. In session one and two it was a common failure to first insert the correct object into the empty tube. This might be due to the change of reward; the white rice waffle may appear more cryptic inside the Plexiglas tube than the peanut. Difficulties with avian vision through Plexiglas have been described before (Wimpeny et al. 2009).

In Task 4 all subjects achieved the reward within the time given from the first trial on. Luke used the most efficient sequence of action possible in conditions B and C already after the first session block, hence after 10 trials of each condition. The group also mastered the highly complex multi-step action sequences of conditions B and C after the second session block, hence after 20 trials of each condition. Since subjects first inserted the ball at the stopper end in 80% of the incorrect trials in the first session block, it is likely that subjects were initially induced to go to the stopper end as this was rewarding in Task 2 and insert the ball (as was rewarding in Task 3). This is most likely a chaining effect that subjects managed to inhibit after the second session block. The results of Task 4 show that kea can quickly accomplish a highly complicated action sequence in the correct order. Stringing together such elaborate successions (means-means-end sequences) within a few trials can be cognitively demanding since it requires disregarding the final goal in the beginning in order to concentrate on the necessary steps in the sequence according to its order in time and space (Santos 2005). The keas seem to be highly sensitive to the contingencies of reinforcement of these tasks. The performance of some subjects reflects a susceptibility to learning sets (learn how to learn) as shown in primates by Harlow (1949). They seem to be able to learn to execute strategic rules to situations that help to solve problems more efficiently.

We can gain cues about some of the mechanisms involved when looking at the supplementary data collected from the cases when the reward was not available after the correct sequence of actions. The adult male Luke reacted immediately in the most efficient manner if the reason for the unattainability of the reward was that the spaghetti had not broken (reinsert the object at the open end). He also spontaneously attained the correct reaction when the spaghetti was broken but the reward was still loosely inside the tube (Lift the closed end and the reward will fall out).

Luke was able to flexibly apply his knowledge from either Task 2 (Lift at the stopper end) as well as from Task 3 (insert tool) depending on the state of the reward (Pierced or loose). To investigate his perception of tool function in further detail we need future experiments in which we alter the weight of the object.

Concluding Remarks

From the Tube Lifting Paradigm (Task 2) we learn that captive kea rapidly develop a sensitivity for stoppers in a set up testing for zero order relationships.

The results of the Spaghetti Breaking Paradigm (Task 3) indicate that the animals can flexibly apply previous experience about tool size assessment and their Tube lifting experience (Task 1 and 2) to a new context that even involves simple planning mechanisms (Gajdon et al. submitted, Visalberghi et al. 2009). Most importantly we can show at this point that captive kea, which are not natural tool users, are the first non-corvid birds to be capable of mastering a second order tool use paradigm (Fragazy et al. 2004_1, Taylor 2007, Bird & Emery 2009, Wimpenny et al. 2009).

All avian species that have previously been tested on complicated tool use tasks are, to our knowledge, nest builders. The kea, in contrast, breed in simple burrows and do not construct complex nests (Jackson 1964). It has been debated whether tool use can be explained by low level processes, since most birds are already routinely establishing more complex object relationships during nest building (Hansell & Ruxton 2008). Although we cannot determine the cognitive prerequisits of complex tool use in birds, the present findings suggest that sophisticated nest construction is not crucial here.

Acknowledgments

We would like to thank Auguste v. Bayern, Lukas Auersperg and Orlaith Fraser for useful comments on earlier versions of the manuscript. This experiment was funded by the Austrian Science Fund, FWF. We would also like to thank the WAF as well as Werner Zecchino for additional sponsoring and the 'Tiergarten Schönbrunn' for providing one of our subjects.

References

Auersperg, A.M.I., Gajdon, G.K. & Huber, L. 2009. Kea (Nestor notabilis) consider spatial relationships between objects in the support problem. *Biology Letters,* **5**, 455-458.

Beck, B. B. 1980. *Animal tool behavior: the use and manufacture of tools by animals*. New York; London, Garland STPM Pres

Bird, C. D.& Emery, N. J. 2009. Insightful problem solving and creative tool modification by captive non tool-using rooks. *Proceedings of the National American Society*, **106**, 101370-10375.

Diamond, J.& Bond, A. B. 1999. *Kea, Bird of Paradox*. Oxford University Press

Diamond, J.& Bond, A. B. 2004. Social play in kaka (*Nestor meridionalis*) in comparison to kea (*Nestor notabilis*). *Behaviour* ,**141,** 777 – 798.

Fragaszy, D. M., Vishalberghi, E.& Fedigan, L. M. 2004. *The Complete Capuchin*, Cambridge University Press

Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E. B., de Oliveira M. G. 2004. Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology,* **64**(4), 359-366

Gajdon, G. K., Lichtenegger M. & Huber L. 2009 Toddler like affordance exploration helps captive mountain parrots to innovate tool use behaviour. Submitted

Hansell, M. & Ruxton, G. 2008. Setting tool use within the context of animal construction behaviour. Trends in Ecology and Evolution, **23**,73–78

Harlow, H. F. 1949. The formation of learning sets. *Psychol. Rev.,* **56**, 51-65,

Jackson, J. R. 1963. The nesting of keas. *Notornis,* **10**, 319-326.

Kacelnik, A. 2009. Tools for thoughts or thoughts for tools? *Proceedings of the National Academy of Sciences of the United States of America* ***106***, 10071-10072.

Reader, S. M., Laland, K. N. 2002. Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences of the United States of America*, **99**(7), 4436-4441

Schaik, C. P., Deaner, R. O., Merrill, M. Y.1999. The conditions for tool use in primates: implications for the evolution of material culture. *Journal of Human Evolution*, **36**, 719–741

Santos, L., Rosati, A., Sproul, C., Spaulding, B., Hauser, M. D. 2005. Means-means end tool choice in cotton top tamarins (*Saguinus oedipus*): finding the limit of primates' knowledge of tools. *Animal Cognition* **8**, 236-246

Taylor, A. H., Hunt, G. R. , Holzhaider, J. C., Gray R. D. 2007. Spontaneous metatool use in New Caledonian Crows. *Current Biology* **17**, 1504-1507

Taylor, A. H., Hunt, G. R., Medina, F.S., Gray, R. D. 2009. Do New Caledonian crows solve physical problems through causal reasoning? *Proceedings of the Royal Society, London* B **276**, 247-254

Visalberghi, E., Spagnoletti, N., Ramos da Silva, E. D. , Andrade, F. R. D, Ottoni, E., Izar, P., and Fragaszy, D. 2009. Distribution of potential suitable hammers and transport of hammer tools and nuts by wild capuchin monkeys. *Primates,* **50**, 95-104**.**

von Bayern, A. M. F., Heathcote, R. J. P., Rutz, C., Kacelnik, A .2009.The role of experience in problem solving and innovative tool use in crows. *Current Biology*, **19**(22),1965-8

Werdenich, D., Huber L. 2006. A case of quick problem solving in birds: string-pulling in keas (*Nestor notabilis*). *Animal Behaviour,* **71,** 855-863

Wimpenny, J. H., Weir, A. A. S., Clayton, L., Rutz, C., Kacelnik A. 2009. Cognitive Processes Associated with Sequential Tool Use in New Caledonian Crows. *PLoS ONE,* **4**(8), e6471. doi:10.13

Chapter Four

Flexibility in problem solving and tool use of Keas and New Caledonian Crows in a Multi Access Box paradigm

[*]Alice M.I. Auersperg, Auguste M.P. von Bayern, Gyula K. Gajdon, Alex Kacelnik, Ludwig Huber

Submitted

[*] The exact order of the authors list (except the corresponding author) is not yet finalized and may be changed before publication

Flexibility in problem solving and tool use of Keas and New Caledonian Crows in a Multi Access Box paradigm

Alice Marie Isabel Auersperg[1,3]*, Auguste Marie Philippa von Bayern[2], Gyula Gajdon[1,3], Alex Kacelnik[2], Ludwig Huber[1]

[1] Department for Neurobiology and Cognition Research, Althanstr.14, 1140 Vienna

[2]Department for Zoology, Tinbergen Building, Southparks Road, Oxford OX1 3PS

[3]Konrad Lorenz Institute for Ethology, Savoyenstr. 1a, 1160 Vienna

*corresponding author: Alice MI Auersperg (e-mail:alice_bayern@hotmail.com; Telephone: +43(0)6769390392; Fax: +43(0) 1 4277 9761)

Key Words

Problem solving ◆ Tool use ◆ Flexibility ◆ Physical Cognition◆ Birds

Short title (50 characters):

Flexible problem solving in keas and New Caledonian crows

Abstract

Corvids and psittacines have recently attracted much attention due to their innovativeness and problem solving skills. Yet, few comparative paradigms exist and none has investigated how different species approach and resolve the same problem in different ways and how flexibly they respond if the problem changes. Here we expose New Caledonian crows (NCC), and keas, to a problem solving task with four possible solutions. Two solutions required the birds

to insert a tool (a ball or a stick) in a specific opening while the other two did not involve the use of tools (opening a window and pulling a string). We investigated how which solutions were approached in which order. The Keas were more explorative and flexible than the NCC discovering two or three solutions within the first ten trials and switching more quickly to new solutions than the NCC if the previous was blocked. One kea and one NCC discovered all four options. The stick-naive kea's success, the first incidence of experimental stick tool use in a parrot, was surprising because, besides the cognitive challenge, keas' morphological constraints makes inserting a stick a complex motor task. This study presents a new method for intraspecific comparison and highlights how species differences in object exploration and affordance learning affects problem solving.

Introduction

Unfolding the evolution of intelligence requires cross-species comparisons which are usually notoriously problematic: cognitive mechanisms are to a large extent heritable phenotypic traits, and as such they evolve in response to selective pressures peculiar to each species' ecology (including social organization), physiology and morphology. Because of this, the obvious expectation is for cognitive processes to be qualitatively different across species. In order to unfold the selective evolution of the species' different cognitive abilities in the physical domain we should focus on the specific mechanisms underlying problem solving abilities rather than ranking their intelligence.

Previous studies in comparative psychology suggest that in order to compare taxonomic differences in problem solving, it is necessary to offer not just one but rather a battery of different tasks (Bitterman, 1965; Herrman et al., 2010). Among such tasks should be solutions that fit for the species' different behavioral preferences and other, more deviating ones. Offering several different tasks consecutively may allow us to reveal only limited information in how different species approach a problem. We could gain more information by offering several tasks at the same time and removing options that have been successfully mastered: this allows for the detection of differences on which tasks are approached first, which tasks

are problematic to which species and why, how many solutions are discovered, and then mastered, how quickly can they switch between solutions, adapt to changes and when do they give up. This may reveal species specific differences in cognitive mechanisms such as flexibility, exploration strategy, or learning the operational characteristics of objects.

As subjects we chose members of the two avian taxa (parrots and corvids), that produce the largest encephalization quotients, as well as the greatest innovation scores and whose performance in various cognitive tests, compares with that of the great apes (Auersperg et al., 2009; Auersperg et al., 2010; Bird & Emery, 2009; Emery & Clayton, 2004; Emery, 2006; Levfebre et al., 1997; Overington et al., 2009; Pepperberg, 1999; Taylor et al., 2007; Tebbich et al., 2007; Timmerman et al., 2000): the kea (*Nestor notabilis*), a neophilic mountain parrot from New Zealand renowned for its manipulative skills but not known to be using tools in its natural habitat and the New Caledonian crow (*Corvus moneduloides*), which is using and manufacturing stick tools in the wild. Both species are famous for their problem solving abilities in various physical cognition tasks (Auersperg et al., 2009; Auersperg et al., 2010; Gajdon et al., 2010; Taylor et al., 2007; Taylor et al., 2009; von Bayern et al., 2009; Weir et al., 2002; Werdenich & Huber, 2006;). Both of them are generalists that live in social groups and within complex environments with fluctuating resources (Diamond and Bond, 1999). Both species pursue a food extracting foraging style, the kea digging for roots in the ground of mountain plains and the crows fishing for larvae in the bark of trees (Hunt 1996, Diamond & Bond, 1999). Our captive keas also innovated to use compact objects, such as wooden blocks, as tools to access rewards in the lab (Auersperg et al., 2010; Gajdon et al., 2010). This gives us the unique opportunity to investigate flexibility and tactic in tool use behaviour as well as other extractive techniques in these two different families.

