Can you teach an old parrot new tricks?

Individual variation in the problem-solving abilities of
wild kaka (*Nestor meridionalis*)

by

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“It is not only fine feathers that make fine birds.”

Aesop, The Jay and the Peacock

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ABSTRACT

Identifying factors that may influence cognitive variation in the wild is essential for furthering our understanding of how ecological and evolutionary mechanisms shape cognitive phenotypes. Yet, studies on cognitive variation in the wild and its causes and consequences are still rare. In both the wild and captivity, birds have become a centre of attention, revealing striking cognitive abilities that may rival the great apes. While much of this research has focused on corvids, few parrot species have been studied thoroughly. One of these species is the kea (*Nestor notabilis*), which has shown remarkable social and physical cognitive skills, including the use of tools. This thesis explores the innovative problem-solving skills of the only other *Nestor* species, the kaka (*Nestor meridionalis*), with the overall aim to investigate ecological, developmental and genetic factors influencing within-species variation of these abilities in the wild.

When confronted with a series of novel problems at a familiar feeding station, juvenile kaka outperform adult kaka, especially in their ability and efficiency to find an innovative solution to acquiring the food reward. This is particularly the case when modification of a pre-learned behavioural response is required and is further expressed in the juveniles' higher individual persistence and exploration diversity, which suggests they may be more behaviourally flexible. Testing for this hypothesis using a Multi-Access-Box approach confirmed faster, more flexible discovery of alternative solving strategies in younger birds.

Further analysis of the kaka's innovation abilities uncovered potential genetic effects on solving ability as shown by full sibling comparison. This provides first potential evidence for heritability of a cognitive trait in the wild and thus presents an important step for furthering our understanding of how natural selection may act on cognitive traits. Between-species comparison of kaka and kea in the physical and social cognitive domains reveals striking similarities. This suggests that the differences in the life histories of these two species play a secondary role in the evolution of *Nestor* parrot cognitive abilities, which may instead be retained from their common ancestor.

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STATEMENT OF AUTHORSHIP

I hereby confirm that this thesis is my own work and that all sources quoted, paraphrased or otherwise referred to have been properly acknowledged in the references. I confirm that this thesis has not been previously submitted for the award of a degree by this or any other university. Any parts of this thesis that resulted from the contribution of others are detailed below or in the Acknowledgements.

Chapters 2 to 4 were written as independent manuscripts intended for publication. As these chapters included contributions of collaborators, they were written in first person plural tense. I am the primary author of each of these papers, with my supervisors, AProf Kevin C. Burns and Dr Rachael C Shaw, as co-authors. Chapters submitted for publication are reproduced in published form in the style of the journal, but with minor modifications to the formatting, and with added cross-references between chapters. As a collection of papers, there is unavoidably some repetition between chapters, particularly in the introductions. Any results which could not be included in manuscripts due to constraints of time or space are included in appendices at the end of the thesis.

In all instances, I designed the studies, carried out the field work and data collection, and drafted the manuscripts. My supervisors provided advice throughout and contributed to study designs, data analyses and the editing of the manuscripts.

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1 GENERAL INTRODUCTION

1.1 EVOLUTION OF COGNITION

In order for natural selection to act on cognitive traits and result in adaptive evolutionary changes, these traits need to be variable, heritable and confer fitness benefits (Darwin 1871; Croston et al. 2015). While many studies have shown that individuals do vary consistently in their cognitive abilities and have tried to determine the factors influencing this variation (Liker and Bókony 2009a; Cole et al. 2011; Morand-Ferron et al. 2011; Thornton and Lukas 2012; Benson-Amram and Holekamp 2012; Aplin et al. 2013; Rowe and Healy 2014; see also section 1.2), evidence for heritability (reviewed in Croston et al. 2015) and fitness consequences (Keagy et al. 2011; Boogert et al. 2011; Cole and Quinn 2012; Cole et al. 2012; Cauchard et al. 2013; Hollis and Kawecki 2014; Morand-Ferron and Quinn 2015) in non-human animals remains rare.

There are currently many different hypotheses on the ecological and evolutionary mechanisms that may underpin individual cognitive variation. Some of the experimental findings led to the assumption that specific cognitive abilities evolve in response to a species' habitat and hence are a reflection of a species' natural history. Kamil and colleagues provide examples of that by comparing four seed-caching corvid species with different elevational distribution resulting in differential dependence on cached food (Kamil 1988; Olson et al. 1995; Balda et al. 1996). They found that those species with the highest dependence on cached food also show the best performance in spatial memory tasks. Similar results have been found for other bird species (Brodbeck 1994) and kangaroo rats (Barkley and Jacobs 2007).

The cognitive buffer hypothesis on the other hand focuses on the correlation of high innovation rate and large relative brain size found in birds and primates (birds: Lefebvre, Whittle, and Lascaris 1997; Timmermans et al. 2000; primates: Reader and Laland 2002; Byrne and Corp 2004; reviewed in Lefebvre, Reader, and Sol 2004). It suggests that large brains provide a higher capacity for general cognitive processes such as innovation, learning and planning, which enable behavioural flexibility and modified responses to changes in the environment. In this way large brains buffer the individual against social and ecological challenges leading to increased survival chances and a longer reproductive

life (Allman et al. 1993; Deaner et al. 2003; Sol 2009). In other words: Large brains make for better problem-solvers. This hypothesis is supported by recent evidence showing a direct correlation between relative brain size and performance in problem-solving tasks in primates and mammalian carnivores (MacLean et al. 2014; Benson-Amram et al. 2015). Additionally, both avian and mammal species with larger relative brain size are more successful at establishing themselves in novel environments (Sol et al. 2005a; Sol et al. 2008) and have a longer lifespan (Allman et al. 1993; Ricklefs and Scheuerlein 2001). Sol et al. (2007) also found lower rates of adult mortality in larger-brained bird species in the wild. Furthermore, true tool use is found in bird species with larger relative brain size (Lefebvre et al. 2002) and the families of the animal kingdom which seem to have evolved the most complex cognitive abilities, parrots and corvids in birds and the great apes in mammals, have the same relative brain size and much larger brains than predicted for their body size (Jerison 1973; Emery 2006). Together, these findings suggest that relative brain size may reflect an animal's cognitive capacity and it is argued that the evolution of larger brains was driven by the need to cope with environmental changes (Lefebvre et al. 1997; Sol 2009; Lefebvre 2010; Reader et al. 2011).

Alternatively, the Social Intelligence hypothesis suggests that complex cognitive abilities evolved to solve problems brought about by increasing social complexity (Jolly 1966; Humphrey 1976; Byrne and Whiten 1988). When living in a social group, each individual must recognize the members of its group, remember social relationships with other individuals and understand various types of communicative signals as well as the others' intentions (Tomasello and Call 1997). Several studies found an association between social complexity and cognition (e.g. Dunbar 1992; Bond et al. 2003; Krasheninnikova et al. 2013).

The Technical Intelligence hypothesis was postulated to complement the Social Intelligence hypothesis to explain the evolutionary changes in the great apes compared to the rest of the monkey clade (Byrne 1997). It is argued that the need to solve technical problems that arise from more complex foraging (e.g. remembering the location of wide-spread food sources or extracting foods) presented an additional stimulus to the evolution of enhanced cognition and larger brains. A recent study by Navarrete et al. (2016) provides support for this hypothesis by showing a strong direct relationship between technical innovations and both absolute and relative brain size, whereas non-technical innovations were only indirectly linked to brain size through diet and life history variables. Huber and

Gajdon (2006) proposed that the Technical Intelligence hypothesis can be applied to birds as well based on their findings of high physical cognitive abilities and technical innovations in a mountain parrot species. This idea is further supported by the finding that the diversity of technical innovations demonstrated by bird families is much better predicted by relative brain size than the number of food type innovations suggesting that the positive relationship between innovativeness and brain size in birds may be explained by the cognitive capacity required to discover new foraging techniques (Overington et al. 2009). Additionally, Ducatez et al. (2015) found larger relative brain size and higher technical innovation rate in dietary generalists when comparing 765 avian species suggesting that technical intelligence might favour an increase in diet breadth in birds.

1.2 INNOVATIVE PROBLEM-SOLVING ABILITIES

Innovation can be defined as either the product of a creative process, i.e. a novel behaviour or an existing behaviour applied in a novel context, or as the process of acquiring such a novel pattern of behaviour for coping with the environment (Reader and Laland 2003). Operationally, innovation is most commonly defined as (finding) “a solution to a novel problem, or a novel solution to an old one” (Kummer and Goodall 1985, p. 205) and thus experimentally evaluated using problem-solving tasks (e.g. Morand-Ferron et al. 2011; Overington et al. 2011; Griffin and Diquelou 2015).

Natural innovation frequency of species is measured by counting the number of anecdotal feeding innovations reported in the literature (Lefebvre et al. 1997; Reader and Laland 2001; Lefebvre and Bolhuis 2003). This includes food-type innovations, i.e. eating a new type of food, as well as technical innovations, i.e. demonstrating a new foraging technique. Webster and Lefebvre (2001) were able to show that there is indeed a positive relationship between natural innovation frequency and performance in a novel problem-solving task. Three passeriform species significantly outperformed two columbiform species in the ability to obtain food from a novel puzzle box as was predicted by their higher natural innovation rate. This relationship between innovation rate and problem-solving performance has recently been re-evaluated with the conclusion that problem-solving tasks provide indeed a valid experimental measure for innovation ability (Griffin and Guez 2014).

Both comparative studies on innovation rate as well as experimental studies on innovative problem-solving have revealed a number of possible fitness benefits such as increased success in surviving in new (Sol et al. 2002; Sol et al. 2005a) or seasonally changing environments (Sol et al. 2005b), increased mating success (Keagy et al. 2009; Boogert et al. 2011), and producing more or fitter offspring (Cole et al. 2012; Cauchard et al. 2013). Furthermore, innovation ability is positively correlated with large relative brain size (Lefebvre et al. 1997; Reader and Laland 2002; Lefebvre et al. 2004; Sol et al. 2005a; Benson-Amram et al. 2015) and linked with abilities thought to be cognitively demanding such as tool use (Reader and Laland 2002; Lefebvre et al. 2002), behavioural flexibility (Auersperg et al. 2011b; Leal and Powell 2012; Manrique et al. 2013; Lefebvre et al. 2013; Reader et al. 2016) and social learning (Reader and Laland 2002; Bouchard et al. 2007; Aplin et al. 2013), suggesting that innovation ability is associated with a species' cognitive capacity (Lefebvre et al. 1997; Chiappe and MacDonald 2005; Lefebvre 2010; Reader et al. 2011).

Competitive ability, on the other hand, is negatively correlated with innovativeness in male guppies and male great tits (Laland and Reader 1999a; Cole and Quinn 2012), which has led to the 'necessity drives innovation' hypothesis, which assumes that poor competitors are forced to innovate when good competitors monopolise limited resources (Laland and Reader 1999a; Reader and Laland 2001). A number of personality traits such as low levels of neophobia (Webster and Lefebvre 2001; Greenberg 2003; Overington et al. 2011), high exploration behaviour (Kendal et al. 2005; Overington et al. 2011; Quinn et al. 2016), and high persistence (Thornton and Samson 2012; Cauchard et al. 2013; Griffin et al. 2014) have also been linked with high innovative problem-solving success, however, not consistently (no correlation with neophobia: Liker and Bókony 2009; Aplin et al. 2013 ; no correlation with exploration: Biondi et al. 2010a; Cole et al. 2011; no correlation with persistence: Benson-Amram and Holekamp 2012). Recent research suggests that rather than temporal or spatial exploration measures, which have been used in the past predominantly (e.g. Verbeek et al. 1994; Dingemanse et al. 2003; Kendal et al. 2005; Overington et al. 2011; Cole et al. 2011), the variety of exploratory behaviours exhibited may predict innovative problem-solving success more accurately (Benson-Amram and Holekamp 2012; Benson-Amram et al. 2013; Griffin et al. 2014; Diquelou et al. 2015). Exploratory diversity may increase the chance of discovering a behaviour pattern suitable for a novel situation the same way larger groups of animals may show higher innovation

efficiency than smaller groups because they contain more diverse individuals (Liker and Bókonyi 2009; Morand-Ferron and Quinn 2011).

It is because of this consistent relationship between exploration diversity and problem-solving performance, amongst other things, that there is ongoing debate whether innovativeness indeed reflects an animal's domain-general cognitive abilities (Chiappe and MacDonald 2005; Sol 2009; Bird and Emery 2009; Lefebvre 2010; Cole et al. 2011; Lefebvre 2013) or if non-cognitive differences provide the source for innovation (Griffin and Guez 2016; see also Thornton and Lukas 2012; Rowe and Healy 2014; van Horik and Madden 2016). For example, it is argued that environmental variability selected for both enhanced cognition and dietary generalism but that there is no causal link between the two (Griffin and Guez 2016). Dietary generalism may then have affected exploration diversity which in turn favoured innovativeness. On the other hand, several authors support the idea that an increase in behavioural repertoire and flexibility may have been the necessary first step for the incorporation of new foods into one's diet and thus becoming a dietary generalist (Emery 2006; Ducatez et al. 2015) or favouring adaptive radiation (Nicolakakis et al. 2003; Tebbich et al. 2010; Lefebvre et al. 2016). The increase in nutrition through dietary generalism may then have further contributed to brain development (Aiello and Wheeler 1995; Ducatez et al. 2015). Furthermore, to my knowledge, there is to date no empirical research that directly investigated the underlying mechanisms of exploration diversity. While it is suggested that large brains increase the amount of control and precision of movement of the body which may enable exploration diversity (Griffin and Guez 2016), there is also evidence indicating that producing a diverse range of exploratory actions may indeed be underpinned by cognitive mechanisms. For example, it has been shown that animals that are rewarded for producing new behaviours become more behaviourally diverse (Jensen et al. 2006; Kuczaj and Eskelinen 2014; Pryor and Chase 2014), which suggests that learning might influence an individual's behavioural repertoire and that it is not solely determined by morphological aspects. It has also been pointed out that changes in behaviour are underpinned by cognitive mechanisms (Griffin et al. 2015) and that selecting exploratory actions may be cognitively demanding and involve processes such as associative learning, causal reasoning and behavioural inhibition (Diquelou et al. 2015). Additionally, a diverse behavioural repertoire may require creative thinking for generating new behavioural variants or combinations of behaviours (Reader and Laland 2003). Thus more research is needed to determine the cognitive and/or non-cognitive

mechanisms underpinning the relationship between personality traits such as exploration or persistence, and innovation.

1.3 COGNITION IN PARROTS

Among birds, corvids and parrots are the families with the largest relative brain size, much larger than predicted for their body size and similar to that of great apes (Iwaniuk et al. 2005; Emery 2006). While there has been an extensive number of cognitive studies on several members of the corvid family, cognition in parrots has, by comparison, rarely been investigated so far and predominantly focused on only two species: African grey parrots (*Psittacus erithacus*) and kea (*Nestor notabilis*). Piagetian object permanence and means-end comprehension (using the string-pulling task) are the only two cognitive problems that have been investigated in several parrot species (Pepperberg and Funk 1990; Pepperberg et al. 1997; Funk 2002; Pepperberg 2004; Schuck-Paim et al. 2009; Auersperg et al. 2013; Krasheninnikova et al. 2013). Results showed that all of the tested species were competent in these tasks, although in some cases high inter-individual and inter-species differences appeared.

Within the research of African grey parrots, one bird in particular contributed to our understanding of parrot cognition: Irene Pepperberg's Alex has taught us not only about the extraordinary language and communication skills a parrot is capable of (he had a vocabulary of 150 English words, learned to label 50 objects and was able to answer questions about their characteristics) but also about their understanding of concepts such as size, colour, shape, same/different, and quantity up to six, including absence of quantity (Pepperberg 1999; Pepperberg and Gordon 2005; Pepperberg 2006). More recent studies on African grey parrots showed that they are also able to infer the location of a hidden food reward by exclusion (Mikolasch et al. 2011) as well as by acoustic cues (Schloegl et al. 2012), but perform poorly in a delay of gratification task (Vick et al. 2010). Interestingly, when tested for their cooperative problem solving abilities, Grey parrots were able to act simultaneously and in accordance to the absence or presence of a partner but failed in the delayed partner arrival task (Péron et al. 2011).

Early studies on the kea, an alpine parrot endemic to New Zealand known for its mischievous, extraordinarily explorative, curious, and playful behaviour, focused on their social cognition. For example, kea were able to cooperate with a conspecific in two

different experimental settings, a seesaw apparatus and a double-sided box, but, similar to chimpanzees, never shared the reward (Teblich, Taborsky, and Winkler 1996; Werdenich, unpubl. data; Huber et al. 2008; cf. Melis, Warneken, and Hare 2010). There is also indication that kea learn from each other about the properties or functionalities of a stimulus (Huber et al. 2001). In the wild, however, kea showed no such signs of social learning (Gajdon et al. 2004). In a comparative tube removal task, all of the six captive kea succeeded either individually or after up to nine demonstrations by a proficient subject. Even after 26 demonstrations only two of at least 15 wild birds succeeded in removing the tube and it remained unclear whether those two individuals discovered the solution individually or by social learning.

Similarly, when tested in the string-pulling paradigm, differences between wild and captive kea were remarkable (Johnston 1999; Werdenich and Huber 2006). All but one of the seven captive individuals solved the task in their first trial, whereas in the wild only seven out of the 19 kea tested succeeded. Another study on wild kea showed their ability to innovate new foraging strategies (Gajdon et al. 2006). Five individuals of a local population in Mount Cook National Park learned how to open the lids of rubbish bins to obtain food scraps inside. That kea are also able to use tools was first shown in captive settings (Auersperg et al. 2010; Auersperg et al. 2011b; Auersperg et al. 2011a). Only recently have anecdotal observations suggested that wild kea learned to use tools too (Ibbotson 2011; Price 2012). Rangers of the Department of Conservation had seen kea inserting sticks into stoat traps to fish for the eggs used as bait. This again shows their highly innovative nature as well as the potential of experimental studies to reveal the cognitive capacity of a species. Other examples of tool use by captive parrots include hyacinth macaws (*Anodorhynchus hyacinthinus*), who use pieces of wood as a wedge to open nuts (Borsari and Ottoni 2005), greater vasa parrots (*Coracopsis vasa*), who use pebbles and date pits to scrape on or break apart seashells for ingestion (Lambert et al. 2015) and Goffin cockatoos (*Cacatua goffini*) who use sticks to retrieve out of reach objects (Auersperg et al. 2012b). Palm cockatoos (*Probosciger aterrimus*) are to my knowledge the only other example of a parrot species using tools in the wild. These birds use sticks and nuts for drumming on trees during social displays (Wood 1988).

1.4 THE NESTOR PARROTS

As introduced in the preceding section, kea have been subject to many cognitive studies and shown remarkable abilities both in the physical and social domain. Its closest relative, the kaka (Figure 1.1), however, has received little attention so far. Kea and kaka are the only two remaining species in the genus *Nestor* and belong with the kakapo (*Strigops habroptilus*), the third and final large parrot species endemic to New Zealand, to the family Strigopidae (Gill et al. 2010). Both kea and kaka are dietary generalists and extractive foragers (Moorhouse 1997; Diamond and Bond 1999), and have a similar, large relative brain size (Iwaniuk et al. 2005), characteristics that have been linked with high innovation rates (Lefebvre et al. 2004; Ducatez et al. 2015). However, kea and kaka differ in their personalities and life histories. While kea are neophilic and inhabit the mountainous regions of New Zealand's South Island (Diamond and Bond 1999; Gajdon et al. 2004), kaka are neophobic and inhabit the lowland forests of all three main islands as well as some offshore islands (Wilson et al. 1991; Diamond and Bond 2004; Gsell 2012). The kea's harsh environment with its scarce resources may require them to continuously invent new foraging strategies and could thus be a major driver in the evolution of their cognitive abilities and personality (Diamond and Bond 1999; Laland and Reader 1999a). Kea and kaka also differ in their development to independence from adults. Kea are dependent on adult foraging for about one year longer than kaka (Diamond and Bond 2004), who become largely independent of adults about five months after fledging (Moorhouse and Greene 1995; Diamond and Bond 1999). Kaka, additionally, lose their juvenile characteristics at about one year of age, whereas subadult kea remain distinguishable from adults for at least three years (Moorhouse and Greene 1995; Diamond and Bond 1999). Furthermore, the kaka's social play has been described as "briefer, more predictable and less sequentially diverse than that shown by keas", lacks object play and is restricted to fledglings and juveniles (Diamond and Bond 2004). Both species are thought to live to about 20 years in the wild (Bond and Diamond 1992; Moorhouse and Greene 1995; Heather and Robertson 2005; Leech et al. 2008).

Figure 1.1: A kaka in Zealandia, a wildlife sanctuary in Wellington, New Zealand.

Morphologically, kea and kaka are very similar, although kea are larger (780 – 960 g on average, compared to 340 – 400 g in kaka; Higgins 1999). The most conspicuous difference lies in their beaks (the upper mandible of a kaka is shorter and deeper than a kea's; Higgins 1999) and points out one of their dietary differences. Beside nectar, pollen, seeds, fruits, sap and scale insects, kea and kaka also consume wood-boring invertebrates (Moorhouse 1997; Diamond and Bond 1999), however, kea do so by tearing apart rotten logs while kaka excavate live as well as dead wood. As of now, we still don't know what cues kaka use in finding larvae inside the trees. One behaviour that has been observed in this context – they drum with their tongue on the bark and in this manner move along the tree – suggests they possibly create sound information and detect the pitch difference between the cavity of the larva and the solid wood (Moorhouse 1992). This would also fit well with the observation that kaka often attack the tree from the side opposite of the tunnel entrance (K. Yule, personal communication), which indicates that they are able to discern where the distance to the grub is shortest. Thus the kaka presents an ideal candidate for studying technical innovations in the wild and furthering our understanding of the influence of personality and life history on cognitive evolution.

1.5 THESIS OUTLINE

This thesis explores the innovative problem-solving skills of wild kaka with the overall aim to identify factors influencing individual variation of such abilities in the wild. Main focus is thereby given to age differences as this is an area which has received little attention in non-human animals so far and is of importance for furthering our understanding of how behavioural plasticity and cognitive traits change during development (Thornton and Lukas 2012). A better understanding of the range of plasticity in relation to heritable components of cognitive abilities will in turn contribute to our interpretation of evolutionary mechanisms and help us to estimate how animals may respond to rapidly changing environments (Croston et al. 2015). Additionally, social effects are investigated and taken into account throughout the thesis and their influence on technical innovations in this wild population of forest parrots is discussed.

In Chapter 1, I gave an overview of the existing literature on the relevant topics. Chapter 2 gives a general assessment of the kaka's problem-solving abilities in different contexts. Here, I present wild kaka at a wildlife sanctuary with a series of three different tasks, of which the first two constitute manipulations of familiar feeders. The kaka thus have to solve a familiar foraging problem in a novel way. By contrast, the third task involves an entirely novel foraging apparatus and problem. To explore possible correlates of inter-individual variation in the kaka's ability to solve these problems, behavioural factors such as exploration diversity and persistence are compared for different age groups.

Secondly, in order to better understand the adaptive value of cognitive abilities and how they are selected under natural conditions, we must also elucidate the heritability of cognitive traits in the wild (Thornton et al. 2014; Croston et al. 2015). Chapter 3 therefore investigates effects of relatedness on the innovative problem-solving abilities of wild kaka. Here, I reanalyse the dataset originally presented in Chapter 2 using a subset of individuals for which information on parentage was available. In doing so, the distribution of solvers across clutches is examined and heritability of overall problem-solving performance assessed. Additionally, 11 months of microchip reader data are included to reveal the individuals' typical social environment and its possible influence on the effects observed in the data.

To evaluate a hypothesis raised in Chapter 2 and further investigate the potential role of behavioural flexibility for the adaptation to new or changing environments, Chapter 4 tests for developmental changes in the kaka's flexibility to solve a novel foraging problem. A Multi-Access-Box is used to explore differences in the speed of younger and older kaka to discover an alternative solution when the one initially used is no longer functional.

Chapter 5 then summarises the findings of these chapters and discusses ecological and evolutionary consequences as well as implications for conservation measures for this endangered parrot species.

2 CAN YOU TEACH AN OLD PARROT NEW TRICKS? COGNITIVE DEVELOPMENT IN WILD KAKA (*NESTOR MERIDIONALIS*)

Despite recent efforts to characterise innovative individuals within a species we still know very little about the ontogeny of innovation ability. A number of studies have found that innovation rates are correlated with personality traits such as neophilia and exploration. Juvenile birds are frequently more neophilic and explorative, yet few studies have found evidence of age-related differences in innovative problem-solving success. Here we show consistently higher innovation efficiency in juveniles of a wild, omnivorous parrot species across a variety of tasks and contexts. We tested 104 kaka (*Nestor meridionalis*), ranging in age from four months to 13 years. Twenty four individuals participated in all three of our problem-solving tasks, two of which involved a familiar feeder and one an entirely novel apparatus. Juveniles were the most efficient problem-solvers in all three tasks. By contrast, the adults' success was context-dependent and limited to the novel apparatus, which did not require modification of a pre-learned behavioural response. This suggests greater behavioural flexibility in the juvenile birds, who also showed higher persistence and exploratory diversity than adults. These traits may enable young kaka to discover efficient foraging techniques, which are then maintained throughout adulthood.

2.1 INTRODUCTION

Behavioural innovations can be observed as behaviour patterns not previously found in the population and frequently arise in response to a novel problem, or as a novel solution to an existing problem (Kummer and Goodall 1985; Reader and Laland 2003). Innovative problem-solving abilities are of high adaptive value and increase individual survival chances in changing environments (Sol et al. 2002; Sol 2003; Sol et al. 2005a). Foraging innovations, for example, enable an individual both to exploit new food sources and find alternative means of exploiting familiar food resources as conditions change (Kummer and Goodall 1985; Lefebvre et al. 1997; Benson-Amram and Holekamp 2012). Thus more innovative individuals can be expected to be more successful foragers (Byrne 1997). This in turn can have fitness consequences including longer lifespan, increased mating success

(Keagy et al. 2009; Boogert et al. 2011) and producing more or fitter offspring (Cole et al. 2012; Cauchard et al. 2013).

Studies looking at within species variation in the tendency to innovate frequently reveal correlations with personality traits such as high exploration rates and low levels of neophobia (Webster and Lefebvre 2001; Greenberg 2003; Overington et al. 2011). Social factors such as larger group size (Liker and Bókony 2009; Morand-Ferron and Quinn 2011), rapid social learning (Reader and Laland 2002; Bouchard et al. 2007) or lower competitive ability (Laland and Reader 1999a; Cole and Quinn 2012) may also increase innovativeness. Studies on wild and captive hyenas (*Crocuta crocuta*) and birds (*Sturnus tristis*, *Cracticus tibicen*, *Corvus coronoides*, *Ocyphaps lophotes*, *Sturnus vulgaris*, *Acridotheres tristis*, *Grallina cyanoleuca*, *Manorina melanocephala*) recently suggested that the range of exploratory behaviours an individual exhibits, rather than temporal or spatial exploration measures, determines innovative problem-solving success (Benson-Amram and Holekamp 2012; Benson-Amram et al. 2013; Griffin et al. 2014; Diquelou et al. 2015). Exploratory diversity may increase the chance of discovering a behaviour pattern suitable for a novel situation the same way larger groups of animals may show higher innovation efficiency than smaller groups because they contain more diverse individuals (Liker and Bókony 2009; Morand-Ferron and Quinn 2011).

While several studies suggest that juveniles tend to be more explorative and less neophobic (Reader and Laland 2003; Biondi et al. 2010a; Benson-Amram and Holekamp 2012), few have found a correlation between age and innovation ability (no effect of age reported by Keagy et al. (2009); Biondi et al. (2010a); Benson-Amram and Holekamp (2012)) and those that have report varying results (see also Thornton and Lukas (2012)). In primates there is evidence suggesting increased innovation in adults, potentially due to their greater experience and foraging competence (Reader and Laland 2001; Kendal et al. 2005; Hrubesch et al. 2009). Whereas in passerines, two studies indicate higher innovative problem-solving abilities in juveniles (Vince 1958; Morand-Ferron et al. 2011). This has been explained by the ‘necessity drives innovation’ hypothesis (Laland and Reader 1999b) arguing that juveniles are poorer competitors and so more in need of innovative alternative solutions. Furthermore, age-related differences in innovation tendency have rarely been studied across a variety of tasks. Thus it remains unclear whether any differences found reflect a general difference in problem-solving ability between juveniles and adults, or are task- or context-dependent. In wild kea (*Nestor notabilis*) for example, research on a

naturally occurring foraging innovation revealed that the most successful individuals were the oldest (Gajdon et al. 2006). However, when wild kea were confronted with a novel string-pulling task, juvenile kea outperformed adults (Johnston 1999).

As foraging innovation frequency has been linked with larger–relative brain size (Lefebvre et al. 1997; Lefebvre et al. 2004; Sol et al. 2005a; Benson-Amram et al. 2015), we investigated age-related differences in innovative problem-solving abilities in a large-brained parrot species (Iwaniuk et al. 2005), the forest-dwelling kaka (*Nestor meridionalis*). Kaka are an especially interesting species for studying the effects of personality and ecology on innovative problem-solving skills as they are generalist, extractive foragers (Moorhouse 1996), characteristics thought to be associated with increased problem-solving success (Lefebvre and Bolhuis 2003; Emery 2006). Yet kaka are also neophobic (Wilson et al. 1991; Diamond and Bond 2004; Gsell 2012), a trait that has been linked to the inhibition of problem-solving abilities (Greenberg 2003; Benson-Amram and Holekamp 2012). Kaka are closely related to the mountain-dwelling and neophilic kea (Diamond and Bond 1999; Gajdon et al. 2006). Both species are thought to live to about 20 years in the wild (Bond and Diamond 1992; Moorhouse and Greene 1995; Heather and Robertson 2005; Leech et al. 2008), are endemic to New Zealand and the only species in the tribe Nestorini. While both social and physical cognition has been well studied in the kea (Huber et al. 2008; Range et al. 2009; Auersperg et al. 2011b; Gajdon et al. 2013), the kaka's cognitive abilities have not yet been investigated. We presented free-ranging kaka with a series of three foraging problems in varying contexts and measured individual differences in problem-solving performance, exploratory strategies and persistence. Individuals ranged in age from 4 months to 13 years, allowing us to explore the development of innovation ability and related behavioural traits or prerequisites in this species.

2.2 METHODS

2.2.1 Subjects, study site and general procedure

We tested free-ranging kaka at Zealandia, a 225 hectare large wildlife sanctuary surrounded by a pest-exclusion fence, in Wellington, New Zealand. Since the founding of Zealandia and ensuing reintroduction of kaka into the region in 2002, the population has been monitored by banding nestlings with a unique colour combination of two narrow aluminium bands on one leg and one wider cohort steel band on the other (except for the

2013/2014 breeding season when kaka were banded with the cohort band only – see Appendix A.1 for more information). From 2008 to 2013 nestlings also received an RFID tag. The exact age was therefore known for all of the subjects in this study and individual identification was possible. During our study the kaka population was estimated at 350 to 400 individuals. This estimate included a number of unbanded birds from unmonitored nests. Unidentifiable individuals were excluded from data analysis. None of the kaka had previously participated in any cognitive study.

Figure 2.1: (a) A kaka using the feeders at Zealandia. (b) The setup in the block-removal task. (c) A kaka removing the block. (d) A kaka opening the lid in experiment 2. (e) A kaka succeeding in the string-pulling task.

We conducted our experiments at two feeding stations. The stations each have two or three ~1.8 m high wooden platforms where kaka are offered supplementary food (parrot pellets) in stainless steel feeders (Figure 2.1a). All subjects were familiar with these feeders and regularly used them. We installed RFID readers on the platforms to obtain additional information on the bird's identity when band reading was impossible (Figure A.1.1). Records from RFID readers installed near the feeding platforms suggest that prior to testing the youngest birds had been using the feeders for at least 2 weeks to 3 months. Between February and October 2014 we tested birds up to five days per week. Test sessions lasted 2 h and took place during times that kaka typically frequented feeders. All kaka that came to the test platform during a session and fulfilled trial criteria were included in the analyses (see 'Data scoring' for our trial criteria and details on trials with multiple subjects). Our experiments were (i) a block-removal task (47 sessions), (ii) a lid-opening task (40 sessions) and (iii) a string-pulling task (18 sessions). These experiments are described in detail below. For experiments i) and ii) we removed any feeders that were not required for

the experiment. In the string-pulling task, we removed the feeders on the platform closest to the string and removed food from the other feeders.

Cashew nuts were used as the reward in all experiments. The block-removal and lid-opening apparatuses were always set up and reset out of the subject's view using a brown cloth as cover, but the baiting was then shown to the bird. In the string-pulling task, we directed the kaka's attention to the reward by tapping or holding it up. An assistant recorded all kaka present at the test location to control for potential social learning effects. We filmed all sessions to permit subsequent behaviour coding.

In total, 104 subjects participated in our study and they ranged in age from four months to 13 years. Twenty-seven of these kaka were juveniles (less than one year old), 42 were subadults (one to four years old) and 35 were adults (more than four years old; age classification according to Moorhouse and Greene (Moorhouse and Greene 1995)). Individuals received a total of 1 - 211 trials per task depending on the frequency of their visits to the feeding station (mean $\pm$ SE: block-removal: 8.8 ± 1 , lid-opening: 14.6 ± 3.8 , string-pulling: 20.4 ± 4.9 ; see Table A.1.10 for individual data).

2.2.2 Experiments

Experiment 1: Block-Removal

The kaka feeders (Figure 2.1a and Figure A.1.2) used at Zealandia are $25 \times 22 \times 11$ cm galvanised steel boxes manufactured by Grandpa's Feeders (Windsong Enterprises). The food tray ($10 \times 19 \times 5$ cm) is covered by a lid (11×22 cm) that is connected to an aluminium tread plate (13×30 cm). The tread plate functions as a push-down lever that opens the lid, enabling access to the food when the birds step on it. We positioned two feeders back to back on the test platform, which simultaneously decreased competition between subjects and kept the appearance of the experimental setup as close to the usual setting as possible.

We used the familiar feeders to create a novel problem for the kaka by blocking the tread plate with a wooden block ($7 \times 12 \times 5$ cm, mahogany, untreated) placed underneath (Figure 2.1b). The sides of the blocks featured zigzag-shaped grooves to facilitate grabbing hold of it. The block could be pulled or pushed out by the beak to re-establish the function of the tread plate (Figure 2.1c).

Experiment 2: Lid-Opening

In our second experiment we used the same familiar feeders to create a novel foraging problem, without including a novel object in the experimental setup. This enabled us to

evaluate the possibility that birds failed experiment 1 due to neophobia. Although all kaka approached the block in their efforts to access the feeder, potentially birds affected by neophobia may have avoided touching or interacting with the block in experiment 1.

In experiment 2 we removed the feeder tread plate and connecting rods so that the lid had to be flipped over to access the food. Due to the length of the lid, this was best achieved from the side of the box (Figure 2.1 *d*). To reduce the weight of the lid, hinges were moved 4.5 cm closer to the front and a $5.0 \times 2.0 \times 0.5$ cm piece of metal was attached to the end of the side bars.

We ran two versions of this experiment. We conducted the first 25 sessions with two feeders back to back on the platform to keep the experimental setup as similar to the usual situation and experiment 1 as possible. However, we removed the treadle on only one of the feeders as the lid flipped open would have obstructed the opening of the second feeder. The other feeder was empty during a session. The subsequent 15 sessions were conducted with only one feeder placed in the middle of the platform to ensure that the corner posts of the platform were not obstructing the subjects. As there was no significant difference in performance (proportion of successful out of total number of trials) between the two versions (Mann-Whitney U test: $U = 208$, $N_{V1} = 54$, $N_{V2} = 6$, $p = 0.27$), data was combined for analyses.

Experiment 3: String-Pulling

An entirely novel problem was used for experiment 3. This tested the possibility that any differences in performance could be attributed to routinized behaviour (as may have been the case in experiments 1 and 2).

At each test location, we fitted a ~24 cm long dowel (1.6 cm in diameter) to a branch that was close to one of the feeding platforms and tied a 50 cm long, 3 mm thick light green nylon string to the dowel. We threaded a loop of green 0.35 mm fishing line through each cashew nut as an attachment point for tying the nut to the string (Figure A.1.3). This facilitated rapid re-baiting of the string in the field. In this experiment pulling up the string enabled the kaka to reach the food reward (Figure 2.1 *e*).

2.2.3 Data scoring

A trial started the moment a kaka approached the apparatus (landed on the test platform/branch or noticeably looked at the reward at the end of the string) and stayed for more than 15 sec. A trial ended the moment the subject left the apparatus (left the test

platform or moved >2 m from string) for more than 15 sec, or once the problem was solved. We used trial duration as a proxy for how long an individual spent working on the problem. The task was solved successfully when the subject manipulated the apparatus in a way that allowed it to access the food reward.

For each kaka we recorded the number of successful trials as well as the total number of trials that they completed in each experiment. We calculated two measures for task solving speed: the number of trials and the total amount of trial time a kaka required to find a solution to the problem.

We measured individual persistence as the average ‘time spent per trial’ (in the case of solvers, this was up until a solution was found). Kaka exhibited a range of exploratory behaviours in their efforts to solve the problem. We calculated an individual’s ‘exploration diversity’ as the proportion of the total number of distinct behaviours the subject showed over the course of testing (in the case of solvers, this was up until a solution was found) out of the total possible behaviours used by all kaka during each experiment.

In cases where multiple subjects were working on the problem at the same time, we coded the behaviour for each focal individual and noted that conspecifics were present on the test platform/branch during the trial. We did not include trials that were directly interfered by another subject, whether by chasing away the focal subject or solving the task, in our performance analysis. However, we did include these trials in the analysis of exploratory strategies.