We designed a Multi Access Box paradigm (MAB), which targets the comparison of problem solving abilities in extractive foragers. The MAB features a battery of tasks that all lead to the same goal. Once a subject consistently masters one solution, the same solution is blocked and the acquisition of competence in another options is recorded. Six kea and five crows were exposed to a set up where food extraction could initially be achieved by four different methods, two of them requiring the use of a tool. One opening featured a curved pathway into

which a compact tool (ball) could be inserted while another opening was restricted for food retrieval with a stick tool. Due to the curvature of the ball path, it was not possible to reach the reward with a stick-like object and due to a missing physical connection towards the reward at the stick opening, an inserted ball fell down inside the box in front of the reward without touching it. Thus, both species had the opportunity to retrieve the reward using their preferred tool (the keas with a compact tool, the crows with a stick tool). The birds were allowed to act upon the set up until they reached a competence criterion by any of the four methods. Once a method was mastered, we locked it and recorded the bird's performance in reaching criterion in any of the other options, and so on until all four methods had been mastered. One solution involved pulling a string, tied around the reward. Another solution entailed opening a window by pulling a crank

Animals that naturally use tools, especially if they also create or modify them, have been considered as intelligent overall. With the MAB procedure we aim to enlighten the significance of this ability in terms of general problem solving capacity in comparison to another technically gifted specie that does not use tools naturally. Is tool use a consequence/result of advanced technical intelligence, or is it an adaptive specialisation that is not accompanied by other skills or cannot be easily used to solve other technical problems? Following the later possibility, it may be reasonable to suggest that the adaptive specialisation has canalized the problem solving capacity by narrowing down its operative range or by affecting the approach to other extractive foraging problems. Such especially gifted species may be less explorative, flexible or innovative than species that have similarly high sensorimotor capacities but are less specialised.

Results

First Session

There were qualitative differences in the way the keas and crows related to the physical setup, and this translated in a marked quantitative difference in the number of solutions discovered within the first session. Averaging across individuals, NCCs found on average 0.75 (Range 0-1) and keas 2.33 (Range 2-3) solutions within the first session (see Table 1 for the individual

results). Within the first session, all kea touched all 4 openings and both tool types, while the NCCs rarely touched any of the openings (except the string) provided. The keas directly manipulated the openings more often than the crows did (Mann-Whitney U test; U=2,34; p=0,01).

Table 1 Number of trial and session in which the different solution were performed successfully for the first time. Asterisks denote discoveries of solutions that occurred within the first session.

Species	*Ind*	***1st solution***	*Trial /Session*	***2nd solution***	*Trial/ Session*	***3rd solution***	*Trial/ Session*	***4th solution***	*Tria/ Session*
Kea	Br	String	1/1*	Window	2/1*	Ball	9/4	-	-
	Fr	Window	1/1*	String	2/1*	Ball	3/1*	-	-
	Ke	String	1/1*	Ball	6/1*	Window	1/5	Stick	1/8
	Lu	String	1/1*	Window	3/1*	Ball	6/1*	-	-
	Pi	Window	1/1*	String	2/1*	Ball	9/5	-	-
	Ta	String	1/1*	Ball	5/1*	Window	1/5	-	-
NCC	Bk	String	1/2	Stick	1/9	-	-	-	-
	Ey	String	1/1*	Stick	1/6	Ball	1/10	-	-
	Ti	String	1/1*	Stick	1/4	-	-	-	-
	Uek	String	1/1*	Stick	9/2	Ball	2/10	Window	1/13

Sequence of solutions discovered and established (met criterion)

After an initial period, all subjects of both the kea and the crows focussed on one particular solution, namely, the string option. After the string was removed, the subsequent order of solutions established differed between the two species and, in keas, between individuals (see Table 2).

As befits their natural predisposition for tool use, the NCC next reached criterion using the stick tools (3 individuals; between session 4 and 12) and, only when this option was blocked, 2 individuals reached criterion with the ball tool (in sessions 8 & 13; see Table 2). All crows except for Uek (as the last option) failed to open the window. This is probably due to the fact that, although they did touch the window with the stick (average 31,77 % ineffective tool actions per crow of the trials in which tools were used were directed against the window), they did not explore the crank of the window in a pulling manner. In the following trials, Uek

always reached for a stick tool after opening the window, and pocked the reward out, instead of sticking her head through the window and taking the reward directly.

The keas established either the 'ball' or the 'window' option after the string solution was blocked (all of them established these three solutions). After these options were closed as well, all keas had touched the box with the stick several times at the appropriate appropritate side. They combined the stick with the opening, but failed to insert it there. Only one kea, Kermit, succeeded to develop an successful technique to retrieve the reward with the stick. Kermit (1) took the tool end *laterally* into his beak and pushed it against the tool entrance. (2) He then switched from grabbing the stick with the beak to grabbing it with the foot, continuing to press the tool end against the opening, (3) Meanwhile he shifted the beak to the other end of the tool securing its position with the foot at the tool entrance. Finally (4) he directed that tool end through the opening with his beak and manoeuvred it until it hit the reward (see movie 1 in online SI). Kermit successfully used the stick tool for the first time three sessions after all other openings had been closed (in session eight) and reached criterion in session ten.

Table 2 Order and session in which each individual reached criterion (8 consecutive times correct or 9 out of 10 correct) for each of the four solutions (string, window, ball and stick). The columns headed "interval" indicate how many sessions lay in between the blocking of one solution and reaching criterion for the next solution.

Species	*Ind*	***1st solution***	*Session*	***2nd solution***	*Session*	***3rd solution***	*Session*	***4th solution***	*Session*
Kea	Br	String	3	Window	4	Ball	6	-	-
	Fr	String	2	Window	3	Ball	5	-	-
	Ke	String	2	Ball	4	Window	5	Stick	10
	Lu	String	2	Window	4	Ball	5	-	-
	Pi	String	3	Window	4	Ball	6	-	-
	Ta	String	3	Ball	4	Window	6	-	-
NCC	Bk	String	2	Stick	-	-	-	-	-
	Ey	String	2	Stick	8	Ball	13	-	-
	Ti	String	1	Stick	12	-	-	-	-
	Uek	String	2	Stick	4	Ball	8	Window	12

Speed in switching from one solution to the next

There was also a notable difference in the speed in which the keas and crows established, i.e. met criterion in the next solutions once the previous method was blocked. The keas took on average an interval of 2.5 sessions, while the crows required 5.4 sessions to establish the next strategy (see Table 2). Even discovering/establishing the stick solution (which we expected to be solved readily by the NCC that are naturally predisposed for stick tool use), after the string solution had been blocked, took the three successful crows 5.8 sessions on average (Table 1 & 2).

The balls had to be removed after three unsuccessful sessions for all kea except Kermit, at the time they reached criterion in all options except the stick. Nevertheless, no additional kea managed to reach the food with the stick. We also had to remove all sticks after three unsuccessful sessions before Ebony and Uek consitantly used the ball entrance. These were the only crows that reached the criterion with the ball option.

Tool preference and analyses related to the tool solutions

The crows only successfully used the thin sticks and Kermit the kea only the thicker sticks, both species used both sizes of ball tools.

After the string opening had been blocked, the kea showed a preference for using the ball, 'combining' it (i.e. carrying the tool to an opening and touching it with the tool) more often with openings then the stick (Wilcoxon signed-rank; T=2,02; p=0,043). For the crows the reverse situation was true; they tended to 'combine' the stick more often than the ball (Wilcoxon signed-rank; T=1,87; p=0,06; mean % of trials in which the stick was combined with an openings=57.8; for the ball=0.78). The crows tried to insert the stick more often into openings than the kea did (Mann-Whitney U test; U=2,59; p=0,01) whilst the kea combined the ball more often than the crows did (Mann-Whitney U test; U=1,9; p=0.05).

In trials in which the reward was retrieved using a tool, the animals conduced many ineffective tool actions (ITA), in which the tools were inserted or combined with ineffective openings before they started to carry the tools directly to the appropriate openings (see Table 3). The average number of ITA per trial was similar in cows and kea in trials in which the ball or the stick was used. The crows however used the stick much more often at ineffective

openings (even in trials in which the stick entrance was closed and the reward was finally retrieved using the ball) while the kea tended to conduct more ITAs using the ball (see Table 3).

Table 3. Ineffective Tool Actions (ITA), in trials in which either the Ball or the stick was used to retrieve the reward. This table depicts the mean number of ITA per trial in which the reward was finally retrieved using the ball tool (colum 3) or the Stick tool (colum 6) as the % of ITA in which the stick (or the ball respecitvely) was inserted into ineffective openings before succeeding with one of the two tools

		Ball			*Stick*		
Species	*subjects*	*Mean No. ITA/trial*	*% ITA Stick*	*% ITA Ball*	*Mean No. ITA/trial*	*% ITA stick*	*% ITA Ball*
Kea	Fr	1,38	0	100			
	Br	1,27	17,85	82,14			
	Ke	0,61	23,07	76,92	0,45	33,33	66,67
	Lu	0,4	0	100			
	Pi	1,33	10,71	89,28			
	Ta	0,58	14,28	85,71			
NCC	Ey	1,06	79,41	20,59	0,52	100	0
	Ti				0,75	100	0
	Uek	1,41	61,29	38,71	0,357	100	0
Mean	Kea	0,93	10,98	89,01	0,45	33,33	66,67
	NCC	1,23	70,35	53,09	0,54	100	0

Discussion

The kea were more flexible and faster in discovering multiple solutions and showed more individual variation than the naturally tool-using NCC: within the first session, all kea successfully employed at least two or three solutions while none of the crows used more than one by this time. The keas also behaved more flexible once openings were blocked, switching to other solutions quicker than the NCC. Using the ball should have been similarly demanding to both species but was successfully applied much faster by the kea. Only in the stick option, the parrots were less successful than the NCC; although they readily applied the stick tool at the appropriate opening of the box, only one individual (Kermit) was able to insert it precisely enough to push out the food reward.

Differences in exploration mode and affordance learning as well the difference the neophilia / neophobia of the keas and crows respectively, seem to be responsible for these differences in

performance. The kea showed more haptic exploration while the corvids, probably due to their higher level of neophobia seemed to explore more in a visually guided manner. Similar results have also been found in comparisons between kea and common ravens (Schloegl et al., 2008). The kea's strong urge to manipulate i.e. act on novel objects, may be helpful to detect functional object affordances. In their naturally low-risk and variable environment, this could have been an adaptive strategy (Huber & Gajdon, 2006; Mettke-Hoffman et al., 2002). The crows, in contrast, approached the apparatus more neophobically and touched it less than the kea did. Two crows stayed timid and did not start to explore it thoroughly. It took the remaining three crows a surprisingly long time to establish successful and reliable tool use as an alternative to string pulling. Not only did the crows insert the balls (the type of tool they were less familiar with than with the sticks) into inadequate openings for food retrieval, they did so with the stick tools as well. Their performance was no different to the kea in this respect. Thus, there were neither indications that they extrapolated any physical knowledge from stick tools to the functionality of the ball tools, nor that they used the stick tools in a goal-directed way (focusing on functional food removal).

These results are in agreement with Wimpenny (2010) that NCCs also use their tools in a non-selective way for object exploration. It can be argued that it is more convenient for the neophobic crows to touch the box not directly with their body (beak) but with an extension such as the stick. However, contrary to this assumption, the crows first established a retrieval solution in which they had to touch the apparatus directly with their bill and not with a tool. Neophobic tool exploration should also be concentrated within the initial phases, but inefficient tool applications occurred throughout testing.

The kea seem to use much more violent and destructive object manipulation when touching the apparatus, involving a lot of pulling an tearing actions (the kea Luke even managed to break the Plexiglas at top of the box, while trying to force it open and most kea attempted to overthrow the MAB, which had to be fixed on the aviary floor). Wild keas are well-known for their curiosity, playfulness and urge to tear apart any interesting object they encounter, e.g. cars' windshield wipers or picnic baskets, (Diamond & Bond, 1999).

Wild NCCs do also use tearing actions when manufacturing long, pointed tools from pandanus leaves (Hunt, 1996). They however hesitated to use such behaviours in this setup and were consequently disadvantaged in situations where the functionalities of the objects are not detectable by simply applying pressure, such as in the case of the window option We can at this point speculate that tearing behaviours may solely be orientated towards tools making and nest building while their foraging is much more focussed on probing and skewering with the tool. Very recently Rutz et al. (2010) were able to show that a substantial amount of the crows' protein and lipid intake came from wood boring beetle larvae obtained with stick tools, also indicating that explorative foraging is more concentrated on probing actions. It seems therefore possible that the range of exploration techniques during foraging in NCC may be constrained by the adaptive specialization for tool use and that this will affect the "zone of latent solutions" (Tennie et al., 2009) within the species' cognitive repertoire. In order to filter out the role of neophobia in this matter it would, however, be necessary to additionall test another physically competent, non-tool using and neophobic corvid, that shows tearing actions during foraging (such as the common raven which is tearing pieces of meat out of carcasses).

Our results provide the first experimental evidence of stick tool use as a behavioural innovation in a parrot. Keas are neither natural tool users like New Caledonian crows, nor do they construct nests with twigs as all corvids do, which may genetically predispose them for handling twigs and other elongated stick-like objects (Hansell & Ruxton; 2008). Instead, they use or dig burrows for laying their eggs (Jackson 1963). Also importantly, the kea's bill morphology, i.e. a strong beak curvature and a pronounced size difference of mandible and maxilla, precludes a good grip and control of long tools. NCCs, maybe as an adaptation to tool use (Kenward et al. 2005), have short straight beaks with the mandible almost as big as the maxilla, allowing them to effectively hold a stick in a straight manner, elongating their beaks and increasing their reach.

Nevertheless, in less than 30 minutes, the successful kea had developed a complicated stepwise technique (see description above and SI, movie 1) that permitted him to insert and to manouvre a stick tool despite his morphological constraints. Kermit's performance indicates a high degree of deliberate control, possibly even involving an anticipation of their effect and at least a representation of the goal to insert the stick into the opening. It is however yet unclear whether he understood the functional connection between his beak, the tool and the reward. This will be subject to further experiments.

The finding that a non-tool using species may conjure up stick tool use as behavioural innovation is significant because it sheds further light about the role of tool use in the evolution of intelligence. Currently two competing hypotheses about the relation between tool use and intelligence have been discussed (Kacelnik 2009). One hypothesis concludes that tool use brought about the evolution of sophisticated cognitive skills in the physical domain, which, in a second evolutionary step, led to more general abstract reasoning abilities. The opposite hypothesis assumes that tool use is one of many derivates of a general purpose intelligence (Emery & Bird 2009). Finding stick tool use in a large-brained species that neither meets the anatomical requirements (flat maxilla under surface, evenly sized maxilla and mandible) nor possesses genetic predisposition for nest construction, provides prima facie support for the general purpose intelligence hypothesis (Bird&Emery, 2009).

Although exercised on the example of just two species, the paradigm we introduce in this study is suited for comparative research into the cognitive mechanisms underlying species differences in problem solving and innovative abilities. Applying this paradigm in a large scale interspecies comparison would allow testing hypotheses about the relationship between ecological factors, exploration strategies and foraging style, and the processes involved in innovation and flexibility.

Methods

Subjects

Six male kea (Frowin, Kermit, Pick, Tammy, Bruce and Luke), as well as five New Caledonian crows (Boycott, Annie-Claude, Tino, Ebony and Uék), two of which were male (Boycott and Tino) participated in this study. Three kea (Kermit, Pick and Tammy) as well as one crow (Uék) were hand-raised. Bruce, Luke and Frowin were parent raised in captivity; Annie Claude, Tino, Ebony and Boykott were wild caught but had various lab experiences. Bruce and Luke were seven, Frowin, Pick and Kermit five, Tammy three and Uek, five years old. All subjects had similar experience with compact tools, the NCC had participated in a test that required dropping stones into vertical tubes (von Bayern et al. 2009) and the kea had placed compact objects in tubes lying horizontally on the ground and then lifted the tube up (Auersperg et al 2010). Both the NCC and the kea used had similar experiences with strings by participating in a vertical string pulling task (Werdenich & Huber, 2006).

The kea were group-housed in a large outdoor aviary (15m x10 m x 4 m) in a group totalling 20 kea, the crows were kept in pairs in outdoor aviaries of various shapes (with an average volume of aproximately. 20m^3) with access to heated indoor divisions (ca. 8m^3) and food and drinking water was available ad libitum. All studies are strictly non-invasive and based purely on behavioral tests. All subjects were housed in accordance with the Austrian and German law.

Apparatus

We designed a Multi-Access-Box (MAB) consisting of a square box (23cm x 23cm x 23cm; for further dimensions see Figure 1) with four exchangeable transparent walls (the dimensions were considered adequate for both species). Each wall contained an opening that could be used to access a food reward presented in the centre of the box, either directly or by means of a tool. The food reward (half a peanut in its shell for the kea; a mealworm inside half a peanut shell for the NCC) was positioned on a vertical pole in the centre of the box (Figure 1), which was attached to a slanted platform. Once the food fell off the pole it rolled down the platform and out of the box (Figure 1).

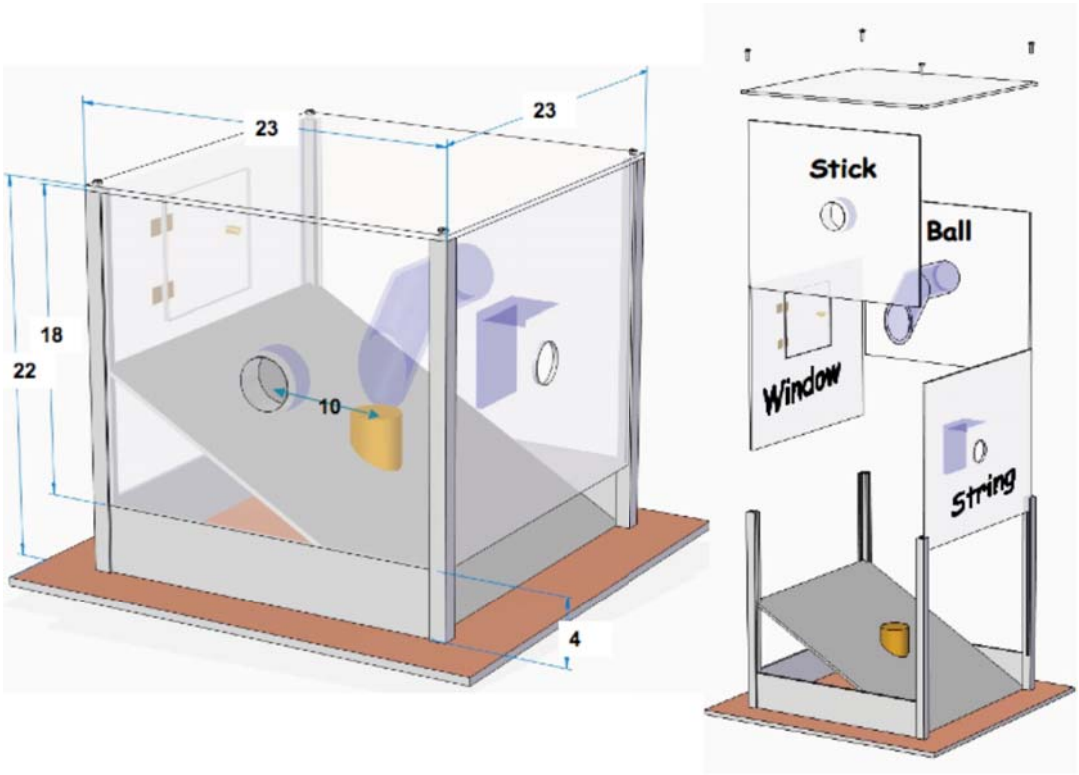


Figure 1: Basic apparatus of the Multi-Access-Box (MAB) and the four exchangeable transparent walls with the openings corresponding to the 4 possible solutions (string, window, ball and stick).

There were four possible solutions (‘string’, ‘window’, ‘ball’ and ‘stick’) through which the out-of-reach food could be obtained, two of which (‘ball’ and ‘stick’) involved the use of tools (Figure 1). (i) The ’string’ solution required the subjects to pull a horizontal string (20 cm) hanging out of the opening in the respective wall, the other end of which was tied to the reward. (ii) In case of the ‘window’ option, the food could be obtained by pulling open a window using a crank and thereafter reaching into the box to retrieve the food from the pole. (iii) To exploit the ‘ball’ option, a compact tool (a marble) had to be inserted into the respective opening, which connected to a transparent tube pathway bending towards the central pole. When inserted into the tube the ball rolled down the pathway and knocked the reward off the pole. (iv). Finally, the opening corresponding to the ‘stick’ solution was connected to a (8mm) short straight horizontal tube at the same height as the food, but with a ten centimetre gap to the pole (Figure 1). Here, the food could be obtained by inserting a stick

tool in the correct, hence unobstructed opening, manoeuvring it towards the pole and hitting the peanut (kea) or stuffed peanut shell (NCCs).

All openings except for the window had the same round shape and diameter, hence were superficially perceptually similar, but could be distinguished by the visible internal structure (see Figure 1). Four sticks tools (15 cm long) and four balls, all painted with yellow childproof acrylic varnish, were provided in two different sizes. Two stick tools were broad and two thin (0.5 cm and 1,.5 cm in diameter respectively), whilst the ball tools were two large and two small marbles. The tools were placed in the four corners of the MAB so that each corner had one stick and one marble (the possible combinations of tool diameters were randomly assigned). The MAB was turned around before each trial and the walls were switched, so that the openings were at randomly changing positions.

Experimental procedure

Prior to the start of the actual tests, the birds received at least four familiarization trials, in which each of the walls was missing once so the birds just could reach into the box and take the food reward. The crows, which are more neophobic than the keas, received as many familiarization trials as necessary to recover the reward in less than three minutes.

During testing, subjects were visually isolated from their group/mates and received a maximum of ten trials per session. A trial continued until the reward was recovered or until ten minutes had passed. If an animal did not obtain the reward within ten minutes testing continued the following day. A trial was scored as correct if the bird obtained the reward by applying one of the four solutions described above without prior unsuccessful attempts to solve the problem in a different way, e.g. previously manipulating other openings or combining the tools with wrong openings. The first successful retrieval of the food from a new opening (the bird may have manipulated other entrances in the same trial) was scored as a ‘discovery’.

Initially all openings were open. Once a subject reached criterion for one solution (if the reward was consistantly recovered using the same solution for two consecutive sessions but also after nine correct trials within one session or eight consecutive correct trials using the same solution within one sessions respectively), the respective opening was blocked (the window was cemented into its frame, the string was removed or the tool entrance was blocked with a wooden stopper), so as to force the subject to shift to other solutions. Testing continued until the animals failed to recover the reward within 10 minutes in three consecutive trials or until all openings were closed. If just one tool opening remained open, and the birds failed to solve it three times consecutively, we gave them a 'second chance' (another three trials) and removed the tools that belonged to the tool task they had previously solved, so as to remove possible distracting factors. For instance, the birds may fail to solve a tool task simply because they might not be able to inhibit using a tool which has been strongly associated to food before.