For each trial we also scored whether the subject was naïve, had previously been present (but had not participated) during a session, had witnessed manipulations of the apparatus that indicated how the problem could be solved or had directly observed a conspecific solve the task and retrieve the reward. These four different levels of social information were used to determine whether social learning affected the likelihood to complete a trial successfully. For more details on data extraction see Appendix, Table A.1.1 to Table A.1.3.

2.2.4 *Statistical Analysis*

We used a generalized linear mixed model (GLMM) with a binomial distribution and logit link to explore possible predictors of whether an individual solved the task (Y/N) for the 104 individuals that participated in at least one task. We included task, age, individual persistence and exploration diversity as well as the relevant interactions with task as fixed factors. For task the reference category was set to block-removal, for age the reference

category was set to adults. Subject was included as a random factor to control for repeated measures (Schall 1991). We subsequently dropped those terms from the model with the least explanatory power until the minimal model only contained variables that significantly predicted problem-solving success. Wald statistics and p values for significant terms were obtained from the minimal model and for nonsignificant terms by individually including them in the minimal model.

We then investigated whether the factors that were retained in the minimal model for the overall solving ability (Y/N) of all 104 subjects also affected task performance (measured as the proportion of successful trials) for the 24 individuals that participated in all three experiments. For this GLMM with a binomial error structure the response variable was the number of successful trials out of the total number of trials.

To investigate the effect of age and task type on persistence and exploration diversity we included these as fixed factors in GLMMs with a normal distribution and identity link (using robust estimation). We included data from all 104 kaka and specified subject as a random factor.

Using GLMMs we analysed how age, persistence and exploratory diversity affected the number of trials (Poisson distribution with log link) and absolute amount of time (normal distribution with identity link) until a solution was found. To limit the number of potentially confounding variables, we only analysed the first experiment (12 solvers), when all subjects were still naïve at the time of their initial success in the task. In the follow-up experiments solvers differed not only in their amount of testing experience but also in the level of social information they may have gathered by watching other individuals solve the problem. Model selection criteria were the same as described above.

To test whether competition at the apparatus affected the outcome of a trial, we used GLMMs with success as the binary response variable (Y/N) with a logit link and presence of a conspecific on the test platform/branch (Y/N; reference category set to N) as fixed effects as well as subject ID as a random factor to control for repeated measures. To avoid pseudo-replication across experiments (a subject may have had several trials in more than one experiment), we analysed each task separately. Similarly, we tested for the effect of social information a subject had had opportunity to gather by observing conspecifics interact with the apparatus (reference category set to “naïve”). Here, we excluded all trials that were conducted after the subject’s initial success.

2.3 RESULTS

2.3.1 Problem-solving performance

In total we tested 104 kaka ranging in age from four months to 13 years, with 24 participating in all three tasks (4 juveniles, 13 subadults, 7 adults). Of the 24 individuals, 18 solved at least one task and five solved all three (for the total number of subjects and solvers in each of the experiments see Table 2.1). Per trial, on average kaka spent 45.5 ± 2 s (mean $\pm$ SE) in the block-removal task, 38 ± 2.3 s in the lid-opening task and 19.1 ± 1.5 s in the string-pulling task. Kaka exhibited an average of three different exploratory behaviours in each of the tasks ($SE_{BR} = 0.1$, $SE_{LO} = 0.2$, $SE_{SP} = 0.3$) in their efforts to solve the problem. Furthermore, they found two different successful techniques in the lid-opening and eight different successful techniques in the string-pulling task (see Table A.1.4 in the Appendices).

Table 2.1: The number and percentage of kaka that were successful out of the total number of individuals tested in each of the three experiments.

Age group	Block-Removal			Lid-Opening			String-Pulling		
	Solver	Total	%	Solver	Total	%	Solver	Total	%
Juveniles	9	21	42.86	6	11	54.55	8	8	100
Subadults	3	34	8.82	6	28	21.43	8	15	53.33
Adults	0	32	0.00	1	22	4.55	4	7	57.14
Total	12	87	13.79	13	61	21.31	20	30	66.67

For the 104 kaka that participated in at least one task, task type, age and exploration diversity were the only significant predictors of an individual's ability to solve the task (minimal model, Table 2.2). All of the interactions with task type were non-significant, as was individual persistence, measured as the average time spent per trial (Table 2.2; see Appendix A.1 for additional analysis on individual persistence and exploration diversity).

Table 2.2: GLMM analysis of the factors affecting whether an individual solved the task.

	F	df 1	df 2	p
Full model				
Exploration diversity	22.487	1	169	4.5E-6
Task	6.336	2	169	0.002
Age group	6.379	2	169	0.002
Time spent per trial	1.021	1	168	0.314
Task*Exploration diversity	0.742	2	167	0.478
Task*Age group	0.328	4	165	0.859
Task*Time spent per trial	0.071	2	166	0.932
Minimal model				
	Coefficient estimate		SE	
Exploration diversity	-9.110		1.921	
Task: Block-Removal	0			
Task: Lid-Opening	-0.187		0.567	
Task: String-Pulling	-2.304		0.680	
Age group: Juveniles	-2.232		0.716	
Age group: Subadults	-0.368		0.639	
Age group: Adults	0			

Data were fitted to a binomial distribution with a logit link. We conducted the analysis on all 104 subjects ($N_{BR} = 87$, $N_{LO} = 61$, $N_{SP} = 27$) and included bird ID as a random factor (estimated variance component for bird ID in the minimal model = $2.7E-9$). Please note, for three individuals it was not possible to extract the exploration diversity value and mean time spent per trial (until a solution was found) in the string-pulling task from the video record due to technical failure.

Examining the proportion of successful trials for the 24 kaka that completed all three tasks, we found main effects for task and age (Table 2.3; Figure 2.2). The string pulling experiment had the highest success rate and block-removal the lowest, while juveniles performed better than subadults and adults (Table 2.3). No adults solved the block-removal task and only one succeeded in the lid-opening. Subadults tended to perform better than adults in both of the feeder experiments, however, this difference disappeared in the string-pulling task and was not significant overall (Contrast estimate (Subadults – Adults) = 0.206 ± 0.119 , $p = 0.088$). Although more explorative kaka tended to have a higher proportion of successful trials, exploration diversity did not significantly influence the proportion of successful trials for the 24 individuals that participated in all three experiments (Table 2.3).

Figure 2.2: Mean proportion of successful trials $\pm$ SE for each experiment and age group for the 24 individuals that participated in all three tasks.

Table 2.3: GLMM analysis of the factors affecting the number of successful trials for the 24 kaka that completed all tasks (the fixed factors were based on the minimal model reported in Table 2.2).

	F	df 1	df 2	<i>p</i>
Full model				
Task	21.079	2	67	7.9E-8
Age group	16.826	2	67	1.2E-6
Exploration diversity	3.872	1	65	0.053
Minimal model				
	Coefficient estimate		SE	
Task: Block-Removal	0			
Task: Lid-Opening	1.358		0.465	
Task: String-Pulling	4.052		0.625	
Age group: Juveniles	3.506		0.807	
Age group: Subadults	1.087		0.754	
Age group: Adults	0			

Data were fitted to a binomial distribution with a logit link. The total number of trials was used as denominator. We conducted the analysis on only those 24 subjects that participated in all three tasks and specified a repeated measures design ($N_{BR} = N_{LO} = N_{SP} = 24$ in the minimal model). Please note, for one individual it was not possible to extract the exploration diversity value for the string-pulling task from the video record due to technical failure ($N_{BR} = N_{LO} = 24$, $N_{SP} = 23$ in the full model).

2.3.2 Individual variation in behavioural measures

Juvenile kaka were more persistent than subadult and adult kaka (GLMM: $F_{2,173} = 12.634$, $p = 7.6E-6$; $N_{BR} = 87$, $N_{LO} = 61$, $N_{SP} = 28$) and showed greater exploratory diversity (GLMM: $F_{2,166} = 9.019$, $p = 1.9E-4$; $N_{BR} = 87$, $N_{LO} = 61$, $N_{SP} = 27$). However, the difference in exploratory diversity was present only in the lid-opening and string-pulling tasks, as indicated by the significant interaction of task and age group ($F_{4,166} = 4.895$, $p = 0.001$; Figure 2.3). For full model outputs see supplementary Table A.1.5 and Table A.1.5.

Figure 2.3: Mean $\pm$ SE (a) time spent per trial (individual persistence) and (b) proportion of exploratory behaviours for the different age groups as well as solvers and nonsolvers. Data is shown for all individuals for whom these measures could be scored (N is given at the base of the bars).

2.3.3 Speed in solving the first task (block-removal)

Juveniles solved the block-removal task faster than subadults, both in terms of the number of trials (GLMM: $F_{1,10} = 65.790$, $p = 1E-5$; $N = 12$ solvers) and the absolute amount of time required to find a solution (GLMM: $F_{1,10} = 16.797$, $p = 0.002$; $N = 12$ solvers). Juvenile kaka pulled the block out within their first four trials, whereas it took subadults at

least 10 trials to do so (no adults solved this task). Speed in solving the block-removal task was not correlated with either persistence or exploration diversity (see Table A.1.7 and Table A.1.8 in the Appendices).

2.3.4 *Social effects*

The presence of conspecifics on the test platform or branch did not affect the outcome of a trial in any of the experiments (GLMMs: block-removal: $F_{1, 759} = 0.092$, $p = 0.762$, $N = 761$ trials; lid-opening: $F_{1, 880} = 2.764$, $p = 0.097$, $N = 882$ trials; string-pulling: $F_{1, 575} = 0.520$, $p = 0.471$, $N = 577$ trials).

Watching another individual solve the problem did not increase the likelihood of an individual successfully completing a trial in the block-removal and lid-opening tasks (block-removal: $F_{3, 619} = 0.300$, $p = 0.826$, $N = 623$ trials; lid-opening: $F_{3, 480} = 2.119$, $p = 0.097$, $N = 484$ trials). However, trials in the string-pulling experiment that were conducted after the subject had directly observed another kaka succeed were more likely to be successful ($F_{2, 94} = 5.577$, $p = 0.005$, $N = 97$ trials; see also Figure A.1.4 and Table A.1.9).

2.4 DISCUSSION

Juvenile kaka outperformed adult kaka in all three of our problem-solving tasks. This was expressed both in terms of more individuals solving the task and higher individual success rates in juveniles. This finding is consistent with results in passerines (Vince 1958; Morand-Ferron et al. 2011) and provides the first evidence for age-related differences in innovative problem-solving abilities in parrots and across different tasks. In addition, success rate in adults was context-dependent, suggesting that decreased behavioural flexibility, rather than neophobia, inhibited the adults' innovation abilities in our tasks.

Whether an individual eventually solved the task also correlated positively with the diversity of exploratory behaviours displayed by the kaka, which is consistent with findings in hyena (Benson-Amram and Holekamp 2012) and other bird species (Diquelou et al. 2015) and confirms the importance of creative and flexible behaviour in generating innovations (Simonton 2003). Even in experiment 1 where juveniles and adults did not differ in their proportion of exploratory behaviours, a more creative approach to the problem was chosen almost exclusively by the younger birds. For example, almost all adults tried to force open the feeder by grabbing the lid with the beak from the front and

lifting it up, but juveniles and subadults did so from various angles of the box and exhibited alternative strategies such as trying to hold the lid open with one foot. Juveniles were also more persistent than adults, spending more time per trial trying to find a solution to the problem.

Interestingly, problem-solving success, persistence and exploratory behaviours all appear to decrease gradually with age. Subadult individuals tended to perform better, show greater exploratory diversity and be more persistent than adult birds in both feeder experiments. Furthermore, juveniles solved the block-removal problem faster than the subadult solvers with regards to both number of trials and absolute time.

In addition to the effect of age, success rates also increased across experiments, possibly due to differing levels of task difficulty, habituation to experimenter and test procedures (Thornton and Lukas 2012), or the visibility of the food reward. The performance difference between tasks was most prominent in adults: none were able to solve the block-removal, only one succeeded in lid-opening, yet over half the adults tested were successful in the string-pulling task. By contrast, the increasing success rate across tasks was far more gradual in juveniles and sub-adults. This suggests that the familiarity with the feeders may have inhibited the adults' success in the first two experiments. Potentially, adults failed to modify their learned behavioural response to the familiar problem (opening the feeder) to fit the new situation (blocked or missing tread plate). This may suggest that juveniles are more flexible in their behaviour, which is also supported by their higher scores in exploratory diversity and consistent with research suggesting that behavioural plasticity decreases with age (Wecker et al. 2005; Deary et al. 2009; Croston et al. 2015; Stamps and Frankenhuis 2016). However, juveniles also had less reinforcement for the normally functioning feeders and hence less reinforcement history to overcome. Potentially, this could mean that in a similar situation, in which adults and juveniles had been using the apparatus for the same period of time before being forced to find an alternative solution, adults may have shown the same behavioural flexibility as the juveniles in this study.

It is unlikely that the individual differences in problem-solving performance in our study were mainly caused by motivational or competitive differences as has been found previously (Birch 1945; Morand-Ferron et al. 2011; Cole and Quinn 2012; Sol et al. 2012). Supplementary food is freely available to kaka at the wildlife sanctuary throughout the day. It is therefore unlikely that juveniles were under increased competitive stress as a consequence of their not yet fully developed foraging skills, thus the 'necessity drives

innovation' hypothesis (Laland and Reader 1999b; Morand-Ferron et al. 2011) may not apply here. It is also likely that all individuals landing on the platform and trying to access the feeders were indeed motivated for food. However, juveniles may have been more reliant on the feeders as a food source, whereas the adults, who are more experienced foragers, may have been more likely to abandon the task in favour of foraging for alternative food resources, which could have resulted in their high failure rates in the feeder experiments. Indeed, our analysis showed that adults were less persistent in all tasks than juveniles. However, the adults' increased success rate in the string-pulling task suggests that they were in fact motivated to work for the high value food reward in the context of a novel feeding situation.

It is unlikely that neophobia greatly inhibited the adult's problem-solving success (Greenberg 2003; Overington et al. 2011). Although it is conceivable that neophobia caused the adults to avoid touching or moving the novel block in experiment 1, adults also failed the lid-opening task where no novel object was present. However, the adults had the greatest success in the string-pulling task, where the entire apparatus was novel. Furthermore, with the exception of one bird, all adults attempted to use their beak to prise open the front of the feeder in the block-removal task and 18 out of 22 adults did so in the lid-opening. Thus adults interacted with feeders and tried to open them, which would have been unlikely to occur if neophobia prevented them from engaging with the problem (for additional analyses of the latency to approach the problem, which supports this hypothesis, see Appendices A.1).

Similarly to other problem-solving studies on wild, social living animal populations (Gajdon et al. 2004; Morand-Ferron et al. 2011; Benson-Amram and Holekamp 2012) but in contrast to findings in captivity (Huber et al. 2001; Huber and Gajdon 2006; Federspiel 2010), we found little evidence that social learning contributed to immediate or eventual success in a task. Several individuals directly observed a conspecific pull out the block in experiment 1, yet none of them subsequently tried to move the block themselves. A similar pattern was found in experiment 2. It was only in the string-pulling task that observing a conspecific solve the problem increased the likelihood of an individual succeeding. Social learning may have been facilitated in this experiment because of the novelty of the task, or the visibility of the food reward. Thus social learning may have contributed to the adults' elevated success rate in experiment 3. Indeed, three of the four adult solvers had observed another kaka solve the problem at least once before their own success in the string-pulling.

2.5 CONCLUSION

Our results suggest that, in kaka, juveniles have the highest potential for foraging innovations and display greater exploratory diversity and persistence. Furthermore, the adults' innovative problem-solving success appears to be context-dependent and limited to those situations that are entirely novel and for which no pre-learned behavioural response pattern is available. This suggests that adults are able to use newly available food sources, but might fail to adapt to changes in the environment that require the use of a familiar resource in a different way. The juveniles' greater behavioural flexibility and explorative nature might help them to learn about their environment and to shape their foraging skills. In this way juveniles might find the most efficient behavioural response to common foraging situations, which is then maintained throughout adulthood.

3 IT'S IN THE GENES! HERITABILITY OF PROBLEM-SOLVING ABILITY IN A WILD FOREST PARROT

Although the heritability of cognition has been extensively studied in humans, similar effects have rarely been investigated in non-human animals and never been shown in the wild. Yet studying heritability of cognitive traits in the wild is essential for furthering our understanding of their adaptive value and the ecological and evolutionary mechanisms that may act on cognitive variation. Here we investigate inter-individual variation in performance in three different problem-solving tasks in relation to the subjects' relatedness in a wild forest parrot, the New Zealand kaka (*Nestor meridionalis*). We found that solving ability was associated with clutch: successful individuals were more likely to originate from the same clutch than expected at random. Furthermore, overall solving performance was predicted by clutch ID and significantly correlated between clutch-mates with upper-limit heritability estimated at 0.69. Analysis of 11 months of RFID readers data on visitation rates to feeding stations suggests that kaka were more likely to forage on their own or with other conspecifics than together with their siblings from the same clutch. Thus our results are unlikely to be solely due to subjects' social environment and instead indicate that problem-solving ability in this parrot species may have a heritable component. This provides the first potential evidence for heritability of cognitive abilities in a wild non-human animal species. However, our heritability estimate only provides an upper boundary as it likely includes non-cognitive and non-genetic components such as nutritional differences during the nesting period, which could not be separated from the heritable cognitive differences in the current study.

3.1 INTRODUCTION

Several authors have recently highlighted the importance of investigating the heritability of cognitive abilities for furthering our understanding of the ecological and evolutionary mechanisms that may underpin individual cognitive variation (Thornton and Lukas 2012; Quinn et al. 2014; Thornton et al. 2014; Croston et al. 2015). In order for natural selection to act on cognitive traits and generate adaptive cognitive phenotypes, these traits need to be variable, heritable and confer fitness benefits (Darwin 1871; Croston et al. 2015). While

many studies have shown that individuals do vary consistently in their cognitive abilities and have tried to determine factors influencing this variation (Liker and Bókonyi 2009; Morand-Ferron et al. 2011; Cole et al. 2011; Thornton and Lukas 2012; Benson-Amram and Holekamp 2012; Aplin et al. 2013; Rowe and Healy 2014), evidence for heritability (reviewed in Croston et al. 2015) and fitness consequences (Keagy et al. 2011; Boogert et al. 2011; Cole and Quinn 2012; Cole et al. 2012; Cauchard et al. 2013; Hollis and Kawecki 2014; Morand-Ferron and Quinn 2015) in non-human animals remains rare.

In humans, where heritability of cognition has been extensively studied, 32 - 86 % of cognitive variation has been attributed to genetic effects (Thornton and Lukas 2012; Croston et al. 2015). Mostly, these studies use general cognitive ability (g) as trait for determining heritability estimates. g represents a single factor that is positively correlated with diverse cognitive processes and is usually assessed through test batteries (Plomin 2001; Croston et al. 2015; Shaw et al. 2015). Heritability of g in humans has been shown to increase with age (Deary et al. 2009), suggesting decreasing environmental influence on g (or in other words decreasing plasticity of g) with developmental time (Croston et al. 2015). g has also been demonstrated in several non-human species in the laboratory (e.g. Galsworthy et al. 2005; Herrmann et al. 2007; Banerjee et al. 2009; Amici et al. 2012; Schmitt et al. 2012) and field (Isden et al. 2013; Shaw et al. 2015). Yet, so far the heritability of g has been examined only in rodent and primate species (Galsworthy et al. 2005; Hopkins et al. 2014). Additionally, there is evidence for the heritability of specific cognitive traits such as learning ability in fruit flies (*Drosophila melanogaster*), honey bees (*Apis mellifera capensis*), three species of fish (*Girardinus falcatus*, *Poecilia reticulata* and *Rhodeus ocellatus*), zebra finches (*Taeniopygia guttata*) and pigs (*Sus domesticus*; Willham et al. 1964; Brandes 1988; Brandes 1991; Lofdahl et al. 1992; Bisazza et al. 2000; Karino et al. 2005; Forstmeier et al. 2009; Woodgate et al. 2014; Smith et al. 2015). However, all of these studies have been conducted in the laboratory, mostly through artificial selection experiments (Wahlsten 1972; Lofdahl et al. 1992; Galsworthy et al. 2005), in-vitro fertilisations (Smith et al. 2015) or breeding and cross-fostering in individual cages (Forstmeier et al. 2009; Woodgate et al. 2014).

However, investigating the heritability of cognitive traits in the wild is essential for understanding their adaptive value and unravelling the relative contributions of environmental and genetic effects on cognitive variation (Thornton et al. 2014; Croston et al. 2015). A better understanding of the range of plasticity in relation to heritable

components of cognitive abilities will in turn help us to better estimate how animals may respond to rapid environmental changes (Croston et al. 2015).

Here we investigated whether individual variation in problem-solving ability in a wild population of large forest parrots may have a heritable basis using full sibling comparison (e.g. Brandes 1988; Galsworthy et al. 2005; Woodgate et al. 2014, also see Falconer and Mackay 1996). Parrots are known for their remarkable physical cognitive and language skills (Pepperberg 2006; Auersperg et al. 2009; Auersperg et al. 2010; Miyata et al. 2011; Schloegl et al. 2012) and their large relative brain size (Iwaniuk et al. 2005; Emery 2006). The kaka (*Nestor meridionalis*) investigated in our study inhabit temperate lowland forests and are generalist, extractive foragers (Moorhouse 1997) with neophobic tendencies (Wilson et al. 1991; Diamond and Bond 2004; Gsell 2012). Kaka are endemic to New Zealand and one of two species in the tribe Nestorini. Their closest relative is the mountain-dwelling, neophilic kea (*Nestor notabilis*; (Diamond and Bond 1999)), whose cognition has been studied across a variety of physical and social cognitive tasks both in the field and in captivity (Huber and Gajdon 2006; Werdenich and Huber 2006; Huber et al. 2008; Schloegl et al. 2009; Auersperg et al. 2011b). The kaka's cognitive abilities have recently been assessed for the first time in a series of problem-solving tasks in which juvenile kaka outperformed adult kaka, especially when modification of a pre-learned behavioural response was required (Loepelt et al. 2016).

Here we reanalyse this dataset using a subset of individuals for which information on parentage was available. Additionally, we analyse 11 months of microchip reader data to elucidate the individuals' typical social environment. More specifically, we examined (1) the effects of relatedness on problem-solving performance, (2) the heritability of overall problem-solving performance and (3) the degree to which the individuals' social environment is likely to explain the observed effects.

3.2 METHODS

3.2.1 Subjects and study site

Subjects were free-ranging kaka tested at Zealandia, a 225 hectare large wildlife sanctuary surrounded by a pest-exclusion fence, in Wellington, New Zealand. The kaka population at Zealandia has been monitored for 14 years by banding nestlings with a unique colour combination of two narrow aluminium bands on one leg and one wider cohort steel band

on the other (with the exception of one breeding season when kaka were banded with a cohort band only – see Appendix A.1 for more information). From 2008 to 2013 nestlings also received a radio frequency identification (RFID) tag. As a result, individual identification of kaka was possible and records on the subjects' age and family histories available.

Originally, 104 kaka were tested of whom 24 participated in all three of our tasks (see Loepelt et al. (2016) for more information on all original subjects). In order to analyse sibling effects on problem-solving ability we include only those 51 individuals for whom we tested at least one sibling from the same clutch (Table 3.1; see Table A.2.1 for individual data; please note, clutch-mates were not necessarily tested in the same experiments, see section 3.2.4 for more details). We base our analysis on clutches as this enabled us to include individuals of unknown parentage (because kaka are banded as nestlings, all banded individuals can be unambiguously assigned to a clutch). Additionally, because we previously found that juvenile kaka outperformed adult kaka in our problem-solving tasks (Loepelt et al. 2016), analysing clutches enabled us to explore potential genetic effects without the confounding effect of age (For an additional analysis of siblings from different clutches in the third task see Appendix A.2). Kaka ranged in age from four months to 12 years and were classified as juveniles when less than one year old ($N = 14$), as subadults when between one and four years old ($N = 21$), and adults when older than four years ($N = 16$; age classification according to Moorhouse and Greene (Moorhouse and Greene 1995)).

In the sanctuary, kaka are offered supplementary food (parrot pellets) at two feeding stations, which are regularly visited by a large number of kaka. This is where we conducted our experiments (described below). None of the kaka in this study had previously participated in any cognitive tests.

3.2.2 *Experiments*

We conducted three problem-solving experiments from 30.01.2014 to 31.10.2014, which differed in context and/or the action required to solve them. For experiments 1 and 2 we manipulated the kaka's regular feeding boxes (Figure 2.1a), which are continuously available on approximately 1.70 m high wooden platforms. All kaka had previously learned to open these boxes by stepping onto a tread plate that functions as a push-down lever. In experiment 1 (block-removal; 47 sessions; Figure 2.1b and c) we blocked this tread plate by placing a wooden block underneath, which had to be pushed or pulled out to re-establish

the functionality of the feeder. This task potentially tested for the kaka's understanding of cause and effect as looking for the blockage of the tread plate instead of manipulating the lid likely required comprehending that stepping on the tread plate causes the lid to open. For experiment 2 (lid-opening; 40 sessions; Figure 2.1 *d*) we removed the tread plate so that kaka had to flip over the lid to access the food. Due to the length of the lid (21.5 cm), kaka were not able to lift the lid far enough from the front of the box (which they would normally approach to open the feeder and retrieve the food) to push it over the pivot point. However, this could be achieved in one swift movement if the subject moved to the side of the box and flip it over from there. Thus, solving this task likely required an understanding of the spatial relationship between lid and box (Huber and Gajdon 2006). In experiment 3 (18 sessions; Figure 2.1 *e*) we used the string-pulling paradigm to test for the kaka's means-end-understanding (Heinrich and Bugnyar 2005; Werdenich and Huber 2006). Here we hung a 50 cm long piece of string from a branch near a feeder platform and tied a food reward to the end of it. As it was too far from the ground to reach from below, kaka had to use the string as a means for pulling up the reward.

In all experiments, we used cashew nuts as reward to increase the kaka's motivation to solve the problem as this is a favoured food which is not usually available to the kaka in the sanctuary. For more details on procedure, measurements and trial numbers see Loepelt et al.(2016).

3.2.3 *RFID readers and data*

There was a total of four RFID tag readers installed in the sanctuary during our testing period, two at each feeding station. As these readers recorded the kaka's RFID tag numbers whenever a tagged bird used the feeding station, we used these data to estimate how often kaka foraged together with their clutch-mates compared to on their own (or together with other conspecifics). This enabled us to evaluate possible effects of social environment against potential heritable genetic effects.

We included data from all except one reader (which proved unreliable) in our analysis. From the two readers on our testing platforms, we used all readings from installation of the readers until the end of the testing period (Station 1: 21.05.2014 - 31.10.2014; Station 2: 27.05.2014 - 31.10.2014). The second reader at station 2 had been installed prior to our testing period at a nectar feeder reader (drink bottles with a nozzle filled with sugar water) approximately 3 m away from the testing platform. Here we included the two months

preceding our testing phase to cover the fledging period of the juvenile subjects (29.11.2013 – 23.10.2014).

We quantified foraging events based on ten minute intervals as kaka typically stayed around eight minutes at a feeding station during our observations (mean $\pm$ SE: 7 min 58 s $\pm$ 15 s; $N=1234$ events). Thus, if an individual's tag was logged more than ten minutes apart, it is likely that the individual had left the station in between the two logging events. If the same individual was logged multiple times, each time within ten minutes of the next, we considered this one event. Similarly, if siblings from the same clutch were logged within ten minutes from each other, it is likely that they were at the station at the same time and this was considered one foraging event with those birds together, which continued until at least one of them left the station.

In addition to this, we analysed observations made during our test sessions, when an assistant recorded all kaka arriving and leaving the station irrespective of whether they participated in the task. Here we analysed both whether clutch-mates arrived and/or left within ten minutes of each other and whether juveniles arrived and/or left within ten minutes of a parent. The latter analysis could not be done with the logged data as no kaka older than five years was microchipped, which included the majority of parents. Although every attempt was made, it was not always possible to record exact arrival and leaving times. Cases where only one of the two times was available were included in our analyses.

3.2.4 *Statistical Analysis*

For each experiment we recorded the number of successful trials (i.e. trials where the reward was obtained) and the total number of trials a subject participated in (Table A.2.1) and classified birds as either solvers (obtained the reward in at least one trial) or nonsolvers (never obtained the reward in the respective task).

We used Fisher's exact tests to investigate whether the distribution of successfully and unsuccessfully completed tasks across clutches (pooled for individuals) differed from random. To examine this effect independently of any possible influence of the subjects' age (Loepelt et al. 2016), we additionally ran the analysis on juvenile clutches only. We used a generalized linear mixed model (GLMM) with a binomial distribution and logit link and repeated measures design to investigate the effect of clutch on the number of successful trials out of the total number of trials. In this analysis, we only included individuals of whom we tested at least one sibling from the same clutch in the same experiment (Table

A.2.2). We could not include age as a factor in the analysis (either fixed or random) as due to the structure of the data (many different clutches, few individuals per clutch) this did not leave enough degrees of freedom.

Another way to balance the experimental design and investigate clutch effects in the absence of varying task participation as potentially confounding variable is to analyse one task only which we do on the block-removal task for reasons of sample size and because it was the first experiment, thus the level of testing experience was the same for all subjects (none of them had previously participated in any cognitive studies). We used Fisher's exact test to investigate whether the distribution of solvers in the block-removal task was different from random. We used a generalized linear model (GLM) with robust estimation to assess whether the proportion of successful trials in block-removal was predicted by clutch and weight the model for the total number of trials a subject participated in ($N = 36$). We estimated heritability of performance in the block-removal task as twice the intra-class correlation coefficient between siblings from the same clutch using a one-way random effects model.

As the string-pulling task was the only task with a number of adult solvers, we additionally analysed the distribution of solvers across sibling groups (full siblings from different clutches and therefore of different age but same parentage) for this task only using Fisher's exact test. For this analysis, we excluded all subjects for whom one or more parents were unknown. We included subjects for whom there was a concrete indication to who the parents are (see Table A.2.1). Additionally, we used a GLM with robust estimation to investigate whether the proportion of successful trials in the string-pulling task was predicted by sibling groups from different clutches.

To further analyse the effect of clutch on the kaka's overall problem-solving performance, we averaged the proportion of successful trials across experiments for each of the subjects. This enabled us to include all 51 subjects in our generalized linear model (GLM) and to explore whether clutch predicted overall solving performance. It should be noted, however, that not all of the kaka participated in all experiments (c.f. Table 3.1 and Table A.2.1 for individual data). For this reason the analyses were weighted for the number of experiments and trials within an experiment each subject has participated in. Additionally, we ran the same analysis on juvenile birds only to exclude the potentially confounding effect of age. For an alternative method of combining problem-solving performance into a single variable using a principal components analysis, please see Appendix A.2.

Heritability is defined as the ratio of additive genetic variance to phenotypic variance and can be estimated from the degree of resemblance between relatives (Falconer and Mackay 1996). For our full sibling analysis heritability was estimated as twice the intra-class correlation coefficient of the average proportion of successful trials using a one-way random effects model (Bisazza et al. 2000; van Oers et al. 2004; Galsworthy et al. 2005). This method provides an upper-limit heritability estimate as it is likely inflated by effects of common environment and genetic dominance (but see (Dohm 2002)). In cases where we tested more than two kaka per clutch, we used those two individuals that participated in the higher number of experiments and trials per experiment for the correlation.

We examined the subjects' social foraging environment using R software (version 3.1.2) to quantify how many visits to the feeding station a kaka (or juvenile) undertook together with one or more siblings from the same clutch (or parent). We then used Wilcoxon signed-ranks test to determine whether for individual kaka (or juveniles) the number of visits made with a sibling from the same clutch (or parent) differed from the number of visits made without a sibling present. Additionally, we used Fisher's exact test to investigate whether the distribution of individuals who foraged together at least occasionally across successful and unsuccessful clutches differed from random.

Table 3.1: Number and percentage of individuals that were successful out of the total number of individuals tested in each of the three experiments and the number of clutches they originate from.

Age group	Block-Removal				Lid-Opening				String-Pulling				Total	
	S	T	%	Cl	S	T	%	Cl	S	T	%	Cl	Ind	Cl
Juveniles	6	13	46.2	5	2	5	40	4	3	3	100	2	14	5
Subadults	2	18	11.1	10	4	16	25	9	4	11	36.4	8	21	10
Adults	0	15	0	8	1	10	10	8	2	3	67.7	3	16	8
Total	8	46	17.4	23	7	31	22.6	21	9	17	52.9	13	51	23

J = juveniles, S = subadults, A = adults, S = solvers, T = total, Cl = clutches, Ind = individuals. This table contains all 51 individuals for whom we tested at least one sibling from the same clutch (not necessarily in the same experiment). Numbers in bold indicate the totals for each age group as well as each experiment.

3.3 RESULTS

3.3.1 *Effects of relatedness*

Of the 51 individuals for whom we tested at least one sibling from the same clutch (23 clutches; Table 3.1; see Table A.2.1 for individual data), 15 participated in two of our tasks

and 14 participated in all three. Siblings that participated in one task only, did not necessarily participate in the same tasks (However, see below for a GLMM analysis that includes only those clutch-mates tested in the same experiment). Overall, two clutches always solved any task they participated in and 12 clutches never solved any task. The total number of successfully and unsuccessfully completed tasks per clutch (pooled for individuals) differed significantly from random (Table A.2.3; Fisher's exact test: $p < 0.001$). This effect remained when we removed age as possible confound and investigated juvenile clutches only (Table 3.2; Fisher's exact test: $p = 0.001$). For the juveniles, two clutches were always successful, two clutches were always unsuccessful and one clutch was a mix of successful and unsuccessful individuals as well as one individual that was successful in one task and unsuccessful in another. Furthermore, clutch significantly predicted the proportion of successful trials in all three tasks (binomial GLMM: $F_{17,50} = 2.370$, $p = 0.009$; $N_{BR} = 41$, $N_{LO} = 19$, $N_{SP} = 8$) when only including individuals with at least one sibling from the same clutch tested in the same experiment (Table A.2.2).

Table 3.2: Solving events across juveniles clutches. Data of individual kaka is pooled to show the total number of successfully and unsuccessfully completed tasks each clutch participated in.

Clutch ID	Solved	Unsolved	# of individuals
6	7	0	3
20	2	0	2
41	2	4	4
59	0	2	2
4	0	4	3

Fisher's exact test: $p = 0.001$

When restricting our analyses to the first task only (block-removal) to investigate clutch effects in the absence of varying task participation and testing experience, the distribution of solvers and nonsolvers across clutches was significantly different from random (Table A.2.4, Fisher's exact test: $p = 0.003$, $N = 36$) and the proportion of successful trials was predicted by clutch (GLM: $\chi^2_4 = 235.583$, $p < 0.001$, $N = 36$).

The problem-solving performance of groups of full siblings from different clutches (therefore of different age but same parentage) was only assessed on the string-pulling task as this was the only task with a number of adult solvers. Consistent with the preceding analyses, the distribution of solvers and nonsolvers across groups of siblings of various age

differed from random (Table A.2.5; Fisher's exact test: $p = 0.049$, $N = 16$) and performance in the task (proportion of successful trials) was also predicted by full sibling groups (GLM: $\chi^2_{55} = 5058.144$, $p < 0.001$, $N = 16$).

3.3.2 Heritability estimate for overall problem-solving performance

Average problem-solving performance (proportion of successful trials) was significantly predicted by clutch when all 51 subjects from 23 clutches were included (GLM: $\chi^2_{11} = 409.693$, $p < 0.001$, $N = 51$) as well as for juveniles only (GLM: $\chi^2_3 = 367.672$, $p < 0.001$, $N = 14$). Intra-class correlation of the average proportion of successful trials of siblings from the same clutch was significant ($t = 0.345$, $p = 0.047$, $N = 23$ pairs) and yielded a heritability estimate of $h^2 \leq 0.69$.

3.3.3 Social environment

As no kaka older than five years was microchipped and the tag of one kaka (GL-O) was undetectable, our analysis of the subjects' visit to the feeding stations as recorded by RFID readers are based on 37 subjects from 16 clutches (Table A.2.6).

All individuals used the feeders more often without their clutch-mates than together with one or more of their siblings from the same clutch (Figure 3.1; Wilcoxon signed-ranks test: $T = 0$, $p < 0.001$, $N = 37$). Nine individuals were never detected foraging with one of their siblings and a further ten did so on less than 10 occasions over the 11 month period. However, there was no association between siblings that were recorded together at the feeders at least once and their ability to solve our tasks (Table A.2.7; Fisher's exact test: $p = 0.558$), neither was there one for those that were recorded together more than 10 times (Table A.2.8; Fisher's exact test: $p = 0.586$) or more than 30 times (Table A.2.9; Fisher's exact test: $p = 1$).

Similarly, kaka were recorded more often to arrive and leave the feeding stations without any clutch-mates during our test sessions (Figure A.2.1; Wilcoxon signed-ranks test: $T = 0$, $p < 0.001$, $N = 44$). Furthermore, apart from 4 instances, juveniles arrived and left independently of their parents (Figure A.2.2; Wilcoxon signed-ranks test: $T = 3.5$, $p < 0.001$, $N = 21$).

Figure 3.1: Number of events ($\pm$ SE) kaka were recorded foraging without and with siblings from the same clutch by the RFID readers at the two feeding stations ($N=37$).