All data was videotaped. We used SPSS for statistical analysis

Acknowledgements

We would like to thank the FWF and the WAF for financial support as well as Lukas Auersperg for technical support in constructing and drawing the apparatus. We declare that we have no conflicts of interest

References

Auersperg A. M. I. Gajdon G. K., Huber L. 2009. Kea consider spatial relationships between objects in the support problem. *Biology Letters* **5**, 455-458

Auersperg A. M. I., Gajdon G. K., Huber L. 2010. Kea (Nestor notabilis) produce dynamic relationships between objects in a second order tool use task *Animal Behaviour.* Published online

Bird, C. D. & Emery, N. J. (2009). Insightful problem solving and creative tool modification

by captive rooks. *Proceedings of the National Academy of Sciences:* **106**, 10370-1037

Bitterman, M.E. (1965). The evolution of intelligence. *Scientific American*, **212**, 92–100.

Diamond, J. & Bond, A.B. (1999) *Kea, Bird of Paradox: The Evolution and Behavior of a New Zealand Parrot.* Berkeley, CA: U. of California Press

Emery, N. J., and Clayton, N.S, (2004) The mentality of crows: convergent evolution of intelligence in corvids and apes, *Science* **306,** 1903–1907

Emery, N. J. (2006) Cognitive ornithology: the evolution of avian intelligence. *Phil. Trans. R. Soc. B* **361**, 23–43

Gajdon G. K., Aman L., Huber L. 2010. Keas rely on social information in a tool use task but abandon it in favour of overt exploration, *Interaction Studies,* In Press

Hansell, M. & Ruxton, G. (2008). Setting tool use within the context of animal construction behaviour. *Trends in Ecology and Evolution*, **23**,73–78

Herrmann, E., Hernández-Llored, M. V., Call, J., Hare, B., Tomasello, M. (2010) The Structure of Individual Differences in the Cognitive Abilities of Children and Chimpanzees**.** *Psychological Science* **21**: 102-110

Huber, L. & Gajdon, G. (2006). Technical intelligence in animals: the kea model. *Animal Cognition* **9,** 295–305.

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

Jackson, J. R. 1963. The nesting of keas. *Notornis*, **10**, 319-326

Kacelnik, A. 2009. Tools for thoughts or thoughts for tools? *Proceedings of the National Academy of Sciences of the United States of America **106***, 10071-10072

Lefevre L., Whittle P., Lascaris E., Finkelstein A. (1997) Feeding innovations and forebrain size in birds. *Animal Behaviour,* **53** (3), pp. 549-560

Mettke-Hofmann, C., Winkler, H. & Leisler, B. (2002) The significance of ecological factors for exploration and neophobia in parrots. *Ethology*, **108**, 249-272.

Overington, S. E., Boogert, N. J., Morand-Ferron, J., Lefebvre, L. 2009. Technical innovations drive the relationship between innovativeness and residual brain size in birds. *Animal Behaviour,* **78**, 1001-1010.

Pepperberg (1999) *The Alex Studies.* Harvard University Press

Rutz, C., Bluff, L. A., Reed, N., Troscianko, J., Newton, J., Inger, R., Kacelnik, A., Bearhop, S. (2010) The Ecological Significance of Tool Use in New Caledonian Crows**.** *Science*, **329** (5998), 1523 - 1526

Schloegl, C., Dierks, A., Gajdon, G. K., Huber, L., Kotrschal, K. & Bugnyar, T. 2009. What You See Is What You Get? Exclusion Performances in Ravens and Keas. *PLoS ONE*, **4**, e6368.

Taylor, A.H., Hunt, G.R., Holzhaider, J.C., and Gray, R.D. (2007). Spontaneous metatool use by New Caledonian crows. *Current Biology,* **17**, 1504-1507

Taylor, A.H, Hunt, G.R., Medina, F.S., Gray, R.D. (2009) Do New Caledonian crows solve physical problems through causal reasoning? *Proceedings of the Royal Society, London B,* **276**, 247-254

Tebbich, S.; Seed, A. M., Emery, N., Clayton, N., S. (2007) Non-tool-using rooks, Corvus frugilegus, solve the trap-tube problem. *Animal Cognition* **10**, (2), 225-231

Tennie C., Call J., Tomasello M. 2009 Ratcheting up the ratchet: on the evolution of cumulative culture. *Phil. Trans. R. Soc. B* **364**, 2405–2415

Timmermans, S., Lefebvre,' L., Boire' D., Basu, P.(2000) Relative Size of the Hyperstriatum ventrale Is the Best Predictor of Feeding Innovation Rate in Bird Brains. *Behaviour and Evolution*. **56**:196-203

von Bayern, AMP, Heathcote, RJP, Rutz, C, Kacelnik, A. (2009). The Role of Experience in Problem Solving and Innovative Tool Use in Crows. *Current Biology,* **19**(22): 1965-1968.

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

Werdenich D., Huber L. 2006 A case of quick problem solving in birds: string-pulling in keas (Nestor notabilis). *Animal Behaviour* **71**:
855-863.

Wimpenny, J. (2010) Phd Thesis. Department of Zoology, University of Oxford

Chapter 5

Directive application of a stick tool in a non tool using parrot species, the kea (*Nestor notabilis*)

Alice M.I. Auersperg, Gyula K. Gajdon, Ludwig Huber

Submitted

Directive application of a stick tool in a non tool using parrot species, the kea (*Nestor notabilis*)

Alice MI Auersperg*[1,2], Gyula K Gajdon[1,2], and Ludwig Huber[1]

[1]*Department of Cognitive Biology, University of Vienna, Althanstrasse14, 1090 Vienna*

[2]*Konrad Lorenz Institute for Ethology, Vienna, Savoyenstr.1a, 1160 Vienna*

**Author for* correspondence *(alice_bayern@hotmail.com)*

This study investigates how captive kea, New Zealand parrots, learn using a stick tool to retrieve a food reward despite physical (curved beak) and ecological constraints to handle elongated objects. We demonstrate that the animals can thereafter immediately direct the functional end of the stick at the positive option of two.

Keywords

Birds ◆ tool use ◆ physical cognition

1. INTRODUCTION

In 1971 Jane Goodall defined stick tool use as "the use of an external object as a functional extension of mouth or beak, hand or claw, in the attainment of an immediate goal". Although object relationships, involving other (more compact) agents are presently admitted by various younger definitions of tool use (Alcock, 1972; Beck, 1980; St Aman & Horton, 2008), the use of stick like objects as tools in a food extracting context is rarely observed in nonhuman animals. There are merely two avian species acknowledged to employ true stick tools in the wild. Woodpecker finches use cactus spines and small twigs to dislodge grubs from bark (Tebbich et al. 2002). New Caledonian Crows use and manufacture various kinds of elongated tools from many different materials (Hunt 1996; Hunt 2000) to obtain wood boring beetle larvae from trees. Stick tool use in both species is genetically transmitted (Tebbich et al. 2002; Kenward et al. 2005). Some primates such as capuchin monkeys, which operate

stone tools in the wild, can acquire using sticks in the laboratory (Frangazy & Visalberghi 2004). This has not been achieved in birds until recently, when Bird & Emery (2009) could demonstrate that rooks used elongated objects to push down a platform inside a tube holding a food reward. There is however no evidence to date that they can intentionally appoint the precise direction of the functional tool end such as genetical tool users can.

The kea, a New Zealand mountain parrot, has shown great competence in various lab tasks involving complex object relationships, including the use of compact objects as tools (Auersperg et al. 2009; Auersperg et al. 2010; Gajdon et al. 2010).

In the course of an experimental series the kea Kermit succeeded in poking a food reward off a small wooden platform by inserting a rod shaped tool through a small vertical hole inside the Plexiglas front of a wooden box. The animal manoeuvred the tool with its beak over a gap of ten centimetres between the hole and the platform until it hit the reward. Hereupon the food rolled out of the box towards the bird on a slanted plate (Auersperg et al. submitted). Kermit learned to do so within three trials of ten minutes. Five other subjects failed after six trials of ten minutes although they all attempted to insert the tool end into the opening. Kermit's performance is the first experimental evidence of successful stick tool use in a psittacine. Due to the curvature of his beak and the size difference between his mandible and his maxilla the stick tool could not easily be handled. Surprisingly Kermit quickly developed a sophisticated technique, allowing him to succeed despite this disadvantage: he took one tool end laterally into his beak and held it against the opening. He then exchanged his beak with his foot still pressing the tool end against the opening. Meanwhile he took the other tool end into his beak tip and pushed it through the hole, manoeuvring it until it hit the reward (Auersperg et al. submitted). Although the coordination of different body parts (beak and foot relative to body weight) outside his usual repertoire requires highly complex motor control, it is yet unclear whether Kermit understood the stick as a functional extension of his beak towards the reward or whether he simply learned to insert the tool and to wave it about inside the box until the reward appeared.

The following study investigates whether kea can *navigate* the stick towards the positive option of two. To attain more stick tool using subjects without shaping, we exposed the same

birds that failed to use the stick in the previous study to demonstration trials by Kermit (although testing for social learning is not the goal of this study).

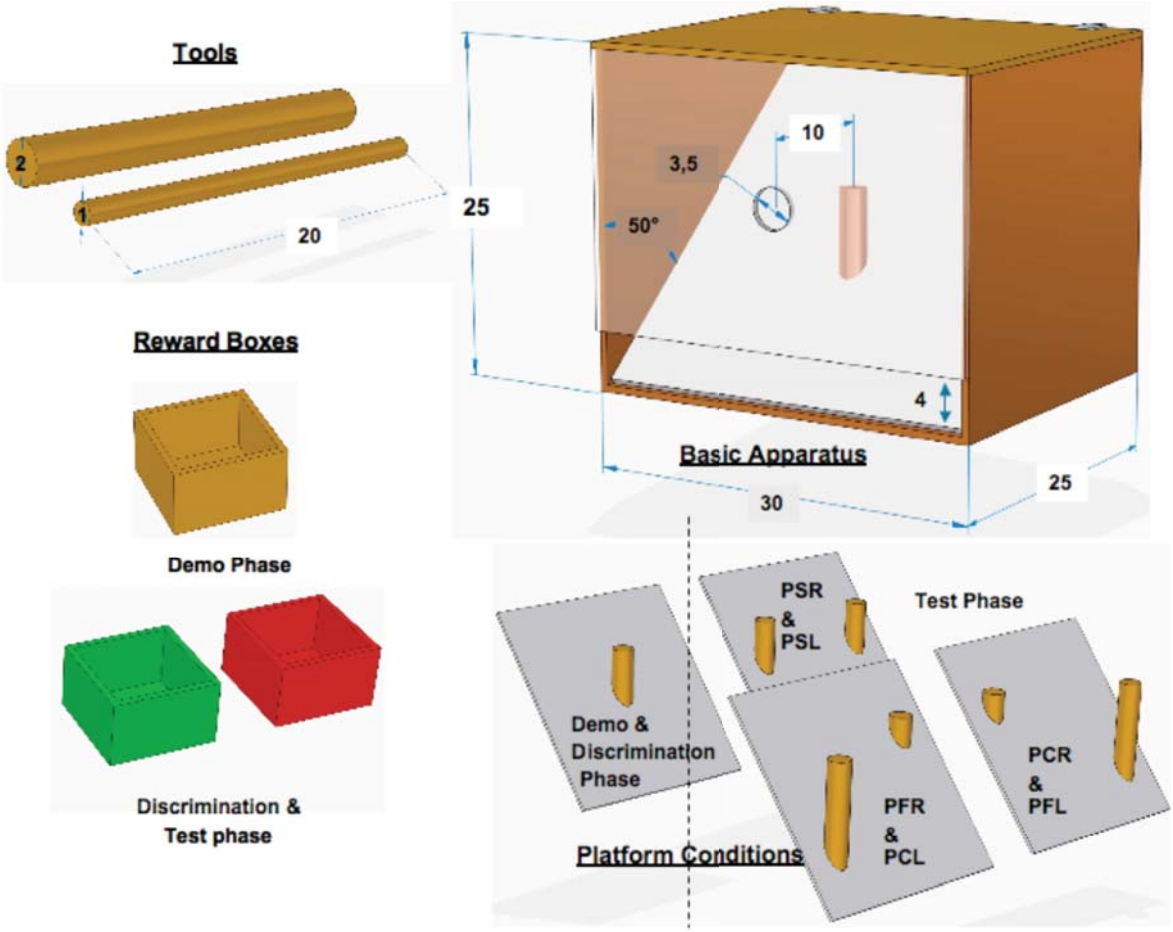


Figure 1 Right : Basic Apparatus with distances in cm. the platforms used during the testing phase. Left: the two tools offered and the reward boxes: Naturell during demo and discrimination phase, red and green during test phase

2. Material and Methods

Subjects

Six adult male kea: Luke, Bruce, Kermit, Frowin and Tammy participated in this study. All were bred in captivity and kept in a large, enriched outdoor aviary (15x10 m and 4 m high) at the Konrad Lorenz Insitute for Ethology in Vienna. Food (fruit, vegetables, seeds, mineral supplements and various protein sources) was spread every day at noon; fresh drinking water was available ad libitum. An experimental compartment (10 x 5 m) could be visually isolated from the remaining enclosure using an opaque sliding door. Since this study is based

purely on behavioural tests, it is classified as a non-animal experiment in accordance with the Austrian Animal Experiments Act (§ 2, Federal Law Gazette No. 501/1989).

Demonstration phase

As basic apparatus we used a wooden box with a transparent Plexiglas front (for dimensions see Figure 1). The front left a gap at the lower end and contained a small round hole (diameter 3,5 cm) in its centre.

A slanted aluminium wall was situated inside the box, which had a small, round, wooden platform placed in its centre. The upper end of the platform was about ten centimetres from the hole in the Plexiglas front (see Figure 1). A food reward (a quarter of a peanut) was placed inside a small wooden reward box onto the platform inside the apparatus. Two rod shaped tools were provided (length 20 cm; 2cm or 1 cm diameter; we used thick tool diameters in order to avoid the parrots' strong beaks breaking them) in front of the box. To retrieve the reward, a stick tool had to be inserted into the small hole and manoeuvred until it hit the reward box, releasing the food through the small gap at the lower end of the Plexiglas front.

Each subject was allowed to observe Kermit retrieving the reward from a distance of one metre in three demo trials before each session. This was followed by a self-trial. If subjects retrieved the reward within ten minutes, they received nine additional trials. Subjects received a maximum of five demo sessions. Animals that did not master the task within this time did not receive further testing. Once subjects retrieved the reward in ten trials they received no more demonstrations but three additional sessions of ten trials on their own in order to improve their technique.

Discrimination phase

We used the same apparatus as in the demonstration phase except there were two different colours of reward boxes: red or green. For half of the subjects green was baited, for the other half red. Subjects received five sessions of ten trials. Within each session the green box was on the platform for half of the trials and the red box for the other half in random order. A trial was scored as correct when the subjects retrieved the reward when the positive stimulus was offered and did not combine the tool with the opening for one minute when the negative stimulus was on the platform.

Test Phase

We used the same basic apparatus as in the previous phases but this time there were two platforms placed next to each other on the slanted wall. Subjects received five sessions of ten trials in which both the red and the green box were placed onto the two platforms. The positive stimulus could be the same distance to the stick opening as the negative (same right positive PSR; same left positive PSL). The positive stimulus could be on the right side and further away from the opening than the negative (Positive Far Right Condition; PFR), on the left side and further away from the hole (PFL), on the right side and closer to the hole (PCR) or on the left side and

closer to the hole (PCL). Each session comprised PCR and PCL once as well as PSL, PSR, PFR and PFL twice. A trial was scored as correct if the positive stimulus was poked off its platform first.

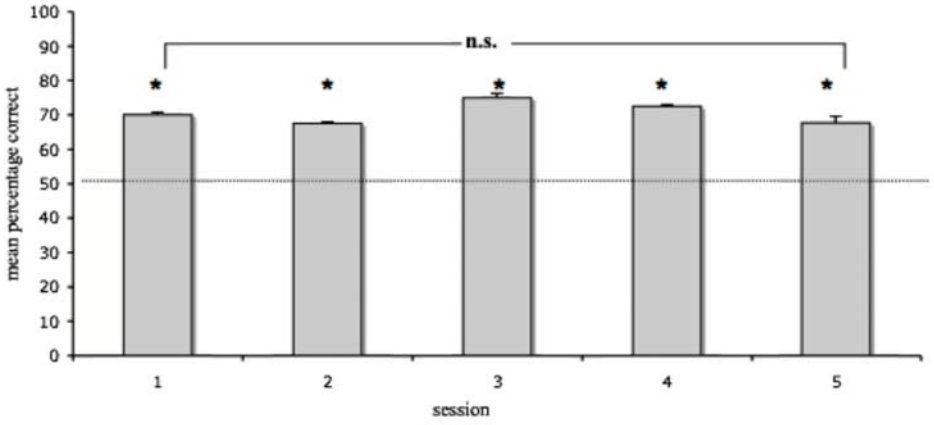
3. Results

Pick successfully employed the stick after only one demo session. Frowin needed three and Luke five sessions. Lacking the appropriate technique, Bruce and Tammy did not succeed within the time given. Pick and Frowin used exactly the same technique as Kermit (described in the introduction, see video supplementary material). Luke, supporting the tool on the rim of the opening, pushed it through the opening by repeatedly shifting his grip backwards until he reached the end of the tool.

During the discrimination phase, red was positive for Kermit and Frowin and green for Luke and Pick. Initially all animals hit the negative stimulus as readily as the positive. Frowin stopped doing so in the session two, Kermit and Pick in session three and Luke in session five.

In each of the five test sessions, the group hit the positive stimulus more often than the negative one (Two Tailed Binominal Test; N=40; p_1=0.008; p_2=0.019; p_3=0.001; p_4=0.003; p_5=0.019). There was no difference in performance between the first and the fifth session (Mc Nemar test N=40; p=1.00; see Figure 2).

Figure 2 Group performance during the test: mean percentage correct in each of the five sessions; *=significantly above chance; two tailed Binominal test; n.s.= not significant; Mc Nemar test



Each of the four subjects had more positive then negative hits within the time given (Two Tailed Binominal Test; N=50; p_{Fr}=0.003; p_{Ke}=0.001; p_{Lu}=0.001; p_{Pi}=0.032).

Kermit's performance was above chance within the first 20 trials (Two Tailed Binominal Test; N=20; p_{Ke}=0.021), the subjects Luke and Pick were already close to significance by this time (Two Tailed Binominal Test; N=20; p_{Lu}=0.057; p_{Fr}=0.057; see Table 1).

Table1 Individual performance in each phase: Session number of first success (demo phase); session number in which subjects ceased to hit the negative stimulus (discrimination training); Number correct out of 20 (first and the last two sessions of test phase)

Subjects	**Demo phase**	**Color Discrimination**		**Test**	
	Succeeded in session	*color positive*	*Session Learned*	*No correct /20 session 1&2*	*No correct/ 20 session 4 &5*
Frowin	3	Red	2	12	15
Kermit	demonstrator	Red	3	15	14
Luke	5	Green	3	14	16
Pick	1	Green	4	14	11

4. Discussion

Kea are not only physically disadvantaged (curvature as well as size difference between upper and lower beak) to use stick tools, they also have no natural predetermination for doing so. Since, unlike many other birds, kea do not construct complex nest cups with twigs but instead breed in simple burrows (Jackson, 1963) they have no disposition to handle elongated objects (Auersperg et al., 2010).

Despite these shortcomings, three out of five subjects mastered the complex motor challenge of handling a stick tool within a short time frame supported by social cues. Pick retrieved the reward on his first try after one demo session. Although we cannot say much about how the subjects acquired their response, previous studies suggest that kea can learn from conspecifics about specific object affordances (emulation learning; Huber et al., 2001).

Pick and Frowin employed the same complex multi-step technique that Kermit had used during the demonstration sessions (see introduction). The high level of body motor control, outside the species' usual repertoire, required to master this technique indicates that the animals actively control their actions anticipating their effects (Auersperg et al. unpublished data).

During the discrimination training all subjects became reluctant to combine the stick tool with the opening if the negative stimulus was displayed, suggesting that the reward was the primary motivation to participate.

Throughout testing, the animals, after only little experience, did not simply manoeuvre the tool arbitrarily inside the opening until a reward appeared but clearly aimed at the baited box. The group performance remained more or less the same throughout the test (about 70 %; see Figure 2). It is likely that many incorrect hits were caused by the technical impracticality of holding a stick tool firmly inside a curved beak. The tool was always juggling slightly between the tips of the maxilla and mandible while the birds were pushing it. Possibly, many mistakes may have occurred because the animals inadvertently hit the negative stimulus while aiming at the positive one

The lack of a learning curve indicates that once the two-choice paradigm was introduced subjects had already grasped the essential properties of the stick tool. They immediately translated the movement of their beak to that of the functional tool end in order to navigate it into the desired direction. This is to our knowledge the first evidence of a non tool using bird appointing the direction of a stick tool as a functional extension of a body part (beak).

Acknowledgements

This Project was funded by the Austrian Science Fund FWF. We would like to thank the WAF and Wener Zecchino for additional sponsoring as well as Lukas Auersperg for constructing the apparatus

Referenences

Alcock, J. (1972). The evolution of the use of tools by feeding animals. *Evolution* **26**: 464-473.

Auersperg, A.M.I., Gajdon, G.K. & Huber, L. (2009) Kea (*Nestor notabilis*) consider spatial relationships between objects in the support problem. *Biology Letters,* **5**, 455-458.

Auersperg, A.M.I., Gajdon, G.K., Huber, L. (2010) Kea (*Nestor notabilis*) produce dynamic relationships between objects in a second order tool use task. *Animal Behaviour.* In Press

Auersperg A.M.I., von Bayern A.M.F., Gajdon G.K., Kacelnik A. Huber. L. Flexibility in problem solving and tool use of Keas and New Caledonian Crows in a Multi Access Box paradigm. Submitted

Beck, B. B. 1980. *Animal tool behavior: the use and manufacture of tools by animals*. New York; London, Garland STPM Press

Bird, C., Emery N. 2009. Insightful problem solving and creative tool modification by captive nontool-using rooks. *Proceedings of the National Academy of Science* **106**(25), 10370-10375

Fragaszy, D. M., Vishalberghi, E.& Fedigan, L. M. 2004. *The Complete Capuchin*, Cambridge University Press

Gajdon G. K., Aman L., Huber L. 2010. Keas rely on social information in a tool use task but abandon it in favour of overt exploration, *Interaction Studies*, In Press

Huber, L., Rechberger, S., Taborsky, M. 2001. Social learning affects object exploration and manipulation in keas, *Nestor notabilis*. *Animal Behaviour* **62** , 945 – 954

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

Hunt, G.R. 2000. Tool use by the New Caledonian crow *Corvus moneduloides* to obtain Cerambycidae from dead wood. *Emu* **100**, 109-11

Jackson, J. R. 1963. The nesting of keas. *Notornis,* **10**, 319-326.

Kenward, B., Weir, A. A. S., Rutz, C. and Kacelnik, A. 2005. Tool manufacture by naïve juvenile crows. *Nature* **433**, 121.

St. Amant, R. & Horton, T. (2008). Revisiting the definition of animal tool use. *Animal Behaviour*. **75:** 1199-1208.