3.4 DISCUSSION

Our results show an association of the kaka's overall problem-solving ability as assessed in three different tasks and the clutch they originate from. Successful kaka were more likely to originate from the same clutch than would be expected by chance and average solving performance was also predicted by clutch. This indicates that problem-solving ability is potentially influenced by genetic factors in this wild parrot species, which is further supported by the significant correlation between siblings from the same clutch. Doubling the ICC coefficient provides a rough estimate for heritability (Falconer and Mackay 1996; Bisazza et al. 2000; Galsworthy et al. 2005) and yields 0.69 in our study. Although this is typically seen as an upper boundary heritability estimate (Falconer and Mackay 1996; Bisazza et al. 2000; Galsworthy et al. 2005 but see Dohm 2002) and in our study possibly inflated by the high number of nonsolvers, it is also higher than most heritability estimates of single cognitive traits or general cognitive ability in non-human animals (cf. Croston et al. 2015) and thus still suggests considerable genetic contribution to the kaka's general problem-solving ability. Additional analyses show that the clutch effect remained when removing potentially confounding variables such as age (by including only juvenile clutches) or varying task participation and previous testing experience (by investigating the first experiment only). Interestingly, there were not only those clutches that excelled at every task they participated in and those that failed every task they participated in, but also clutches sitting in the middle, made up of solvers and non-solvers, task-dependent solvers

(individuals that solved one task but failed in another) and/or individuals with a lower proportion of successful trials.

As indicated by RFID readings at feeding stations and our test observations, kaka in our study more often foraged without their clutch-mates than they did with siblings from the same clutch. It is therefore unlikely that siblings showed similar problem-solving skills because they were exposed to similar environment and experience with the chance to learn from one another. In fact, half of the individuals were detected together with a sibling on less than ten occasions over an 11 month period. It is thus questionable whether these siblings were indeed foraging together on those occasions or whether they met at the feeders by chance. Furthermore, there was no association between those birds who did visit the feeders together with a sibling at least once and their solving ability. Our test observations additionally suggest that juveniles hardly ever visited the feeding stations together with their parents. As our testing period started late January, only two and a half months after the first kaka of that season were due to fledge, this potentially indicates that even at this early stage juveniles spent relatively little time together with their parents. However, as test observations typically covered only two hours of the day and no more than five days a week, they represent only part of the kaka's daily activity.

Previous analyses of the kaka's problem-solving ability in these tasks revealed no effect of individual persistence or neophobia on overall performance (Loepelt et al. 2016). It is therefore also unlikely that these traits greatly contributed to the observed sibling resemblance in our study. Taken together our results thus suggest that the cognitive mechanisms underlying problem-solving ability in kaka are heritable and provide the first potential evidence that cognitive variation has a genetic component in a wild population of non-human animals. However, the current study is limited in that we were not able to measure early live environmental effects such as nutritional differences, which have been shown to affect cognitive and personality development (Brust et al. 2014; Noguera et al. 2015). It is thus possible that some of the variance we observed in our dataset is due to differences in parental care and foraging ability, which is difficult to assess in the wild and furthermore difficult to disentangle from genetic effects. For example, parents that are less skilled foragers may feed their offspring lower quality food, which may negatively affect their cognitive development. At the same time, these parents may be less skilled foragers because of their lower cognitive ability, which they may pass on to their offspring genetically. Lower cognitive ability in the offspring may thus be caused both by nutritional

differences and inheritance. More field research is needed to further our understanding of how cognitive abilities are passed on to offspring in the wild. Additionally, it would be extremely valuable to test wild kea in a similar set of tasks to further investigate environmental effects on the evolution of cognition as this species is the kaka's closest relative but lives in a different habitat.

4 FLEXIBILITY IN PROBLEM-SOLVING: FINDING AN ALTERNATIVE SOLUTION

Behavioural flexibility is an important trait for an animal to adapt to changing environments and thought to be high for generalist species living in complex habitats with dispersed resources. In humans, behavioural flexibility has been shown to decrease with age. However, empirical studies on behavioural flexibility in non-human animals have so far rarely considered age effects. Here we investigate age-related differences in the flexibility in problem-solving of a wild omnivorous parrot species. We tested 20 free-ranging kaka (*Nestor meridionalis*) on a Multi-Access-Box, which featured four different options for retrieving a food reward. Once an individual became proficient in using one of those options, the respective option was blocked, forcing the animal to look for an alternative solution. Of the 15 individuals that participated in more than 10 trials, six were younger than three years and nine were older. We found that the younger birds were significantly faster in discovering a first solution as well as alternative solutions once their previously used option was blocked. Additionally, younger kaka showed a wider range of exploratory behaviours and tended to be more persistent. To our knowledge, this study thus represents the first empirical evidence for an age-related decline in behavioural flexibility in non-human animals.

4.1 INTRODUCTION

Behavioural flexibility, the ability to modify ones behaviour with changing conditions (Easton 2005; Logan 2016), is thought to be a key component for a species' ability to adapt to changing environments. In line with that, behavioural flexibility has been shown to increase a species' invasion success (Sol and Lefebvre 2000; Sol et al. 2002; Sol et al. 2013), feeding innovation rate (Lefebvre et al. 1997; Lefebvre and Bolhuis 2003) and innovative problem-solving ability (Lefebvre and Bolhuis 2003; Auersperg et al. 2011; Manrique et al. 2013; but see Griffin et al. 2013; Logan 2016). However, the study of behavioural flexibility is made difficult by inconsistent nomenclature (Bond et al. 2007; Stamps 2015) and measurement with regards to this trait (cf. Sol et al. 2002; Bolhuis et al. 2004; Auersperg et al. 2011; Chow et al. 2016; Logan 2016; see also Griffin and Guez

2014). As a consequence, we still know little about the mechanisms and correlates of behavioural flexibility (Griffin and Guez 2014; O'Hara et al. 2015; Logan 2016).

A Multi-Access-Box approach has been proposed for revealing species-specific differences in innovative problem-solving abilities alongside psychological profiles as this addresses a number of issues encountered with testing flexibility or problem-solving ability on a single task or with measuring these two factors in different contexts (O'Hara et al. 2011; Auersperg et al. 2012a; Logan 2016). A Multi-Access-Box offers up to four different options for accessing a food reward in the middle of the clear Perspex apparatus (Auersperg et al. 2011b; Manrique et al. 2013). Each option can be blocked once an individual becomes proficient in using it. Thus flexibility in switching between different solving strategies can be measured while the location of the reward and the apparatus stay the same. In this way, using a Multi-Access-Box allows to assess cognitive performance on multiple tasks while simultaneously taking into account differences in behavioural, anatomical and perceptual features between the species (Auersperg et al. 2011b; Auersperg et al. 2012a). As similar behavioural and physiological differences may also be present between juvenile and adult individuals of the same species, we apply this approach to test for age-related differences in the behavioural flexibility of wild kaka in problem-solving.

In humans, behavioural flexibility has been found to decline with age (Wecker et al. 2005; Deary et al. 2009; Haworth et al. 2010; Croston et al. 2015), which is further supported by Bayesian models investigating developmental plasticity (Stamps and Frankenhuis 2016). However, empirical studies on behavioural flexibility in non-human animals have rarely considered age effects. Although two studies of wild parrots indicate that juvenile birds may also be more flexible than adults, this relationship was not directly tested. The first study was conducted on wild yellow-naped amazons (*Amazona auropalliata*) and investigated the behavioural flexibility of these parrots when translocated to a novel environment (Salinas-Melgoza et al. 2013). Here the individual that stayed longest in the new area was a juvenile, which led the authors to suggest that the parrots' response to a novel environment may be associated with age classes. The second study investigated age-related differences in the innovative problem-solving abilities of wild kaka across multiple tasks (Loepelt et al. 2016). From the context-dependent success of the adults it was concluded that juvenile kaka may be more flexible in their behaviour and were thus more efficient at modifying a pre-learned behavioural response than older individuals. Juveniles were also more diverse in their exploratory strategies and showed greater persistence than

adults. Additionally, when first faced with the problem that the mechanism to open known feeders was no longer functional, juvenile kaka found a solution faster than subadult kaka (Loepelt et al. 2016). However, neither study described above directly tested for the effect of age on behavioural flexibility.

Based on our previous research (Loepelt et al. 2016), our predictions for the kaka's performance and behavioural flexibility on a Multi-Access-Box are as follows: (1) we expect general problem-solving performance to be higher in younger kaka than in older ones, (2) we expect younger kaka to discover an initial solution to the problem quicker than adult kaka, (3) we expect adult kaka to struggle discovering an alternative solution once their initial solution is blocked and (4) we expect juveniles to show greater exploratory diversity and persistence.

4.2 METHODS

4.2.1 *Subjects and study site*

We tested 20 free-ranging kaka in total, of whom 15 participated in at least 10 trials (Table 4.1). These kaka live in and around a 225 hectare large wildlife sanctuary (Zealandia) in Wellington, New Zealand. For monitoring purposes kaka nestlings at Zealandia are banded with a unique coloured band combination which enabled us to individually identify subjects of known age. The kaka in this study ranged in age from one to 14 years. We were unable to test any juvenile birds (less than one year of age; age classification according to Moorhouse and Greene (1995)) as the older individuals tended to dominate the apparatus. We therefore compare performance and behaviour for kaka less than three years old ($N=7$) with those three years and older ($N=9$; for additional analyses comparing subadults and adults see Appendices A.3.1 and A.3.2). All subjects had previously participated in non-invasive cognitive studies (Loepelt et al. 2016) and were thus familiar with the experimenter and general procedure. We conducted our study adjacent to an established feeding station where kaka receive supplementary food (parrot pellets). A separate wooden platform (42×71 cm) was tied to a tree in close proximity to but visually shielded from the feeding station five months prior to testing. The platform was installed at a height of approximately 140 cm and featured a perch on each of the long sides (Figure 4.1).

Table 4.1: Subjects that participated in the study with information about age (in years), sex, parents, prior testing experience (in number of tasks the subject had participated in), whether the individual participated in the habituation phase and the total number of trials in each of the test phases with no option blocked (Phase 1), one option blocked (Phase 2), two options blocked (Phase 3) and all but the Stick option blocked (Phase 4).

Subject	Age [y]	Sex	Female Parent	Male Parent	# of prior tasks	Habitua- tion	# of trials in phase			
							1	2	3	4
B-Unb_40472	1	?	BY-W	LB-R?	4	Y	20	11	17	17
B-Unb_40489	1	F	P-WO	BP-P	4	Y	14	19	15	7
B-Unb_40538	1	?	?	?	2	N	1	-	-	-
G-GR	2	?	RR-P	Y-GL	4	Y	16	17	15	4
G-MB	2	?	PW-L	P-WB	3	Y	3	-	-	-
G-OR	2	F	KR-W	?	4	Y	36	-	15	7
KR-G	2	M	PW-L	P-WB	2	N	20	18	15	25
LM-G	2	?	KR-W	?	3	Y	15	14	17	1
Unb-Y	3	F	?	?	4	Y	11	21	18	36
MW-O	4	?	R-GR	OB-P	4	Y	18	27	22	-
O-GW	4	?	BY-W	LB-R	3	Y	24	13	-	-
O-KL	4	?	PW-L	G-GK	1	N	18	14	-	-
LK-Y	5	?	?	?	1	Y	17	1	-	-
Y-GL	5	M	?	?	4	Y	17	15	17	42
B-YP	6	M	?YL-L	?OO-G	1	N	1	-	-	-
LL-B	6	?	R-GR	?OB-P	3	Y	13	-	-	-
W-BB	7	M	UNB/ L-KM	OY-G	2	Y	1	-	-	-
W-Unb	7	M	?	?	3	N	1	-	-	-
RM-S	8	M	20053	B640	3	N	16	5	-	-
RR-P	14	F	?	?	1	N	19	18	11	-

F, female; M, male; UNB, unbanded; Y, yes; N, no. The dotted line separates the two age groups.

4.2.2 Apparatus

The apparatus was adapted from Auersperg's et al. (2011) Multi-Access-Box (MAB) and consisted of an 20×20 cm Perspex cube with interchangeable panels (Figure 4.1 and Figure 4.2a). The food reward (pieces of cashew nut) was placed on a wooden board (7×7 cm) in the middle of the MAB and could be accessed by four different options. These options could be blocked individually to elicit the discovery of another option.

The four available options for accessing the food were (i) Board, (ii) Sliding Door, (iii) Door and (iv) Stick. (i) The Board panel featured a 2 cm wide opening at the bottom through which the handle of the food board protruded. Kaka could retrieve the food by pulling the food board out through the opening (Figure 4.2b). (ii) The Sliding Door panel featured two

rails along which the sliding door could be moved in either direction. Kaka could grab the sliding door by a rectangular handle and push or pull it to uncover the opening in the panel through which the food could be retrieved (Figure 4.2*c*). (iii) The Door panel featured a round opening, 2.5 cm in diameter, by which the kaka could grab the door and pull it open (Figure 4.2*d*). They could then reach into the box to retrieve the food. (iv) A 22 cm long stick (12 mm diameter) was placed along the back panel (Figure 4.2*a* and *e*) and could be inserted through the opening in the Board panel to fish for the food board or the food itself. In the blocked versions, the Board did not feature a handle, the Sliding Door was wedged into the rails and did not feature a handle and the Door was glued shut and did not feature a hole. The fourth panel was a plain ‘back panel’, which we aligned with one edge of the platform to give the kaka more space to move around the other three sides (the platforms dimensions were limited by the size of the tree trunk to which it was attached).

Figure 4.1: The MAB on the testing platform, which is tied to the tree in the background.

All subjects encountered the MAB in the same position (Board panel facing the tree, Sliding Door panel facing away from the tree; Figure 4.1) and the MAB was never rotated between trials. All target parts (the functional elements of the opening) were located in the middle

of the lower part of the panels. Each of the target parts had a different shape to ensure kaka had to actively seek an alternative strategy rather than merely targeting the same shape that had been rewarded before.

Figure 4.2: (a) The MAB, looking through the back panel, with the stick in the front, the opening for pulling the food board on the left, the door on the far side and the sliding door on the right. (b) A kaka pulling out the food board. (c) A kaka opening the sliding door. (d) A kaka opening the door. (e) A kaka breaking pieces off the stick while holding it in one foot.

4.2.3 Procedure

We conducted one session per day on up to five days per week from 14.10.15 to 23.12.15. All sessions were filmed for subsequent behaviour coding.

Habituation

During a habituation phase the kaka were given opportunity to get accustomed to the new box and materials. For this purpose, all panels that feature possible solutions (i.e. the Board, Door and Sliding Door panels) were removed, so that only the back panel, top panel and aluminium bars remained. Cashew nut pieces were placed in the middle of the MAB on the food board. As the kaka had never encountered Perspex before, the MAB was rotated during habituation so that the back panel was in different locations. This ensured that the subjects would come into contact with the Perspex panel and had to manoeuvre around it.

Although every effort was made to give all subjects a habituation phase, this was not always possible as it was increasingly difficult to habituate new individuals to the box after testing had commenced for most of the subjects (see Table 4.1 for the individuals who participated in the habituation phase). However, all individuals that were not habituated had seen conspecifics interact with the MAB before being tested themselves. Thirteen of the 20

subjects had taken food out from under the top panel and 12 of those 13 had come into contact with the Perspex back panel before they were tested. There was no difference in the latency from landing on the platform to contacting the MAB in the first test trial between those individuals who had participated in the habituation phase and those who did not (Mann-Whitney U test: $U = 39$, $N_{NH} = 7$, $N_H = 13$, $p = 0.643$).

Test

Initially, all four options (Board, Door, Sliding Door and Stick) were available to the subject (Phase 1). Once the subject had discovered one of the solutions and was consistently using the same option to retrieve the reward (on at least two consecutive sessions (i.e. days) for at least 11 consecutive trials or a minimum of 14 trials in total; see section 4.2.4 for the definition of a trial), this option was blocked (Phase 2). This process was repeated until only one option remained or the subject failed to find an alternative solution (Phases 3 and 4). The stick was replaced when it fell to the ground or was thrown off the platform by the subject in all trials where Stick was the only option left. When kaka failed to discover the Stick option after all other options were blocked, we inserted the stick halfway into the opening to test whether this would facilitate the stick tool use in kaka (We only did so after a minimum of 10 trials with the stick lying next to the MAB. However, 2 individuals encountered the stick inside the opening after 7 and 2 trials, respectively, when they were participating in other subjects' trials (see section 4.2.4 for more information on these 'group trials')).

One kaka, G-OR, had discovered the Board and Sliding Door options early on and kept switching between these two options. Here, both these options were blocked at the same time once G-OR had used each of them at least 15 times in total.

In an effort to keep the time between the last use of an option and the blocking of that option as similar as possible between individuals, we tried to introduce all subjects to the blocked option the same session they reached criterion in the respective option. This was achieved for nine out of 13 individuals in Phase 2, six out of 10 in Phase 3 and six out of 8 in Phase 4. Kaka received a maximum of 15 trials per session.

4.2.4 Data scoring

All trials were recorded and the videos subsequently analysed to score trial durations and various behaviours of the kaka. A trial started the moment a kaka landed on the test platform and ended with successful reward retrieval, with the subject leaving the testing area (a

radius of approximately 3 m around testing platform) or starting to forage, preen or sleep, or with the interference of another subject. During a trial, if a subject was displaced or left the platform upon the arrival of a conspecific but was able to return to the platform and continue the trial within 5 min, the duration spent away from the platform was deducted from the trial duration. We excluded all trials that were interrupted by a conspecific less than 30 sec after trial start.

We considered an option as successfully used, if the subject retrieved at least some of the reward through this option (or, in the rare case where this happened, if the subject attempted to retrieve the reward but was prevented from doing so by a conspecific). We recorded the number of trials required until an option was discovered (used successfully for the first time) and measured the latency to success in each of the phases in total amount of trial time.

We also recorded the range of exploratory behaviours the kaka exhibited in each trial in their efforts to access the food, as well as the parts of the apparatus an individual explored by nibbling or using force. We additionally recorded whether and when an individual made contact with each of the panels of the MAB. Please see supplementary Table A.3.1 for more details on the coding of the behaviours. The kaka's individual persistence was measured as the mean duration of trials that were unsuccessful and ended with the subject leaving the testing area (or starting to forage, preen or sleep), which was considered 'giving up'.

We made every effort to test kaka individually, in the absence of conspecifics and whilst still naïve to the possible solutions of the MAB. When there were multiple subjects present at the test location we either waited until some of them left, or aimed to test the individual with the least options discovered and distracted other kaka by offering them little pieces of food in a nearby tree. Where this was not possible or successful, we recorded whether the conspecifics were present in the area or on the test platform during the trial and made a note of all instances in which subjects observed another kaka use an option they hadn't discovered themselves at that point. All trials in which more than one kaka was working on the MAB at the same time were classified as 'group trials' (less than 15 % of all trials; the majority of group trials (65 %) happened in Phase 4 when kaka were struggling to discover the stick option and we allowed them to work simultaneously).

4.2.5 *Statistical Analysis*

We include all 20 subjects in all analyses relating to the first trial and in the analysis of individual persistence. In all other analyses, those four individuals that participated in no

more than one trial and the one individual that participated in no more than four trials (G-MB) were excluded. The reason for excluding G-MB from the analysis relating to the latency to discover an option lies in her first trial. In this trial the sliding door was blocked as the MAB was set up for another subject, whom G-MB joined on the platform. As the sliding door was also the first option G-MB discovered (in her second trial, the first one with all options available), her latency to find a solution is not comparable to the other subjects.