Tebbich, S., Taborsky, M., Fessl, B. & Dvorak, M. 2002. The ecology of tool use in the woodpecker finch (*Cactospiza pallida*). *Ecology Letters*, **5**, 656-664.

Chapter 6 Conclusion

My aim was to investigate how kea consider spatial relationships between objects, in particular during tool use. Although there are still numerous open questions, I think we have gained some insight into the mechanisms underlying problem solving in the kea throughout the experiments presented in this thesis.

I will now briefly summarize the main findings as well as describe some possible implications these results may have on present research. Finally I will suggest some future directions, which may be reasonable to affiliate to this work.

6.1 Summary of the Main Findings

Since all experiments presented in this thesis concentrate on physical problem solving, I used chapter one to depict some important background information: I started by explaining how the use of technical information may have been relevant in the evolution of higher cognitive processing (Byrne, 1997) and how physical cognition is presently investigated in non-human animals. I thereafter recapitulated some of the currently most important works on technical problem solving in birds such as the string pulling paradigm or the trap tube paradigm as well as various studies involving innovative tool use. The Introduction illustrates that corvids in particular have been under close investigation in previous years. Especially studies on innovative tool use have lately yielded exciting results: not only genetically tool using New Caledonian crows but also rooks, which are not known to employ tools in the wild, seem to pay attention to many functional properties of their instruments (such as the size, the weight or the orientation of the working end). They can furthermore remodel and manufacture tools and even operate a tool as a means to reach another tool (Bird & Emery, 2009; Taylor et al., 2009; von Bayern et al., 2009; Wimpenny et al., 2009). Since avian problem solving has been rather 'corvicentric' in the past years, it is an appropriate step to confront more parrots with similar problems, since they not only have similar relative brain sizes but have also been competent in various physical problem settings (Funk, 2002; Huber et al. 2001; Ivaniuk et al., 2005; Wedenich & Huber, 2006).

Some relevant ecological details about the kea, the parrot on which the experiments in

this thesis are focussed, are hereupon explained. The main conclusion of this part of the chapter was that the whereabouts of the kea's extreme neophilia and its strong urge investigate objects in its physical environment in a manipulative manner, seem to lie within its evolutionary history: during the ice age the kea was exposed to the harsh conditions of the alpine regions of the Southern alps of New Zealand (Fleming, 1979). Due to a lack of natural predators as well as a seasonality of food availability in this region, the kea developed into a cunning generalist: any possible food source is welcome within its open program foraging repertoire and the affordances of any object that could harbour such a food source are boldly examined in a destructive manner (Diamond & Bond, 1999).

I also summarize some important kea studies. Finding a sensibility to physical connectedness (Werdenich & Huber, 2006), as well as the capacity to use compact objects as tools, (Gajdon et al., submitted) is highly relevant for the experiments presented in this thesis. Chapters three to five are mainly focussed on tool relations in the kea, while chapter two investigates how kea perceive the physical connection between a food reward and the support it rests upon.

In chapter two we learn that, similarly to tamarin monkeys, kea quickly accomplish pulling a piece of support with a food reward resting upon, rather then next to it, whereas another (neotropical) parrot seemed to have problems with a comparable setup (Mendonça-Furtado & Ottoni, 2008). Contrary to juvenile chimpanzees (Povinelli et al., 2000) the kea had little difficulties with a task in which the reward was perceptually more contained by the support in the incorrect than in the correct option (their superior performance may however be due to their, as compared to the apes, considerably better vision). All but one subject did however, have trouble with a task in which the physical connectedness of the support to the reward was disrupted by a gap. We presume that the remaining subjects may be using a rule to always pull if the reward is sitting on top of the support, ignoring the physical connection of that support to their reach.

In the following chapter we picked up where previous studies on tool use in the kea left off: Gajdon et al. (submitted) discovered the capacity in captive kea to use compact objects as tools (as explained in the introductionary chapter). Here, we used a novel paradigm in which the spatial relationships between the tool and the appartus had to be established by the

subjects themselves. All our subjects quickly developed a sensitivity for stoppers in a tube lifting paradigm. Within a short time frame they not only learned to lift a tube at the blocked end in order to pour out its content, but also to attend to the number of stoppers (avoiding tubes with blockages at both ends). They could also almost immediately summon a new second order tool use action (inserting a correctly sized object previous to lifting) from this and former experiences about the functional relevance of tool size (Frangazy et al., 2004; Gajdon et al., submitted). Additionally, subjects quickly learned to apply the most efficient (means-means end) succession to retrieve the reward, initially disregarding the final goal in order to concentrate on the necessary steps in the sequence in a spatio-temporally coordinated manner. (Santos 2005). We therefore argue that the animals are learning to execute strategic rules to situations that help to solve problems more efficiently.

After finding tool capacities along with other physical competencies (Gajdon et al. submitted; Huber et al. 2001; Werdenich et al. 2006) a comparison to a naturally tool using corvid seemed reasonable. In chapter four we introduced a new, Multi Access Box paradigm featuring multiple solutions to reaching the same food reward (two of which included the use of tools) in order to compare problem solving abilities in extractive foragers.

The kea detected more solutions faster and were more flexible in switching between options once solutions were blocked than naturally tool-using New Caledonian crows. One kea even succeeded in retrieving the reward via stick tool use, which has never before been experimentally been shown in a parrot. We suspect that differences in neophobia as well as in exploration technique rather than intelligence seem to be responsible for the differences between the two species (more visual versus more haptic exploration). The exploration of the kea was also much more violent (pulling and tearing actions) while the manipulation of the crows was limited to hitting and probing actions directed at the affordances of the apparatus. We argue that tearing actions in these crows may be restricted to the tools themselves during tool manufacture but are rarely applied during foraging.

Although in the previous study one kea repeatedly succeeded in retrieving the reward by knocking it off an out of reach platform using a stick tool, we could not be sure whether he understood the stick as a functional extension of his beak towards the reward. Chapter five describes how three other subjects mastered using a stick to retrieve a reward after receiving

social cues. Thereafter they succeeded in navigating the stick into a desired direction in a two choice paradigm. Their success rate remained at the same (ca. 70%) throughout testing, which suggests that unsuccessful attempts were caused by technical difficulties rather than from not aiming at the desired goal. This is the first evidence of ability to actively direct a stick tool as a functional extension of a body part in non tool using birds.

6.2 Implications

The results of the support problem, which has already been tested on various primate species, further sustain a range of findings that performance in various aspects of cognition in large brained birds frequently matches that of the great apes (Emery & Clayton, 2004 $_{a,b}$; 2005). Such findings further emphasize a convergent evolutionary path of intelligent behaviour in birds and primates.

In the following experiments we found evidence for sophisticated levels of tool use but had difficulties showing whether insightful cognitive processes were underlying these actions. Although the kea seems to possess many prerequisites necessary for personating a skilled folk physician, it is still hard to determine whether higher levels of mental representations are responsible for its problem solving abilities. In order to exclude associative processes while targeting spontaneously accurate performance in a novel task, it can be advantageous to work with a species which is slightly neophobic and therefore at least vaguely reluctant to touch the apparatus more then necessary, such as most corvids. Due to their exceedingly strong urge to physically manipulate interesting objects, the kea will however literally hijack the experimental apparatus in a violent manner as soon as the experimental compartment is opened. Consequently, even with careful habituation, the kea typically retrieve the reward initially by accident and it is therefore often thorny to evaluate whether and how they may have gained knowledge of the functional properties involved.

Interestingly, when we compared the kea's performance in chapter five with a neophobic corvid, this violent examination technique turned out to be more successful overall. The kea retrieved the food faster and were more flexible in acquiring new solutions. The results of chapters three, four and five additionally indicate that although the kea are

rarely successful on a first trial, their learning as well as their generalization abilities are remarkably fast. Jane Godall and Hans Kummer (1985) suggested using innovativeness as an ecological measure for intelligence. Innovation is the "process that generates in an individual a novel learned behavior that is not simply a consequence of social learning or environmental induction" and innovativeness can therefore be depicted as the frequency with which individuals of a species make behavioural innovations, that are not the domain of most members of the species and differientiate from, genetically coded responses to the environment (Ramsey et al., 2007). It has also been shown that technical innovations in birds correlate with allometrically controlled measures of brain size (Levebre, 2010; Overington et al., 2009; Webster & Levebre, 2001). Our findings throughout this thesis imply that, although we can not yet evaluate whether the kea's behaviour during problem solving has been insightful in each individual case, its rapid generalization abilities and its flexibility in discovering and switching between novel solutions indicates an innovativeness equal to or possibly even higher than in some corvids.

All birds previously tested on problems involving tool use are also constructing complex nest cups out of twigs, such as most corvids. As mentioned in the previous chapters, there has been reasonable doubt whether avian tool use may be explained by high level processing since nest building already requires routinely establishing object relationships that are often more complex than tool use itself (Hansel & Ruxton, 2008). Tool use in nest building species such as for example in woodpecker finches may therefore merely have evolved to avoid morphological adaptations (Kacelnik, 2008). The kea, as many parrots, is breeding in simple burrows, which only entails some digging but not the establishment of complex object relationships (Jackson, 1963). As depicted in the last three chapters, the parrots are still proficient in establishing many innovative functional relationships between objects involving the use of several different kinds of tools: in chapter three we found that, with little experience, the animals can quickly conjure up second order object relationships involving compact tools. In chapters four and five we discovered that under the appropriate circumstances captive kea can acquire the complex motor actions required to handle a stick like tool in an orientated manner despite morphological shortcomings in this respect. The

results of this thesis indicate that complex nest construction is not a requirement for tool use in birds.

There has also been debate on whether complex physical skills are derived as a result of tool use in regularly tool using species such as the New Caledonian crow or whether a more domain general intelligence may be responsible (see for example Bird & Emery, 2009, Kacelnik, 2008, Levebre, 2010). Finding sophisticated tool use in large brained birds, which are no natural tool users such as kea or rooks, support the latter assumption. Although there have been reports of tool use in other parrot species, those incidences were observational and the tool was not directed as a functional extension of a body part. The capacity for various kinds of innovative tool actions has however previously been found in another non tool using corvid, the rook (Bird & Emery, 2009). The findings of this thesis make the kea a perfect representative of the psittacine family for avian tool use coequal to the rook in the corvid family.

6.3 Future Directions

Testing a new species on existing problem solving paradigms can be problematic since the experimental setups of some tasks may involve properties, irrelevant for the target behaviour but not perfectly cut out for some species' morphological or behavioural characteristics. Presenting specific modifications to apparatuses can sometimes notably improve the animals' performance (Martin-Ordas et al. 2008). For example when chimpanzees failed in versions of the classic trap tube paradigm, being required to use a tool to push a food reward out of a tube, it was assumed that they did not attend to the causally relevant features of the task (as described in the introduction; Povinelli, 2000). Apes did however succeed when confronted with another setup in which they could rake the reward towards themselves rather then pushing it away (Mulcahy & Call, 2006). They also improved their performance when the trap tube was exchanged with a trap table or when the tools were removed (Martin-Ordas et al., 2008, Seed et al., 2009). The kea also failed previous attempts at the trap tube paradigm (as described in the introduction; Werdenich et al.; unpublished data). Our subjects have however, gathered new experience from the spaghetti breaking

paradigm in which they lifted tubes while avoiding blockages (as described in chapter three). The keas' success in this task opens the opportunity to new versions of the trap tube paradigm, which may be better adapted to our subjects' specific skills. This would additionally represent an opportunity to find out to what degree the animals have a mental representation of the dynamic path the reward is going to take through their actions. I hereby suggest, for example a tool-less trap tube seesaw apparatus, which can be employed simply by lifting a tube, loosely fixed in a horizontal position at the appropriate site causing the reward to roll out at the opposite end or, alternatively to end up inside the trap (see Figure 1). Another option, involving ball shaped tools, may be a two choice task featuring two tubes fixed in a vertically slanted position as in Gajdon et al. (submitted; described in the introduction), one with a functional and one with a nonfunctional trap respectively.

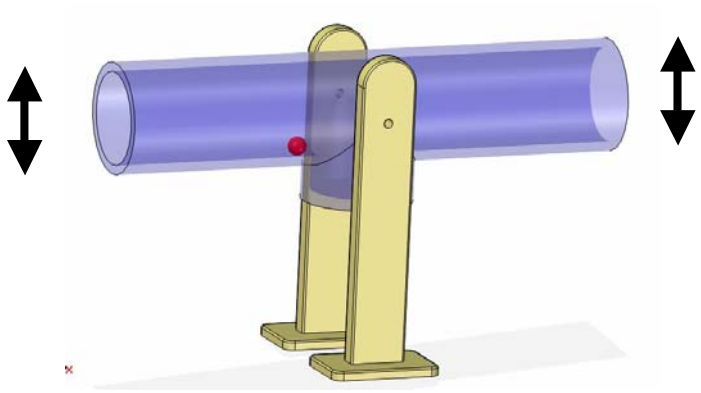


Figure 1. Suggestion for a kea-specific trap tube apparatus. The transparent tube is loosely fixed and can be lifted at either end, dictating the path of the reward

The use of compact objects as tools also opens the gate to future investigations into aberrations of tool challenges, previously tested on corvids such as meta tool use or tool modification as tested on rooks by Bird & Emery (2009). It would furthermore be very exciting to confront other psittacines with similar tool use problems: only a circumstantial intra-family comparison of physical abilities can allow us to determine in sufficient detail how tool use abilities may be influenced by the animals' ecology.

Although we tested the Multi Access Box apparatus only on two species it would be reasonable to also test the same apparatus on more food extracting species. During testing, the New Caledonian crows struggled with the window solution and took longer to detect the ball option than the kea did. It is possible that their behavioural repertoire may be canalized through adaptive specialisation towards stick tool use during problem solving and that their success may depend on whether solutions involve the use of stick like tools. It is, however, equally probable that the difference in performance between the two species was solely caused by their difference in neophobia. It would therefore be decidedly appealing to test other (physically skilled) neophobic corvids, such as rooks or common ravens on the same paradigm. As mentioned earlier, large scale interspecies comparisons, including a large number of different extractive foraging species, might moreover help us to test hypotheses concerning the relationship between ecological factors, exploration strategies and foraging styles, as well as the processes involved in innovation and flexibility.

6.4 References

Bird, CD & Emery, NJ. (2009)$_1$. Insightful problem solving and creative tool modification by captive rooks. *Proceedings of the National Academy of Sciences,* **106**, 10370-10375

Byrne RW (1997) The technical intelligence hypothesis: an additionalevolutionary stimulus to intelligence? In: Whiten A, Byrne RW(eds) Machiavellian intelligence. vol II: extensions and evaluations. Cambridge University Press, Cambridge, pp 289–211

de Mendonça-Furtado O, Ottoni E B (2008) Learning generalization in problem solving by a blue-fronted parrot (*Amazona aestiva*). *Animal Cognition* **11**:719-725

Diamond, J. & Bond, A.B. (1999) *Kea, Bird of Paradox: The Evolution and Behavior of a New Zealand Parrot*. Berkeley, CA: U. of California Press.

Emery, N.J., & Clayton, N.S. (2004)$_a$. *Comparing the complex cognition of birds and primates. In: Comparative vertebrate cognition: are primates superior to nonprimates?* (eds. Rogers, L.J., & Kaplan, G.). Developments in Primatology:Progress and Prospects, pp. 3-55. New York: Kluwer Academic / Plenum
Publishers.

Emery, N. J. & Clayton, N. S. (2004)$_a$. The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science,* **306**, 1903-1907

Emery, N.J., & Clayton, N.S. (2005). Evolution of the avian brain and intelligence. *Current Biology* **15**: R946-R950..

Fleming, C.A.(1979) *The geological history of New Zealand and its life.* Auckland: Auckland University Press

Frangazy, D.M., Visahlberghi, E., Fedigan, L.M. (2004) *The Complete Capuchin.* Cambridge University Press

Funk, M. (2002) Problem solving skills in young yellow crowned parakeets (*Cyanoramphus auriceps*) *Animal Cognition.* **5**(3), 167-176

Gajdon, G.K., Lichtnegger, M., Huber, L. Toddler like object exploration 1 helps captive mountain parrots to innovate tool use behaviour. Submitted

Hansell, M. & Ruxton, G. 2008. Setting tool use within the context of animal construction behaviour. Trends in Ecology and Evolution, **23**,73–78

Huber, L., Rechberger, S., Taborski (2001) Social learning affects object exploration and

manipulation in keas, *Nestor notabilis* . *Animal Behaviour*, **62**, 945-954.

Humphrey, N. K. (1976). The social function of intellect. In: *Growing points in ethology* (Ed. by Bateson, P. P. G. & Hinde, R. A.), pp. 303-317. Cambridge: Cambridge University Press.

Iwaniuk, A. N., Dean, K. M. & Nelson, J. E. (2005). Interspecific allometry of the brain and brain regions in parrots (*Psittaciformes*): comparisons with other birds and primates. *Brain, Behaviour and Evolution*, **65**, 40–59.

Jackson, J. R. 1963. The nesting of keas. *Notornis,* **10**, 319-326.

Kacelnik, A. 2009. Tools for thoughts or thoughts for tools? *Proceedings of the National Academy of Sciences of the United States of America **106***, 10071-10072.

Kummer, H. & Goodall, J. 1985 Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society of London* B **308**, 203–214.

Lefebvre, L., Whittle, P., Lascaris, E. & Finkelstein, A.1997 Feeding innovations and forebrain size in birds. *Animal Behaviour* **53,** 549–560

Levebre, L (2010) Taxonomic counts of cognition in the wild. *Biology Letters.* Published online

Liedtke, J., Werdenich, D, Gajdon, G. K., Huber, L, Wanker, R. (2010) Big brains are not enough: performance of three parrot species in the trap-tube paradigm. Animal Cognition. Published online

Martin-Ordas, G., Call, J**.** & Colmenares, F. (2008). Tubes, tables and traps: great apes solve two functionally-equivalent trap tasks but show no evidence of transfer across tasks. *Animal Cognition,* **11***,* 423-430.

Martin-Ordas, G. & Call, J**.** (2009). Assessing generalization within and between trap tasks in the great apes. *International Journal of Comparative Psychology,* **22**, 43-60.

Mulcahy, N.J. & Call, J. (2006). How great apes perform on a modified trap-tube task. *Animal Cognition,* **9***,* 193-199.

Ramsey, G., Bastian, M.L. & van Schaik, C.P. (2007) Animal innovation defined and operationalized. *Behav. & Brain Sciences* **30**: 393-437.

Reader, S. M. & Laland, K. N. (2002) Social intelligence,innovation and enhanced brain size in primates. *Proceedings of the National Acadademy of Science USA* **99**, 4436–4441.

Povinelli D J (2000) *Folk Physics for Apes. The Chimpanzee's Theory of How the World Works*. Oxford University Press

Santos, L., Rosati, A., Sproul, C., Spaulding, B., Hauser, M. D. 2005. Means-means end tool choice in cotton top tamarins (*Saguinus oedipus*): finding the limit of primates' knowledge of tools. *Animal Cognition* **8**, 236-246

Taylor, A.H., Hunt, G.R., Medina, F.S. and Gray, R.D. (2009). Do New Caledonian crows solve physical problems through causal reasoning? *Proceedings of the Royal Society, London* B **276**, 247-254

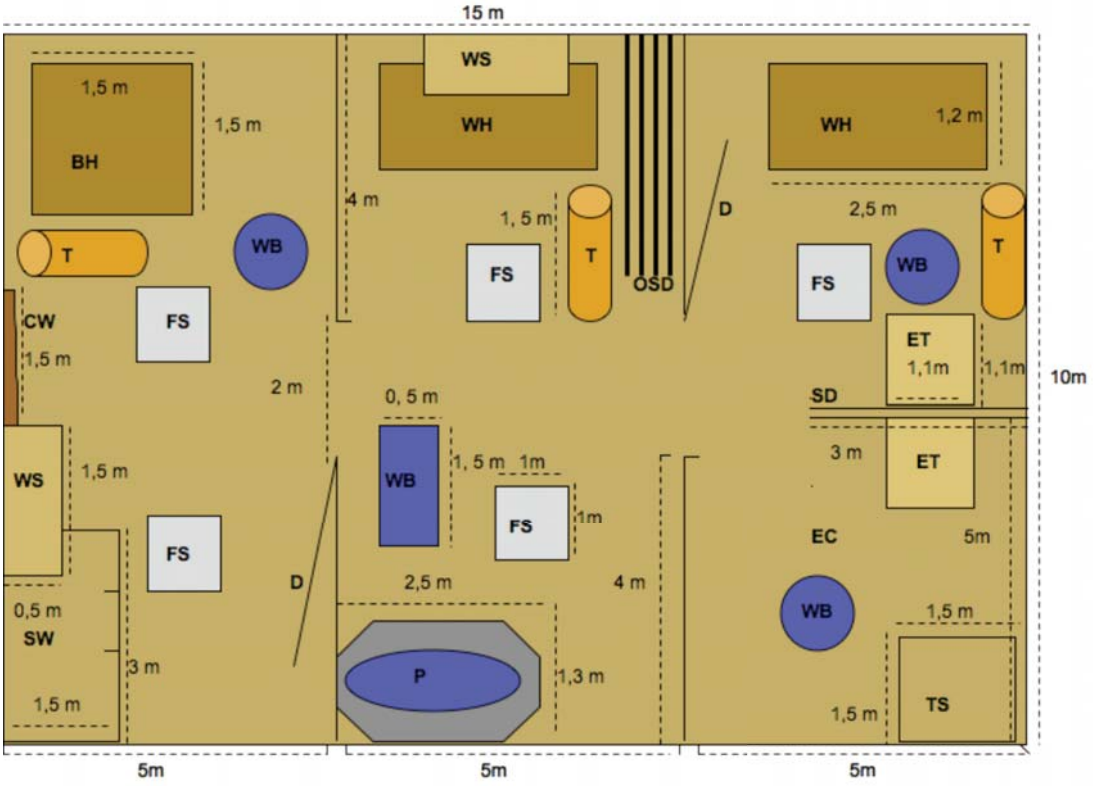
von Bayern, A. M. F., Heathcote, R. J. P., Rutz, C., Kacelnik, A .(2009)The role of experience in problem solving and innovative tool use in crows. *Current Biology*, **19**(22),1965-8

Webster, S. J. & Lefebvre, L. (2001) Problem solving and neophobia in a columbiform–passeriform assemblage in Barbados. *Animal Behaviour*, **62**, 23–32.