To investigate whether age group predicted overall problem-solving success (number of successful trials out of the total number of trials), we use a generalized linear mixed model (GLMM) with a binomial distribution and logit link. We specified age group, the number of blocked options (none blocked, 1 option blocked (Board or Sliding Door), and 2 options blocked (Board and Sliding Door); generally correspondent to Phases 1, 2 and 3, however, we include trials that occurred at later phases, cf. section 4.3.2: Switching back to previous options) and the interaction between the two as fixed factors. We excluded all trials that ended because of the interference of a conspecific. We dropped those terms with the least explanatory power from the final model to receive Wald statistics and p -values for the significant terms.

We also use a GLMM (normal distribution with identity link) to investigate whether age groups differ in the absolute amount of time needed to discover a first and alternative solutions. We additionally included phase and the interaction of phase and age group as fixed factors in the model to analyse whether it is more difficult for older individuals to find an alternative solution compared to finding a first solution.

We use Mann-Whitney U tests to investigate whether kaka one to two years of age differ from kaka older than two years in terms of their exploration, persistence and latency to contact the MAB.

Finally, we use a GLMM with a normal distribution and identity link to test whether the latency to discover an option in each of the phases was affected by prior observation of a conspecific's success in the respective option. For this analysis we excluded individuals who had discovered a second and third option themselves before entering the second and third phase, respectively.

4.3 RESULTS

4.3.1 General problem-solving success

Of the 16 kaka who discovered at least one solution to the MAB, half discovered the Board option first, the other half the Sliding Door option (Figure 4.3; Table 4.3). However, five of the eight kaka that discovered the Sliding Door first, switched to preferring the Board option after two to five trials. The Door option was always the third option the kaka successfully used (9 out of 10 kaka did so; Table 4.3). No kaka in this study learned to purposefully use the stick to retrieve the reward, although most of the eight kaka that advanced to Phase 4 (when all other options were blocked) were very persistent and participated in up to 42 trials and spent 0:06:55 to 2:29:45 h in total trying to find another solution. However, one individual who kept pulling the stick out of the opening to throw it off the platform (in those trials where we had inserted it halfway into the MAB) incidentally moved part of the reward or the food board within reach on a total of four occasions while doing so. Yet, even after this ‘accidental’ use of the stick, she never attempted to purposefully use the stick for reward retrieval (she had 36 trials in Phase 4 in total). And another subject, who observed Unb-Y moving and retrieving at least part of the reward with the stick, also never tried to replicate this action (see also section 4.3.4).

Table 4.2: The number of successful out of the total number of subjects that participated in each of the test phases.

	Overall				> 1 trial per phase			
	Phase 1	Phase 2	Phase 3	Phase 4	Phase 1	Phase 2	Phase 3	Phase 4
1 – 2 years	7/8	5/5	6/6	0/6	7/7	5/5	6/6	0/5
> 3 years	9/12	6/8	3/4	0/2	9/9	6/7	3/4	0/2

Kaka also found two additional solutions, however with limited success. A number of kaka started rocking and tilting the MAB when they were struggling to find another option to access the food. This led to pieces of the reward falling within reach of the opening in the Board panel in two instances. Also, one kaka (Unb-Y) managed to squeeze her head through the opening in the Board panel and thus reached one piece of the reward at a time on three occasions at the beginning of Phase 2 (Thereupon, we decreased the width of the opening from four to two cm). Furthermore, kaka deployed nine different techniques when

opening the sliding door (different combinations of direction, grip and action) and nine different techniques when opening the door (see supplementary Table A.3.2 for descriptions).

Figure 4.3: Mean number of trials $\pm$ SE until the first successful use of the Board, Sliding Door and Door option for the two age groups. All subjects discovered the Board and Sliding Door options first and the Door option third. No kaka learned to use the stick. The number of subjects is given at the base of the bars.

On average, the proportion of successful trials tended to be lower for kaka above three years of age when one or two options of the MAB were blocked (Figure 4.4; see also Table 4.2 for the number of successful individuals in each of the phases and age groups). However, because of the generally high success rates and the greater variance among the older birds, this difference only approaches significance (GLMM: Age group: $F_{1,33} = 3.932$, $p = 0.056$) when the number of blocked options was also included in the model ($F_{2,33} = 3.512$, $p = 0.041$; $N_{\text{Unblocked}} = 15$, $N_{\text{Blocked}} = 12$, $N_{2\text{Blocked}} = 10$; see supplementary Table A.3.3 for coefficient estimates). There was no significant interaction between the two terms ($F_{2,31} = 0.043$, $p = 0.958$). It should be noted, however, that each term on its own was also non-significant (GLMM: Age group: $F_{1,35} = 1.496$, $p = 0.230$; GLMM: Blocked options: $F_{2,34} = 1.617$, $p = 0.213$).

Table 4.3: The trial number in which each of the options was first discovered as well as the latency to success in trials and absolute amount of time in each of the test phases.

Subject	Age [y]	Options used successfully						# of options used in P1	Latency to success (# of trials and total time in mm:ss.ms)					
		1 st	Trial	2 nd	Trial	3 rd	Trial		Phase 1		Phase 2		Phase 3	
B-Unb_40472	1	SD	1	B	2	D	4	3	1	00:26.3	1	00:21.1	1	00:15.7
B-Unb_40489	1	B	1	SD	15	D	34	1	1	00:10.6	1	01:58.0	1	02:15.7
G-GR	2	B	1	SD	17	D	22	1	1	03:00.2	1	02:51.6	1	00:40.1
G-MB ¹	2	SD	-	-	-	-	-	1	-	-	-	-	-	-
G-OR ²	2	B	1	SD	2	D	37	2	1	00:41.2	-	-	1	08:46.2
KR-G	2	SD	1	B	2	D	40	2	1	02:25.4	1	03:17.3	1	01:44.8
LM-G	2	SD	1	B	16	D	33	1	1	01:44.2	1	00:43.1	3	02:23.6
Unb-Y	3	B	1	SD	14	D	39	1	1	07:26.0	2	03:20.4	2	10:40.3
MW-O	4	B	3	SD	28	-	-	1	3	15:40.5	10	31:19.9	-	-
O-GW	4	SD	2	B	5	-	-	2	2	04:23.8	1	00:10.8	-	-
O-KL	4	B	1	SD	19	-	-	1	1	00:55.1	1	01:35.6	-	-
LK-Y	5	SD	1	B	3	-	-	2	1	02:34.1	-	-	-	-
Y-GL	5	SD	1	B	20	D	36	1	1	02:24.4	1	07:47.8	2	08:20.2
LL-B	6	SD	1	B	2	-	-	2	1	00:42.3	-	-	-	-
RM-S	8	B	1	-	-	-	-	1	1	00:28.6	-	-	-	-
RR-P	14	B	5	SD	25	D	38	1	5	09:41.6	6	08:27.2	1	02:26.7

B, Board; SD, Sliding Door; D, Door; P1, Phase 1. ¹G-MB's latency to discover a first option is not used because the sliding door was blocked in her first trial (see section 4.2.5 in the Methods for more information). ²G-OR skipped phase 2 (see 'Test' in section 4.2.3 for more information)

Figure 4.4: Mean proportion of successful trials $\pm$ SE for the two age groups depending on the number of blocked options (generally correspondent to Phases 1, 2 and 3, however this includes trials mentioned in section 4.3.2: Switching back to previous options). The number of subjects is given at the base of the bars. B, Board; SD, Sliding Door.

4.3.2 Speed in discovering different solutions

Younger kaka were significantly faster in discovering a first as well as alternative solutions once their initial option was blocked (Figure 4.5; GLMM: $F_{1, 33} = 6.909$, $p = 0.013$; $N_{\text{Phase1}} = 15$, $N_{\text{Phase2}} = 11$, $N_{\text{Phase3}} = 9$; Coefficient estimate $\pm$ SE: -229.34 ± 87.25). There was no difference between the phases ($F_{2, 31} = 0.810$, $p = 0.454$) or in interaction with age group ($F_{2, 29} = 0.195$, $p = 0.824$), indicating that neither younger nor older kaka needed significantly more time to discover an alternative solution in Phases 2 and 3 than they did to discover an initial solution in Phase 1.

Phase 1

All but one kaka less than three years old discovered a first solution to the MAB in their first trial, whereas it took older individuals up to five trials (1.8 trials on average). None of the four kaka that participated in one trial only were successful (a 1-, a 6- and two 7-year-olds). This difference in trial number until their first success also translated to the total amount of time the kaka spent in those trials. Older kaka needed on average more time to discover a first option than younger kaka (Figure 4.5: Phase 1). The fastest bird, a 1-year-old, successfully retrieved the reward after 11 sec and none of the young birds needed more than 3 min. By contrast, four of the nine older birds took between 4:24 min and 15:41 min to find an initial solution.

Six kaka discovered and used more than one option before any option was blocked (Table 4.3; 3 younger and 3 older kaka). Of those only one kaka, a 1-year-old, discovered and used three options (Sliding Door, Board and Door) and did so within the first four trials.

Figure 4.5: Mean latency $\pm$ SE to successfully use a first option in Phase 1 and an alternative version after blocking of the previous one in Phases 2 and 3 for the two age groups. The number of subjects is given at the base of the bars.

Phase 2

All of the five young kaka, who advanced to the second phase, successfully used an alternative solution within their first trial after their previous option was blocked. Of the eight kaka older than three years that advanced to the second phase, one eight-year old (RM-S) never found a second option to the MAB and stopped appearing at the test location after five unsuccessful trials (8:04 min total trial time). A five-year old kaka that had found an alternative solution during the first phase when no option was blocked, failed to use this option when her preferred option was blocked. However, she only received one trial in the second phase before the end of testing and this trial had to be terminated after 1:27 min due to the interference of a conspecific. The remaining six kaka over the age of three needed between one and 10 trials to successfully use an alternative solution (3.5 trials on average $\pm$ 1.5 SE) in the second phase. Half of the older kaka (4 out of 8 subjects) also needed more time in total to discover a second option after their first one was blocked (7:48 – 31:20 min) than any of the young subadults (overall range of the 1- to 2-year-olds: 00:21 – 3:17 min; Figure 4.5: Phase 2).

Phase 3

A similar pattern to Phase 2 was evident in Phase 3 when both the Board and Sliding Door options were blocked. All six young kaka (this includes G-OR who skipped Phase 2, see below or ‘Test’ section under 4.2.3 for details) discovered the Door option and five of them did so in their first trial. Of the four older kaka, one 4-year-old (MW-O) never discovered the Door option even though she spent 22 trials and 33:22 min in total trying to find an alternative solution and observed another subject successfully opening the door. Similar to RM-S in Phase 2, MW-O eventually stopped participating in the task. She did continue to show up at the test location occasionally, but could not be motivated to come onto the platform. The remaining three older kaka discovered the Door option in 1 to 2 trials and needed 2:27 to 10:40 min (Figure 4.5: Phase 3). By comparison, five of the six younger birds successfully used the Door in 00:16 to 2:24 min. Interestingly, the 2-year-old that took longest (8:46 min, 1 trial) was G-OR who had frequently switched between the Board and Sliding Door in Phase 1 and had consequently both options blocked at the same time. Those two individuals (1 and 2 years old) who were fastest in using the Door option in Phase 3 (16 and 40 sec, respectively) had both discovered this option prior to blocking of their second option.

Switching back to previous options

Eight kaka that had already advanced to a phase where one or more of their options were blocked, encountered the MAB with these options unblocked at least once when they were interfering other subjects’ trials. Of those individuals that encountered a version of the box that allowed reusing previous options, the only one that wasn’t successful was MW-O, a 4-year old (who was also slowest to discover a first and second solution to the MAB in Phases 1 and 2, see Table 4.3). All other individuals readily and quickly took the chance to switch to a previous option and retrieved the reward in 7.5 sec on average ± 18 SE ($N = 18$ trials).

4.3.3 Individual variation in behavioural measures

All kaka touched the MAB with the beak within their first trial and 19 of the 20 subjects did so within five sec of landing on the platform. There was no difference in the latency from landing on the platform to contacting the MAB between the younger and the older birds (Mann-Whitney U test: $U = 52$, $N_{1-2y} = 8$, $N_{>2y} = 12$, $p = 0.792$).

However, overall, younger kaka exhibited more exploratory strategies on more structures of the apparatus than did older kaka (Figure 4.6a; Mann-Whitney U test: $U = 10$, $N_{1-2y} = 6$,

$N_{>2y} = 9$, $p = 0.050$). Younger kaka also tended to contact all three target panels faster than did older kaka, however not significantly so (Figure 4.6*b*; Mann-Whitney U test: $U = 33$, $N_{1-2y} = 6$, $N_{>2y} = 9$, $p = 0.529$).

All but one kaka (14 out of 15) at least touched and moved the stick and 10 kaka investigated it by nibbling. Seven kaka also picked the stick up and held it in one foot. However, no kaka ever tried to combine the stick with the MAB and insert it in one of the openings. Among the strategies the kaka deployed when they were struggling to solve the problem was also ‘Pushing the MAB off the platform’ and ‘Looking at the experimenter’ (the latter was not included as an ‘exploratory’ strategy). Those three kaka who tried to achieve a solution by means of the experimenter most often (in 21 to 35 trials), also occasionally used vocalisation with it, presumably to attract the experimenter’s attention.

Although younger kaka tended to be more persistent and spend on average more time trying to find a solution to the problem before ‘giving up’ than older kaka did, this difference was overall non-significant (Figure 4.6*c*; Mann-Whitney U test: $U = 15$, $N_{1-2y} = 7$, $N_{>2y} = 8$, $p = 0.152$).

Figure 4.6: Mean $\pm$ SE of (a) the number of exploratory actions at different parts of the MAB, (b) the latency to touch all three target panels with the beak and (c) the time a kaka spent trying to find a solution to the problem before ‘giving up’ for the two age groups. The number of subjects is given at the base of the bars.

4.3.4 Social effects

Observing another kaka successfully using one of the available options did not appear to affect performance. Kaka who had directly observed a conspecific's success prior to each of the phases (success in any option prior to Phase 1, success in the respective second and third option prior to Phases 2 and 3) were not faster in discovering an option than those who had not (GLMM: $F_{1,28} = 0.685$, $p = 0.415$; $N_{\text{Phase1}} = 14$, $N_{\text{Phase2}} = 8$, $N_{\text{Phase3}} = 8$). Three individuals (all above 3 years old) that observed the successful reward retrieval of other subjects up to twice before being tested themselves, were not successful in their first trial. And another two individuals (both younger than 3 years) that had watched successful reward retrieval only through the Board option, instead discovered and used the Sliding Door option first. For discovering a second and third option there was an average delay of 8.5 trials between watching an option and using it for the first time (Range = 2 – 22; $N = 12$). Furthermore, MW-O observed another subject solve the Door option but never used it herself in the six trials afterwards with Board and Sliding Door blocked before she stopped participating in the task. However, KR-G learned the Board option when he interfered and actively displaced another subject who was in the process of pulling the board. He then immediately pulled the board the rest of the way himself. Thus it is possible that direct competition plays a role for social learning in this species.

4.4 DISCUSSION

Similar to the closely related kea (*Nestor notabilis*; Auersperg et al. 2011b), kaka show significant flexibility in their problem-solving and are able to adjust their behaviour to a new situation. Consistent with our expectations, kaka younger than three years were faster to discover a first solution to the problem than older kaka. However, kaka were overall so successful in using the different options of the MAB that the difference in general problem-solving performance (proportion of successful trials) between the age groups only approached significance, although younger kaka tended to be more successful when the discovery of an alternative solution was required than older kaka. Two out of eight older kaka failed to discover an alternative solution when the previously used option was blocked (one in Phase 2, the other in Phase 3) and those who did discover an alternative solution again needed more time to do so than the younger birds. Partially contrary to our third

prediction, successful older kaka did not generally need more time to discover an alternative solution than they did for discovering a first solution.

Younger kaka also showed a greater diversity in exploratory actions and tended to be more persistent. This is in line with previous research on wild kaka (Loepelt et al. 2016) and potentially aids their behavioural flexibility. Adults, once they found a possible solution, were more likely to continue to use this solution and abandon further investigation of the problem, whereas the 1- to 2- year-olds were more likely to continue to explore alternative strategies, thus discovering up to three options during the first phase. Adults additionally tended to spend less time per trial trying to find a solution to the problem before ‘giving up’ and two individuals stopped participating in the task after five and 22 trials, respectively, when their previously used options were blocked. The latency to contact the apparatus did not differ between younger and older birds, thus it is unlikely that neophobia greatly influenced our results. Likewise, prior experience of failure does not appear to be the primary source for the lower persistence of the older kaka. For example, the two individuals who stopped participating in the task when they were unable to find an alternative solution (RM-S and MW-O), had both been successful in previous experiments (Loepelt et al. 2016). RM-S was the only adult to solve the lid-opening task and was also successful in the sting-pulling task. The subadult MW-O had even been a solver in all three tasks conducted prior to the present study. It thus appears unlikely that they were less motivated to keep participating in the task due to negative testing experience.

Similar to previous studies in the wild (Gajdon et al. 2004; Morand-Ferron et al. 2011; Benson-Amram and Holekamp 2012; Loepelt et al. 2016), social learning did not appear to increase problem-solving success. Kaka who had observed another kaka successfully using one of the available options were not faster discovering an option than those who had not and did not necessarily use the same option first. However, KR-G learned the Board option when he interfered and actively displaced another subject who was in the process of pulling the board. He then immediately pulled the board the rest of the way himself. Thus it is possible that social learning in this species is driven by direct competition.

That all kaka discovered the board and sliding door option before they discovered the door option indicates that the door option was harder to use or discover, possibly due to the kaka needing to change their position as they opened the door. Another possibility is the location of this option on the MAB. However, kaka often landed on the platform facing the door option and indeed 13 out of 16 kaka made contact with the door panel within four trials and

six kaka either nibbled the door hole or even moved the door (or both) in the first phase. Subjects even investigated the ‘back panel’ even though there was hardly any space for them on that side of the platform. In fact, kaka made contact with the ‘back panel’ more often than with the Door panel. It is therefore unlikely that the location of the Door panel or lack of space were the main reason for using the Board and Sliding Door options first. It rather suggests that those panels that were plainer and allowed unobstructed view inside the box may have been investigated in favour of the Door panel.

No kaka in this study discovered the stick option. Even in cases where the subject accidentally moved the reward within reach when pulling the stick out of the way, kaka did not appear to learn from this experience. Although 14 out of 15 kaka manipulated the stick in some way and seven even picked it up and held it one foot, no kaka attempted to insert the stick into the opening of the MAB. Instead, most often kaka were throwing the stick off the platform. Contrary to this finding, one of six kea discovered the stick tool when being tested on a MAB in the lab (Auersperg et al. 2011b). It is possible, that stick tool use by kaka in the present study was inhibited by the fact that the opening through which the tool was to be inserted was the same opening the kaka had previously used to retrieve the board. This potentially created a mental blockage in form of functional fixedness as has been found in other studies (Duncker and Lees 1945; Adamson 1952; Hanus et al. 2011). Kaka may have associated the opening in the Board panel with the fixed function to grab and pull out the food board, thus failing to use it for insertion of the stick tool. Indeed, five kaka kept trying to reach the board with the beak through the slot when the handle bar was removed from the board.