Werdenich D, Huber L (2006) A case of quick problem solving in birds: string-pulling in keas (Nestor notabilis). *Animal Behaviour* **71**:855-863

Wimpenny, J. H., Weir, A. A. S., Clayton, L., Rutz, C., Kacelnik A. (2009) Cognitive Processes Associated with Sequential Tool Use in New Caledonian Crows. *PLoS ONE,* **4**(8), e6471

Appendix 1 Basic plan of the aviary at the KLIVV



Breeding Hut

CW – Climbing Wall

D - Door

EC – Experimental Compartment

ET - Experimental Table

FS – Foraging Table

OSD – Opaque Sliding Doors

P - Pond

SD – Sliding Door

SW – Sick Ward

T – Hiding Tube

TS – Touch Screen

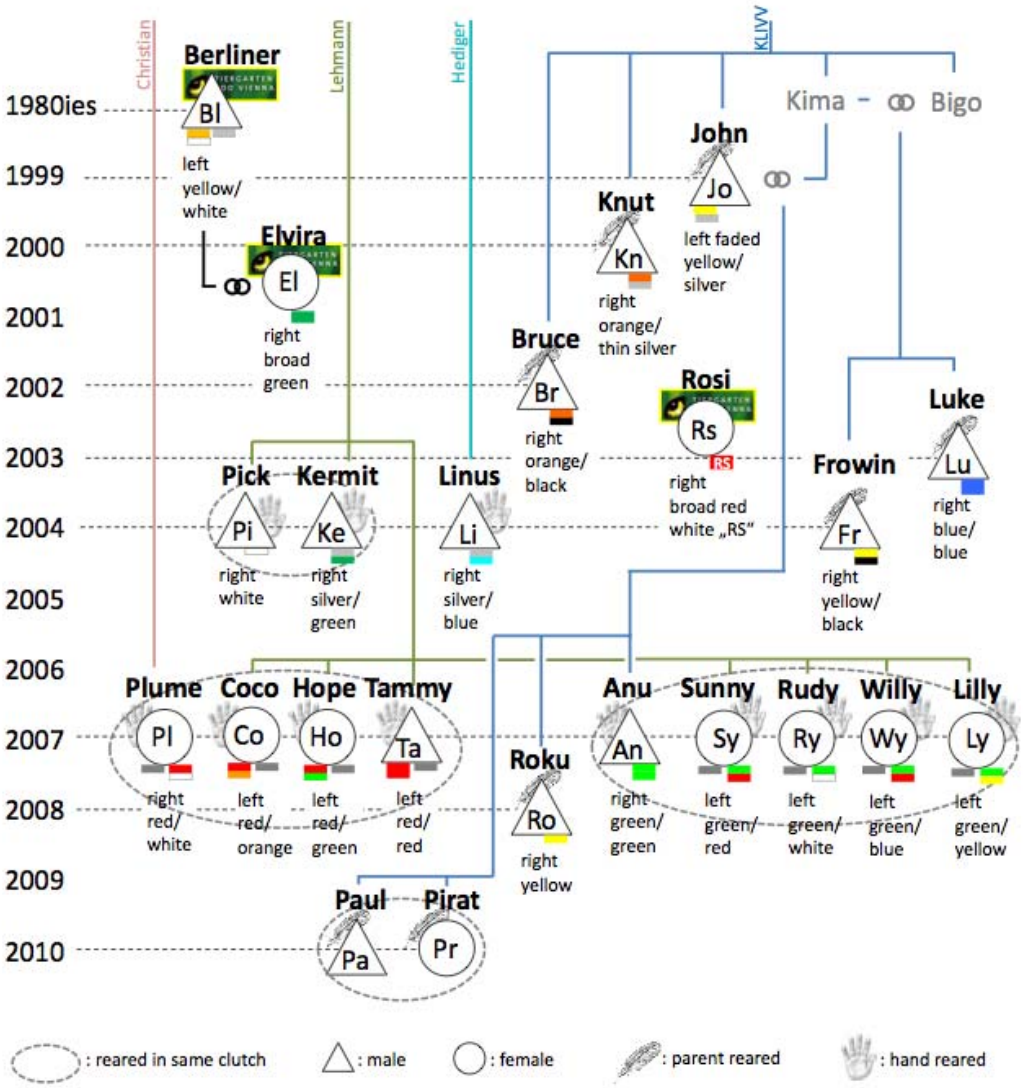
WB – Water Bowl

WH – Weather Hut

WS – Weather Shelter

Appendix II

Current animal stock at the Vienna kea lab



by Dr. Gyula Gajdon

Appendix III

Supplementary Material for: 'Kea (*Nestor notabilis*) consider spatial relationships between objects in the support problem'

1. Extended Materials and Methods

Subjects

Six juvenile kea (Hope, Plume, Willy, Lilly, Gino & Anu), two of which were males took part in this study. All of them were between 13 and 15 months of age. We also used two subadult males (Zappel & Linus) at four years of age. All eight subjects were hand-raised at the Konrad Lorenz Institute for Ethology in Vienna. They were housed together in one large group aviary (15m x10m x 4m) enriched with branches, stones and wooden logs, and occasionally with wooden toddler toys. Food consisted of a mixture of fruit, vegetables, cottage cheese, minced beef, eggs, seeds and vitamin supplements and was offered everyday at 12 am and fresh drinking water was available ad libitum. During testing, an opaque sliding wall was temporarily closed between the experimental compartment (5mx10mx4m) and the remaining aviary in order to visually isolate the test subject from its conspecifics. All subjects had previously participated in several experiments including two-choice-paradigms, but never in this particular setup.

Apparatus

The apparatus consisted of a wooden box (60cm x 30cm x 30cm). The broad front was made of Plexiglas (26cm x 60cm) and left a gap of 4 cm between its lower end and the floor of the box. Since it was not possible to habituate the kea on cloth we used wood as support material: Two red wooden slats, (25cm x 5.5cm x 0.4 cm) were arranged in parallel (20 cm apart) underneath the Plexiglas partition (Figure 1). A peanut was used as food reward, which could only be obtained by pulling the baited slat at the end, sticking out from under the partition (Figure 1). To avoid frustration if a peanut fell off a slat that was pulled too quickly, it was loosely fixed with a drop of cream cheese to the distal end underneath the partition. A thin, translucent layer of cream cheese was smeared on both slats before testing in order to make

sure they both smelled similarly. In order to avoid rushed choices, the subject had to wait ten seconds behind a wire mesh 2.5m from the baited apparatus before trial. The birds were not able to observe the placing of the peanuts.

Training

All subjects received a basic training followed by 5 transfer tests of increasing difficulty (Hauser et al. 1999; Povinelli 2000). Due to diet regulations the number of trials per session varied between the training and the different testing conditions (Table 1). During the training period the distal end of either both, one (right and left respectively), or neither of the slats ('neither condition') was baited with a peanut (Figure 1). Training continued until the animals had chosen the correct slat eight consecutive times in the 'one-side-baited' trials and stopped pulling any slat in the 'no-side-baited' trials. A trial was completed if a subject moved one of the two slats, did not approach the apparatus for one minute or distanced itself one meter from the apparatus after approaching it. Each subject was given one testing session per day and a maximum of ten sessions for each problem.

Immediately before each of the following testing sessions subjects had to successfully complete a given number of trials from the previous set up as a precondition to continue (Table 1). This ensured that the subjects were well motivated and attentive. If they failed the precondition, the procedure started again on the next day.

The 'On'- and the 'Connected Problem'

Subjects were first tested on the 'On Problem', which formed the basis of previous experiments (Spinozzi 1993, Hauser 1999, de Mendonça-Furtado & Ottoni 2008). Two equal rewards were used; one was placed onto the end of one slat and the other was placed one centimeter next to the end of the other slat randomly to its left or right side (Figure 1). After successful completion of the preceding session, three test trials (i.e. one test session) followed comprising one left, one right and one randomly baited trial in random order. Subjects were allowed to advance to the next transfer task after they had always chosen the correct slat in two consecutive sessions

In the 'Connected Problem' both slats were baited but one was interrupted by a 2cm gap. A session consisted of six test trials (three left and three right correct) in random order (Figure 1). The birds were allowed to proceed to the next transfer task after completing 5 consecutive trials correctly within one session.

Control of Perceptual Containment

For the control of perceptual containment we used four wooden slats, the ends of which were cut into distinct shapes (Figure 1). Most of the shapes were based on those Povinelli (2000) had used. First the subjects were tested on Combination A, in which the shape of the correct slat appears less contained within the perceptual field around the reward (option 1), while the incorrect option (option 2) appeared more engulfed in the reward; pulling the slat however, would not create contact (Figure 1). After reaching criterion in Combination A (see below), the animals were tested in Combination B, i.e. option 3 and 4. Here, the shape of the incorrect (4) and the correct option (3) were perceptually very similar and could only be differentiated with great acuity (Figure 1). Subjects would need to pay special attention to the contact between the support and the reward in order to solve the task. In both combinations (A and B) each subject received six testing trials per session with each option allocated three times to each side in a counterbalanced random order. Testing proceeded until a subject chose the correct option in five consecutive trials within one session.

All subjects were tested in visual isolation from other group members. A trial was completed if a subject touched one of the slats with the beak or another body part and each subject was given one testing session per day and a maximum of ten sessions for each problem. Criteria required to fulfil in order that a subject advanced to the next trial are depicted in Table 1. Once a subject had met the criteria in these two combinations, it was confronted with an array of mixed combinations of the same options (Fig. 1). Combination C contained options 1 (correct) & 4 (incorrect), Combination D options 2 (incorrect) & 3 (correct); Combination E options 2 & 4 (both incorrect) and Combination F options 1 & 3 (both correct). Again each session was preceded by trials of the previous task: before testing, each subject had to master two extra trials of Combination A and B, each in random order. Again, a test session

consisted of six trials; subjects were confronted with combination C and D twice (for each the correct choice being once left and once right), and with combinations E and F once. Testing proceeded until the subject had mastered two consecutive sessions without incorrect choices in the trials of Combinations C & D.

Analyses

The individual performance within the first ten test trials of each condition was examined using binominal tests. If a subject did not reach significance within this limit we carried out further trials in the binominal test to identify the trial number at which they did. In the analysis of the training and the last tasks (Combination C-F) we included only trials containing one correct and one incorrect option (i.e. E & F were excluded).

Curriculum Vitae

Alice Marie Isabel

Auersperg

PERSONAL DATA
Doctoral Student, Kea Lab,
Department of Cognitive Biology
University of Vienna
Althanstr.14, 1090 Vienna
Home Adress:
Goldegg 7, 3110
Neidling, Austria
Mobile: ++43-676 9390392
E-mail: alice_bayern@hotmail.com
Date of Birth: 25.Juni 1981
Landsberg am Lech, Germany
Marital status: Married
Nationality: German

EDUCATION

2007/10-	Candidate for a Doctor of Natural Sciences Department for Cognitive Biology **Unversity of Vienna** UZA I, Biozentrum, Althanstraße 14, 1090 Vienna, Austria http://cogbio.univie.ac.at/
2007/05	Bachelor of Science, (Honours, Zoology) School of Biological Sciences **Edinburgh University** Darwin Building, King's Buildings Mayfield Road, Edinburgh EH9 3JR
2002/07	International Baccalaureate **Munich International School** Schloß Buchhof, 82319 Starnberg, Germany

INTERNSHIPS & WORKEXPERIENCE

2005/07-2005/09 **Estacion de Biodiversidad Tiputini Equador**
Field assistant
monitoring behaviour and change in biomass of
red howler monkeys (*Alouatta seniculus*)

2004/06– 2004/08 **Subdepartment of Animal Behaviour**
University of Cambridge
Research assistant (Corvid cognition)
hand-raising and experimentally
monitoring 14 newly fledged Jackdaws (*Corvus monedula*)

2003/08- 2005/09 **Atlantic Whale Foundation Tenerife**
Cetacean student research project
Arona, Tenerife
research coordinator (Pilot whale population ecology)

2006/06-200/07 and
2006/06-2006/07 **Ritterturnier Kaltenberg Veranstaltungs- GmbH**
Klaus Bock/S. König, Marketing & Public Relations
Schloss Straße 8
82269 Kaltenberg
PR & Media

1997/03-1997/04 **Field Trip to Galapagos**
Coordinated by Prof. I. Eibl-Eibesfeldt

SKILLS, COMPETENCIES
Language skills: German (native)
English (fluent, written and spoken)
French (basics, written and spoken)
IT skills: MS Office (Word, Excel, PPT), Adobe, SPSS, Noldus Observer.
Interests: Birds; Physical cognition; tool use; evolution of animal play
Hobbies
Sports: skiing, horse-riding, scuba diving,Rock climbing
Culture: Reading, Central-Southern Africa, S. America, Travelling