One limitation of the present study is that we were not able to test juvenile kaka (less than one year old) with the MAB. Findings from Loepelt et al. (2016) suggest that the differences in problem-solving performance and behaviour are greatest between juvenile and adult kaka, whereas subadults and adults are less divergent from each other. Although subadults were slightly more successful than adults when a familiar problem had to be solved in a different way, both solved a novel problem (string-pulling) with a similar success rate (cf. Figure 2.2). Consistently, subadults and adults found a first solution to the as yet novel MAB with similar speed (see supplementary analysis in Appendix A.3 and Figure A.3.1). In Phases 2 and 3, subadults tended to find an alternative solution to the MAB slightly faster than the adults (Figure A.3.1). This is also consistent with the slightly higher success rates of subadults found by Loepelt et al. (2016) in the two feeder

experiments which required modification of a pre-learned behaviour. However, in the present study only two adults completed Phases 2 and 3 (two adults never found an alternative solution in Phase 2, one of which received only one trial, and another adult could only be tested in Phase 1). Based on the results of Loepelt et al. (2016) it is thus likely, that the differences in problem-solving flexibility between younger and older kaka found in the present study would have been more pronounced, had we been able to include juvenile birds in our dataset. For future research it would be especially interesting to test juvenile kaka in stick tool use as they were the most creative innovators in the previous study (Loepelt et al. 2016), thus being the likeliest candidates for the invention of using sticks to retrieve food.

Nevertheless, our data shows that younger kaka are more flexible in their behaviour than older individuals, adapting to a change in the foraging situation more quickly. This study thus refutes a competing hypothesis raised by Loepelt et al. (2016) which suggested that the younger birds' seemingly more flexible behaviour may have been due to the a shorter reinforcement period with the apparatus. In the present study, all subjects had been using the apparatus for approximately the same amount of time when the first option was blocked and they were required to change their behaviour in order to find an alternative solution. It thus appears that adult kaka are less flexible in their behaviour independent of the reinforcement period they experienced. Furthermore, younger kaka are more likely to persist and be successful at finding alternative solutions when previously used strategies fail. Their more creative and thorough exploration of the problem additionally increases their chances to discover new foraging strategies. Overall, younger kaka thus have the highest potential to survive in dramatically changing environments as they might be brought about by climate change. However, more research is needed to determine whether these results can be generalised to all parrots or birds, or are unique to certain species.

5 GENERAL DISCUSSION

The overall aim of this thesis was to investigate developmental changes in innovative problem-solving abilities and behavioural plasticity in the wild to further our understanding of the relative contributions of environmental and genetic effects on cognitive variation. Innovation ability – operationally defined as the ability to solve a novel problem or find an alternative solution to an old one (Kummer and Goodall 1985) – is frequently associated with large relative brain size (Lefebvre et al. 1997; Reader and Laland 2002; Lefebvre et al. 2004; Sol et al. 2005a; Benson-Amram et al. 2015), behavioural flexibility (Auersperg et al. 2011b; Leal and Powell 2012; Manrique et al. 2013; Lefebvre et al. 2013; Reader et al. 2016) and a number of fitness benefits (Sol et al. 2002; Sol et al. 2005b; Keagy et al. 2009; Boogert et al. 2011; Cole et al. 2012; Cauchard et al. 2013), and therefor thought to reflect domain-general cognitive abilities (Chiappe and MacDonald 2005; Sol 2009; Bird and Emery 2009; Lefebvre 2010; Reader et al. 2011; Muthukrishna and Henrich 2016; but see Rowe and Healy 2014; Griffin and Guez 2016; van Horik and Madden 2016).

A number of studies have found innovative problem-solving ability to be correlated with personality traits such as high exploration rates and low levels of neophobia (Webster and Lefebvre 2001; Greenberg 2003; Overington et al. 2011). Juvenile birds have often been shown to be more explorative and less neophobic (Reader and Laland 2003; Biondi et al. 2010a; Benson-Amram and Holekamp 2012), yet few studies have found evidence of age-related differences in innovative problem-solving success in non-human animals. To further our understanding of how behavioural and cognitive traits change during development, Chapter 2 assessed the innovation ability of 104 wild kaka (*Nestor meridionalis*), ranging in age from four months to 13 years on a series of three problem-solving tasks. Twenty four individuals participated in all tasks, two of which involved a familiar feeder and one an entirely novel apparatus. Juvenile kaka less than one year of age showed consistently higher problem-solving efficiency than adults (> 4 years) across all tasks and contexts with the performance of subadult individuals falling in the middle. Moreover, the adults' success was context-dependent and limited to the novel apparatus, which did not require modification of a pre-learned behavioural response. These results suggest that juvenile kaka may be more behaviourally flexible than adults, which is supported by their higher persistence and exploratory diversity. These traits may enable

young kaka to discover efficient foraging techniques, which are then maintained throughout adulthood.

Studying the heritability of cognitive traits in the wild is essential for furthering our understanding of their adaptive value and the ecological and evolutionary mechanisms that may act on cognitive variation (Thornton et al. 2014; Croston et al. 2015), yet effects of relatedness have rarely been investigated in non-human animals and never been shown in the wild. Chapter 3 therefor reanalyses the dataset presented in Chapter 2 using a subset of individuals for which information on parentage was available to investigate the inter-individual variation in innovative problem-solving performance in relation to the subjects' relatedness. It was found that kaka who were successful at retrieving the reward from the different apparatuses were more likely to originate from the same clutch than expected at random. Furthermore, overall solving performance was predicted by clutch ID and significantly correlated between clutch-mates with upper-limit heritability estimated at 0.69. Analysis of 11 months of RFID readers data on visitation rates to feeding stations further suggested that kaka were more likely to forage on their own or with other conspecifics than together with their clutch-mates. Thus the subjects' social environment and shared experience appear not to be the sole source of similarity in problem-solving performance between siblings. Instead, these results indicate that innovative problem-solving ability in this parrot species has a heritable component. The study is limited in that it was not possible to separate the heritable cognitive differences from potential non-cognitive and non-genetic components such as nutritional differences during the nesting period. Hence, the heritability estimate only provides an upper boundary in the current study. Nevertheless, this provides the first potential evidence for heritability of cognitive abilities in a wild non-human animal species.

In adaptation to the environment, behavioural flexibility is thought to play a central role (Dill 1983; Sol et al. 2002; Tebbich et al. 2010; Snell-Rood 2013). The context-dependent success of the adults found in Chapter 2 raised the hypothesis that juvenile kaka may be more flexible in their behaviour and were thus more efficient at modifying a pre-learned behavioural response than older individuals. Chapter 4 tested for this hypothesis using a Multi-Access-Box paradigm (Auersperg et al. 2012a). This consisted of a Perspex puzzle box featuring four different options for retrieving a food reward, all of which were initially available. Once an individual became proficient in using one of those options, the respective option was blocked, forcing the animal to look for an alternative solution. 20

free-ranging kaka were tested ranging in age from one to 14 years. All of these individuals had previously participated in the study described in Chapter 2 and were thus familiar with the experimenter and general testing procedure. Analysis of the 15 kaka that participated in more than 10 trials, revealed that subjects younger than three were significantly faster in discovering a first solution to the problem as well as alternative solutions once their previously used option was blocked than older subjects. Additionally, consistent with the finding in Chapter 2, younger kaka showed a wider range of exploratory behaviours and tended to be more persistent. This study thus suggests that, similar to findings in humans (Wecker et al. 2005; Deary et al. 2009; Haworth et al. 2010; Croston et al. 2015), behavioural flexibility decreases with age in this omnivorous wild parrot species, potentially indicating that this trait is most important for young kaka when adapting to their environment and in shaping their technical foraging skills. The generally high flexibility that the majority of subjects showed in solving this novel foraging task may further support the assumption that behavioural flexibility is essential for generalist species living in complex habitats with dispersed resources.

5.1 DEVELOPMENTAL CHANGES

The present studies are among the first to show that juvenile birds may be more efficient innovators across a variety of tasks. This is consistent with findings in passerines on single tasks (Vince 1958; Morand-Ferron et al. 2011; Aplin et al. 2013) but contrary to evidence in meerkats (Thornton and Samson 2012) and primates (Reader and Laland 2001; Kendal et al. 2005), where it has been suggested that prior knowledge and experience may play an important role for generating innovations (Koehler 1925; Epstein et al. 1984; Reader and Laland 2003). For example, chimpanzees that were allowed to explore an object prior to a task that required manipulating it, were shown to outperform conspecifics that had no such prior experience with the object (Birch 1945). Based on this premise, adult kaka would have been expected to outperform juveniles in the feeder tasks presented in Chapter 1 as they had been using them many years longer. Especially in the block-removal task, where the normal functionality of the feeder was to be re-established, a better understanding of the feeder's mechanism may have been expected to facilitate finding a solution to the problem. However, adult success was lowest in those feeder tasks, rather suggesting that adults had difficulty modifying their previously learned behavioural response to the feeders. This in turn pointed towards greater behavioural flexibility in juveniles, however,

with the data in Chapter 2, it was impossible to discern whether this difference was general or mainly caused by the adults' greater reinforcement history for the normally functioning feeders. In Chapter 4, however, all subjects were introduced to the Multi-Access-Box at the same time and received a similar number of trials before one of the possible options was blocked. Yet, younger kaka were significantly faster to discover an alternative solution than the older kaka, some of whom abandoned the task altogether. Taken together, the results presented here therefor suggest that juvenile kaka are indeed more flexible in their behaviour, which may favour innovations. This association between greater flexibility and innovation efficiency in juveniles is, however, contrary to two studies which did not find a correlation between flexibility and innovative problem-solving performance in passerines (Griffin et al. 2013; Logan 2016). However, both these studies assessed behavioural flexibility using a reversal learning task, which may indicate that different methodologies capture different aspects of behavioural flexibility.

Additionally, younger kaka showed greater behavioural diversity when exploring the problems presented here. This supports the growing evidence indicating a positive correlation between exploration diversity and innovation success (Benson-Amram and Holekamp 2012; Benson-Amram et al. 2013; Griffin et al. 2014; Diquelou et al. 2015). Their more creative and thorough exploration of the problem may thus additionally increase young kaka's chances to discover new foraging strategies. Furthermore, kaka deployed a range of different solving techniques with some individuals frequently switching between them, which further confirms their flexible and creative approach to problem-solving.

Although sample size may appear small for some analyses, the number of subjects tested in the studies presented here is comparable to similar studies on innovation ability conducted in the wild and larger than in the majority of studies conducted in captivity. For example, Benson-Amram and Holekamp (2012) tested 62 wild hyenas (*Crocuta crocuta*), Cauchard et al. (2013) 45 wild great tits (*Parus major*), and Morand-Ferron et al. (2011) 173 wild great tits and 63 wild blue tits (*Cyanistes caeruleus*). All of these studies assessed the subjects' problem-solving abilities on a single task, whereas the kaka's problem-solving abilities were assessed on three different tasks for Chapter 2 of this thesis. Looking at the tasks separately, 87 individuals participated in the block-removal task, 61 in the lid-opening task and 30 in the string-pulling task. Furthermore, overall solving ability was analysed on the full dataset of 104 individuals as well as the restricted dataset of 24 birds who participated in all experiments. Data acquisition for Chapter 4 was additionally complicated

by the complex nature of the Multi-Access-Box task, which required testing subjects individually and throughout several phases, something that, to my knowledge, has never been attempted with a social animal in the wild before. Yet, 16 individuals (7 kaka less than 3 years old and 9 kaka older than 3) could be included in the main analyses. By comparison, the original study by Auersperg et al. (2011b) included six captive kea (*Nestor notabilis*) and four captive New Caledonian crows (*Corvus moneduloides*) and Shaw et al. (2015) tested 20 territorial New Zealand robins (*Petroica longipes*) in a test battery consisting of six tasks in the wild.

Taken together, the findings presented in this thesis suggest that behavioural flexibility and diversity are important traits for juvenile birds in exploring and adapting to their environment, testing a range of different foraging techniques to discover efficient strategies. This is supported by findings showing, for example, that a juvenile yellow-naped amazon (*Amazona auropalliata*) translocated across dialect boundaries stayed in the new environment and imitated the local contact call, whereas adult individuals either returned to their capture site or remained at the new site but did not alter their contact calls to match the local dialect (Salinas-Melgoza and Wright 2012).

A higher innovation rate in juveniles appears to support the hypothesis that innovations occur when individuals have a reduced cognitive load as may be the case in juveniles that are still cared for by their parents, which additionally allows them time for play and exploration (Kummer and Goodall 1985; Diamond and Bond 1999; van Schaik et al. 2016). However, kaka become independent of their parents about five to six months after fledging (Moorhouse and Greene 1995). Both the lid-opening and the string-pulling task were conducted after this time period, yet juveniles showed significantly higher exploration diversity and innovation efficiency in both these tasks. Another possibility might be that juveniles instead have increased necessity to innovate as they have not yet fully developed their foraging skills (Laland and Reader 1999b; Morand-Ferron et al. 2011). However, during the block-removal task, juveniles were presumably still cared for by their parents to some part and supplementary feeding is available to the kaka at the wildlife sanctuary throughout the day. Even during the 2-hour test sessions, there was always a second set of feeders approximately 220 m away, which kaka could have flown to and likely some of the birds did. The RFID reader data furthermore shows that juvenile individuals were frequenting both feeding stations, so they knew about their location. It seems therefore unlikely that juvenile were under any immediate stress for discovering new food sources.

More research is needed to determine the cognitive mechanisms underlying developmental changes in behavioural flexibility, exploration diversity and innovation efficiency.

5.2 SOCIAL EFFECTS

It has also been suggested that high innovation frequencies may be associated with species with a large relative brain size because these species may be more prone to using social information and thus innovations spread rapidly through social learning making them more likely to be detected by ornithologists (Griffin and Guez 2016). However, a number of studies experimentally investigating innovative problem-solving in the wild found no indication that the subjects used social information when trying to solve the problem (hyenas: Benson-Amram and Holekamp 2012; kea: Gajdon et al. 2004; Gajdon et al. 2006; passerines: Tebbich et al. 2001; Morand-Ferron et al. 2011); a pattern which appears to be confirmed by the studies in this thesis. Neither in the first set of three problem-solving tasks presented in Chapters 2 and 3, nor during the four tasks available through the Multi-Access-Box used in Chapter 4, did I find any indication that observing a conspecific solve the problem generally increased the subjects' likelihood to be successful themselves.

However, there is also research suggesting that juveniles are more likely to learn socially than adults (Biondi et al. 2010b; Aplin et al. 2013). Additionally, Range et al. (2009) found that adult kea were only attentive towards a conspecific demonstrating food-related behaviour if the model was also an adult. Hence, it is possible that I wasn't able to detect many instances of social learning in the innovation context because the youngest kaka were the most efficient problem-solvers in all experiments, so that adults would have had to learn from juveniles. Indeed, in those handful of instances that strongly suggested social learning had taken place, younger birds (up to two years of age) had observed slightly older birds. However, these were also individuals who had successfully solved previous experiments themselves, hence it is similarly possible that this previous individual experience is important for establishing social learning. Indeed, there is growing evidence suggesting that individual (asocial) learning plays a central role for generating innovations (Gajdon et al. 2006; Boogert et al. 2008; Flynn et al. 2016).

5.3 EVOLUTIONARY IMPLICATIONS

Chapter 3 in this thesis suggests that innovative problem-solving ability in this wild parrot species may be underpinned by a heritable component, which provides the first potential evidence for heritability of cognitive abilities in a wild non-human animal and thus contributes to our interpretation of how natural selection may act on innovation ability. This study thus complements previous research showing consistent individual variation (Morand-Ferron et al. 2011; Cole et al. 2011) and fitness benefits of innovativeness (Sol et al. 2002; Keagy et al. 2011; Cauchard et al. 2013).

Additionally, several of the experiments in this thesis are comparable to studies conducted on wild kea and may thus give us valuable insight into the evolutionary mechanisms acting on the cognitive abilities of these two closely related parrot species, both assayed in their natural environment. For example, Gajdon et al. (2006) investigated a natural population of kea that had learned to open the lids of rubbish bins on a hotel ground to obtain food scrapes. The study found that only five kea of 36 banded individuals were successful (13.9 %). Although the apparatus used to test lid-opening in the kaka in this thesis (described in Chapter 1) was considerably smaller than those rubbish bin lids, the behaviour pattern required for successful opening of the lid was similar. Kaka had to approach the feeder from the side, grab the lid at the loose end with the beak and perform a sideways motion to flip the lid over the pivot point. Twelve kaka out of 61 (19.7 %) learned to open the feeder lids in this way. Interestingly, the youngest kea able to open the rubbish bin lids was three years and the two individuals that were most efficient were at least 17 and 20 years, respectively, whereas no kaka above the age of seven was able to open the feeder lids in the study presented in this thesis and the most efficient solvers were the youngest kaka (less than 1 year old).

The string-pulling paradigm (described in Chapter 1) was also tested in wild kea (Johnston 1999). Here, seven out of 19 kea (36.8 %) successfully pulled up the string using beak and feet to retrieve the reward compared to 20 out of 30 kaka (66.7 %). Interestingly, in this task juvenile kea outperformed adults as did juvenile kaka. It should be noted, however, that the string-pulling apparatus used for the kea (a 50 cm long piece of string suspended from a perch inside a Perspex cylinder placed on the ground) was different from the apparatus used in this thesis (a 50 cm long piece of string suspended from a dowel fixed to a tree branch).

Lastly, in a study involving a tube-lifting apparatus, wild kea were tested for their social learning abilities (Gajdon et al. 2004). Surprisingly, only two out of 15 kea (13.3 %) learned to remove a tube from a pole while climbing upwards. Additionally, neither of those two individuals solved the task immediately after observation of the trained demonstrator suggesting that they may have found the solution by individual, instead of social, learning. The results from the experiments in this thesis are strikingly consistent with this finding in kea. Although several kaka closely observed a conspecific solve the problem at hand and some of them did so multiple times, this did not appear to effect solving probability. For example, in the block-removal task, at least 12 individuals attentively observed a conspecific pull out the block from under the tread plate of the feeder but none of them manipulated the block themselves afterwards. Only in the string-pulling task did observing another kaka solve the problem increase the likelihood of success, possibly because here they could follow the movement of the reward. Taken together, it appears that kaka, similar to kea may shape their foraging skills primarily through individual (asocial) learning (see also Diamond and Bond 1999). However, the foraging tasks described above are limited to testing the birds' natural response to a new or altered food source in their environment and how they may overcome problems associated with exploiting it. They do not test for other mechanisms or strategies kea and kaka may use as part of their natural foraging repertoire, such as mechanisms deployed for locating wood-boring invertebrates inside tree trunks, and how kea or kaka may learn these during their early development.

Strikingly, overall kaka appear to perform on par with kea suggesting that their respective life histories and different personalities play a secondary role in their cognitive evolution. Instead, they may have retained their cognitive skill set from their common ancestor. Contrary to some previous findings (Webster and Lefebvre 2001; Greenberg 2003), the neophilia-neophobia difference between the two species does not appear to affect their respective problem-solving performance, neither does the difference in habitat, which further contradicts the hypothesis that the kea's harsh alpine environment drives their innovativeness (Diamond and Bond 1999; Laland and Reader 1999a). The results rather point in the direction that the kea's and kaka's ancestral stem species, the proto-kaka, was innovative and behaviourally flexible, which may have favoured radiation and adaptation to their respective ecological niches (Nicolakakis et al. 2003; Tebbich et al. 2010; Lefebvre et al. 2016). That kaka even appear to outperform kea in some tasks (e.g. the string-pulling task), may be due to the fact that the kaka's more abundant forest habitat provides a more nutritious diet, which may positively affect cognitive development (Brust et al. 2014). In

addition, a low micronutrient diet during sexual maturation has been shown to reduce adult neophobia in zebra finches (Noguera et al. 2015). The different habitats of kaka and kea may thus potentially also explain their personality differences.

Figure 5.1: Sequence of photos showing a kaka on Kapiti Island, New Zealand, opening the zipper on a backpack trying to remove a bag with food. Photo credit: Judi Miller.

The finding that kaka innovation may rival the kea is further supported by recent anecdotal evidence suggesting that at least one kaka on Kapiti Island, New Zealand, learned to open the zippers on backpacks of people visiting the island trying to steal their lunches (Figure 5.1; G. de Lisle and J. Miller, personal communication). This is an example of kaka ingenuity that reminds of kea opening rubbish bin lids. However, as of to date, kea remain superior to the kaka in at least one aspect of their cognition: tool use. Kea did not only show in the laboratory that they are able to use a stick or ball tool to retrieve a reward from an apparatus (Auersperg et al. 2010; Auersperg et al. 2011b; Auersperg et al. 2011a), recently they were also observed using sticks in the wild to set off stoat traps and fish for the egg used as bait (Ibbotson 2011; Price 2012). In contrast, there are no reported instances of tool use by kaka in the wild and the individuals that participated in the study described in Chapter 4 were not able to use a stick to retrieve a reward from the Multi-Access-Box. Whether this is due to lack of necessity for the kaka to show such abilities in the wild and a methodological flaw (see section 4.4) to reveal them in an experimental setting, or whether kea are an evolutionary step ahead of kaka is a question that needs further research.

5.4 CONCLUSION

Together, the findings presented in this thesis reveal the kaka's high innovation potential and behavioural flexibility, which is highest in juveniles and on par with the kea's. Chapter 3 suggests that innovative problem-solving performance in this wild parrot species may be

underpinned by a heritable component indicating that natural selection acts on innovation ability. It is therefore likely that kaka and kea have inherited their innovation skills from their common ancestor, which may have additionally facilitated adaptation and radiation to their respective niches. I found no indication for an influence of neophobia on innovative problem-solving performance in any of the investigated tasks on within-species level and kaka appear to rival the kea despite their between-species difference in neophobia/neophilia. Although younger kaka are more likely to persist in trying to find a solution to problems they encounter, there was no direct correlation between persistence and problem-solving performance. Exploration diversity, on the other hand, was directly associated with problem-solving and higher in younger birds than in adults, consistent with recent research emphasising the importance of behavioural diversity and flexibility for generating innovations.

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APPENDICES

A.1 CHAPTER 2: SUPPLEMENT

A.1.1 *Methods*

Subjects and study site

For identification of kaka wearing only the cohort band we relied on the RFID-tag reader, the number imprinted on the cohort band (read with binoculars while in the field) and any distinguishing features in the video records. Unbanded or unidentified individuals were excluded from data analysis.

The kaka feeding stations where we conducted our experiments are approximately 220 m linear distance apart and not within visual range of one another. Operational feeders were available to the kaka between test sessions.

Experiments

Experiment 1 (block-removal) was conducted from 30.01.2014 to 05.08.2014, experiment 2 (lid-opening) from 18.08.2014 to 31.10.2014 and experiment 3 (string-pulling) from 25.09.2014 to 31.10.2014.

We never conducted more than one session in any one experiment per day. In cases where two different experiments were conducted the same day, the testing location was switched between sessions. This, in combination with the different time of day, increased the likelihood of testing different individuals.

Video clips of successful kaka solving the tasks can be watched online: <http://www.youtube.com/watch?v=MHTn7UZlZgU>

Data scoring

For the 24 subjects that participated in all tasks, we obtained an estimate of neophobia by using the videos to measure an individual's latency from landing on the platform to stepping on the treadle with the block underneath in the block-removal task and the latency from landing on the platform to contacting the feeder in the lid-opening task (touching the feeder or lifting the lid) in the first trial. For one individual in the block-removal task (B-Unb_40469), who pulled the block out before he stepped on the treadle, we used the latency to touch the block instead. For one individual in the lid-opening task we could not extract

a neophobia score as he never touched the feeder. We did not estimate neophobia for the string-pulling task, as there was no suitable equivalent for the latency to touch the apparatus (as touching the string in this experiment is not necessarily a measure of neophobia, but may rather be a consequence of whether the birds understood the task).

Statistical analyses

To investigate the effect of individual persistence on eventual success (Y/N) for each of the age classes separately, we used binomial GLMMs for juveniles and subadults and included all tasks (subject was included as a random factor to control for repeated measures). For adults, we used a Mann-Whitney U test to investigate the effect of persistence on the string-pulling task only (as no adult was successful in the block-removal and only one adult succeeded in the lid-opening task). We also did this analysis for our measure of exploratory diversity.

We used Mann-Whitney U tests to investigate the effect of neophobia on whether an individual solved the task for the two feeder experiments separately. We also used a GLMM to test for the effect of neophobia on problem-solving performance for the two feeder experiments jointly. Here we specified a binomial distribution with logit link and repeated measures structure and used the number of successful trials as response variable with the total number of trials as denominator. We used the same GLMM specifications to examine whether the latency to approach the very first experimental setup (latency to step on the treadle with the block underneath) as a general neophobia score affected problem-solving performance in all three tasks. We also used a GLMM with repeated measures structure to examine if neophobia was predicted by age. Here we specified a normal distribution with identity link and used robust estimation.

With the exception of one juvenile kaka, the subject's sex could only be definitively determined for individuals that were known breeders. As a consequence, all of our solvers in experiment 1 and the majority of solvers in experiment 2 were of unknown sex. For this reason, we used Mann-Whitney U tests to analyse the effect of sex on the proportion of successful trials and on our behavioural measures for the string-pulling experiment only.

A.1.2 Results

Individual persistence

Individual persistence did not influence eventual success when analysed separately for each of the age groups (GLMMs: juveniles: $F_{1,37} = 1.166$, $p = 0.287$; $N_{BR} = 21$, $N_{LO} = 11$, $N_{SP} =$

7; subadults: $F_{1,75} = 2.267$, $p = 0.136$; $N_{BR} = 34$, $N_{LO} = 28$, $N_{SP} = 15$; Mann-Whitney U test: adults in string-pulling: $U = 0.0$, $N_S = 3$, $N_{NS} = 3$, $p = 0.100$).

Exploration diversity

Exploration diversity increased the likelihood of eventual success when analysed as factor on its own for juveniles and subadults separately across all tasks (GLMMs: juveniles: $F_{1,36} = 7.494$, $p = 0.010$; $N_{BR} = 21$, $N_{LO} = 11$, $N_{SP} = 6$; subadults: $F_{1,75} = 15.257$, $p < 0.000$; $N_{BR} = 34$, $N_{LO} = 28$, $N_{SP} = 15$). However, there was no effect of exploration diversity on eventual success for adults tested in the string-pulling task (Mann-Whitney U test: adults in string-pulling: $U = 7.5$, $N_S = 3$, $N_{NS} = 3$, $p = 0.200$).

Neophobia

On average, kaka stepped on the feeder treadle four seconds (SE = 0 sec, Range = 1 – 19 sec) after arriving on the platform in the block-removal task and touched the feeder 19 sec (SE = 5 sec, Range = 1 sec – 1 min 26 sec) after arriving on the platform in the lid-opening task.

The latency to step on the treadle did not differ between solvers and nonsolvers in the block-removal task (Mann-Whitney U test: $U = 62.5$, $N_S = 6$, $N_{NS} = 18$, $p = 0.581$) and the latency to contact the feeder did not differ between solvers and nonsolvers in the lid-opening task (Mann-Whitney U test: $U = 43.5$, $N_S = 10$, $N_{NS} = 13$, $p = 0.186$). Furthermore, there was no effect of these measures of neophobia on the proportion of successful trials in the tasks (GLMM: $F_{1,45} = 0.228$, $p = 0.635$; $N_{BR} = 24$, $N_{LO} = 23$). Likewise, when we used latency to approach the very first experimental setup (latency to step on the treadle with the block underneath) as a general score for each bird's neophobia, it did not affect the proportion of successful trials in all three tasks (GLMM: $F_{1,70} = 1.120$, $p = 0.294$). Moreover, neophobia did not differ between age groups (GLMM: $F_{2,44} = 1.001$, $p = 0.376$; $N_{BR} = 24$, $N_{LO} = 23$).

Sex differences

The proportion of successful trials in the string-pulling task did not differ between males and females (Figure A.1.5; Mann-Whitney U test: $U = 13.5$, $N_M = N_F = 5$, $p = 0.841$). There was also no difference between males and females in their individual persistence or exploratory diversity in the string-pulling task (Mann-Whitney U tests: persistence: $U = 3$, $N_M = N_F = 5$, $p = 0.056$; exploration diversity: $U = 7.5$, $N_M = N_F = 5$, $p = 0.310$).

A.1.3 *Supplementary figures*

Figure A.1.1: RFID-tag reader installed at a feeding platform at Zealandia. (a) The rectangular antenna (38 x 22 cm) runs around the tread plate of the left feeder. The antenna is encased in wood (along the corner posts of the platform), black tent pole (above the tread plate) and dark brown plastic cable raceway (under the tread plate of the feeder, not visible in the photo). The black tent pole fixed above the feeder on the right side is a dummy, to prevent biasing the kaka to one side of the platform (installation of two antennae this close to one another running at the same frequency was not possible, as this causes interference) (b) The white plastic pipe that leads the antenna tail ends to the data logger and battery on the ground inside a black plastic box.

Figure A.1.2: Kaka feeders manufactured by Grandpa's Feeders (Windsong Enterprises). (a) Top view with the tread plate in the front and lid closed. (b) Side view with tread plate pushed down and lid open.

Figure A.1.3: Fishing line threaded through a cashew nut tied to the end of the string used in experiment 3 (string-pulling).

Figure A.1.4: Mean proportion of successful trials $\pm$ S.E. for each of the four different levels of social information in all three experiments. This graph is based on the data of all 104 individuals tested. For 'Watched success' the value is zero in the block-removal. In the string-pulling there were no trials that fit the definition of 'Watched manipulations'.

Figure A.1.5: Mean proportion of successful trials $\pm$ S.E. for males and females in the string-pulling experiment. This graph is based on the data of the ten individuals whose sex was known.

A.1.4 *Supplementary tables*

Table A.1.1: The definitions of start and end time of a trial as well as success and social interference for each of the three experiments.

	Experiment	Definition
Trial Start	1, 2	A trial started the moment a subject arrived on the platform (if it stayed for more than 15 sec or started manipulating the apparatus) or after offered food was consumed.
	3	Trial started the moment a subject landed on the test branch or noticeably looked at the reward.
Trial End	1	A trial ended either the moment the subject left the platform (if it left for more than 15 sec), or once the entire block was removed from underneath the treadle by the focal subject, or once the block was removed by any subject.
	2	A trial ended the moment the subject left the platform (if it left it for more than 10 sec) or once the lid was flipped open.
	3	A trial ended once a subject moved more than 2 m away from the string or the moment the subject held the reward in foot or beak.
Success	1	A trial was considered successful if the entire block was removed from underneath the treadle so that stepping on the treadle opened the lid.
	2	A trial was considered successful if the lid was flipped over completely so that it could not fall shut again.
	3	A trial was considered successful if the string was manipulated in a way that allowed the subject to consume the food reward.
Social Interference	1, 2, 3	A trial was considered interrupted if the subject was displaced by another bird or when the trial ended because a subject other than the focal subject solved the task.

Experiment 1 = block-removal, experiment 2 = lid-opening, experiment 3 = string-pulling

Table A.1.2: The different exploratory behaviours kaka displayed in their efforts to solve the problem and the experiment in which they occurred.

Behaviour	Experiment	Definition
Nibbles tread plate	1	Nibbling the tread plate.
Nibbles feeder	1, 2	Nibbling the feeder (mostly the lid).
Nibbles perch	3	Nibbling the dowel the string was attached to.
Nibbles string	3	Nibbling the string.
Lid Lifted – Front	1, 2	Lifting the lid with the beak from the front of the box.
Lid Lifted – Side	1, 2	Lifting the lid with the beak from one of the sides of the box.
Lid Lifted – Backside	1, 2	Lifting the lid with the beak by grabbing the backside of the lid.
Lid Lifted – Top	2	Lifting the lid with the beak while sitting on top of the box
Lid Lifted – Hinge	2	Lifting the lid by pushing down the end of one of the side bars of the lid with the beak at the hinge.
Lift treadle	1	Grabbing the treadle with the beak and lifting it.
Move feeder	2	Pushing, pulling or lifting the feeder.
Foot to lid	1, 2	Lifting one foot in the direction of the lid which is held open with the beak or grabbing the lid with one foot while it is held open with the beak.
Stand up on food tray	2	Standing up on the rim of the food tray while the lid is pushed up with the beak.
Look	1	The subject noticeably looked at the block e.g. by tilting the head or ducking.
	2	Stopping motion to look at the feeder in an exploratory manner (e.g. by tilting the head).
	3	Briefly looking at the string (as defined above).
Stare	3	Looking at the string for an extended period of time without looking away.
Touch	1	Touching the block with beak or tongue.
	3	Touching the string with beak, tongue or foot.
Move block	1	Pushing or pulling the block.
Shrub	3	Trying to reach the reward from a shrub below the string.
Flying	3	Flying towards string and trying to grab hold of it.
Pull string	3	Pulling the string upwards so that the reward moves closer to the subject.

Table A.1.3: The four different levels of social information a kaka may have had opportunity to gather.

	Definition
Naïve	Subject had not previously been at the test location during a test session. Only applicable for an individual's first trial.
Present before	Subject had previously been present at the test location during a session, where it may have seen other kaka interacting with the experimental apparatus.
Watched manipulations	Subject had noticeably watched another kaka (e.g. being on the platform next to the individual or tilting the head to look at the individual on the platform) manipulate the apparatus in a way that gave a clue to the solution to the problem (i.e. pulling the block, lifting the lid from the side or pulling the string) or had arrived and seen the apparatus after another kaka was successful (i.e. the feeder with the lid flipped open or the string lying on top of the branch or held in another kaka's foot while eating the reward).
Watched success	Subject had noticeably watched (as defined above) another kaka solve the problem and retrieve the reward.

Table A.1.4: Techniques used in the lid-opening (LO) and string-pulling (SP) tasks.

Task	Technique	Definition
LO	Side	Moving to the side of the feeder, grabbing the edge of the lid with the beak and flipping it over the pivot point.
LO	Front	Lifting and holding the lid from the front of the box, stepping onto the edge of the feeder, into the food tray and walking until the lid is pushed all the way over.
SP	Upside down	Hanging upside down and holding onto perch with one foot while pulling the string in with beak and other foot.
SP	Grabbing rope with foot	Pulling the string closer with the beak and then securing the length of string gained by grabbing it with one foot.
SP	Step on rope on perch	Pulling the string closer with the beak and then securing the length of string gained by stepping onto it with one foot.
SP	Step on rope moving sideways	Pulling the string closer with the beak and then securing the length of string gained by moving to the side and stepping onto it with one foot.
SP	Walking sideways pulling rope through beak	Letting the string run through the beak while walking to the side thus gaining more string.
SP	Upright pull	Letting the string run through the beak until stretched up in a completely upright position thus gaining more string.
SP	Fold rope around branch/dowel	Placing a loop of string on the branch and then reaching down on the opposite side of the branch to grab the end of the string.
SP	Flying	Flying towards the string and holding on to it while pulling reward off.

Table A.1.5: GLMM analysis of individual variation in persistence measured as the average time spent per trial.

	F	df 1	df 2	<i>p</i>
Full model				
Age group	12.634	2	173	7.6E-6
Task	0.631	2	171	0.534
Task*Age group	0.286	4	167	0.887
Minimal model				
	Coefficient estimate		SE	
Age group: Juveniles	53.892		10.969	
Age group: Subadults	9.530		4.502	
Age group: Adults	0			

Data were fitted to a normal distribution with identity link. We conducted the analysis on all 104 subjects and included bird ID as a random factor (estimated variance component for bird ID in the minimal model = 497.660, SE = 193.255). Robust estimation was used for computing the parameter estimates covariances.

Table A.1.6: GLMM analysis of individual variation in exploratory diversity measured as proportion of distinct exploratory behaviours a subject showed out of the total possible behaviours used by kaka during each experiment.

	F	df 1	df 2	<i>p</i>
Full model				
Task	13.024	2	166	5.6E-6
Age group	9.019	2	166	1.9E-4
Task*Age group	5.380	4	166	4.2E-4
Minimal model				
	Coefficient estimate		SE	
Task: Block-Removal	0			
Task: Lid-Opening	0.010		0.028	
Task: String-Pulling	0.060		0.044	
Age group: Juveniles	0.046		0.036	
Age group: Subadults	0.066		0.024	
Age group: Adults	0			

Data were fitted to a normal distribution with identity link. We conducted the analysis on all 104 subjects and included bird ID as a random factor (estimated variance component for bird ID in the minimal model = 0.006, SE = 0.002). Robust estimation was used for computing the parameter estimates covariances.

Table A.1.7: GLMM analysis of the factors affecting the number of trials until a solution was found in the block-removal task (experiment 1).

	F	df 1	df 2	<i>p</i>
Full model				
Age group	65.790	1	10	1E-5
Time spent per trial	2.052	1	9	0.186
Exploration diversity	1.243	1	9	0.294
Minimal model				
	Coefficient estimate		SE	
Age group: Juveniles	-1.537		0.190	
Age group: Subadults	0			

Data were fitted to a Poisson distribution with a log link. We conducted the analysis on the 12 solvers of experiment 1 to limit the number of potentially confounding variables. No adult kaka were able to solve experiment 1, hence the reference category for age was set to subadults.

Table A.1.8: GLMM analysis of the factors affecting the total amount of time until a solution was found in the block-removal task (experiment 1).

	F	df 1	df 2	<i>p</i>
Full model				
Age group	16.797	1	10	0.002
Time spent per trial	2.163	1	9	0.175
Exploration diversity	0.805	1	9	0.393
Minimal model				
	Coefficient estimate		SE	
Age group: Juveniles	-296.778		72.413	
Age group: Subadults	0		0	

Data were fitted to a normal distribution with identity link. We conducted the analysis on the 12 solvers of experiment one to limit the number of potentially confounding variables.

Table A.1.9: GLMM analyses of the effect of social information on the outcome of a trial in the string-pulling experiment.

	F	df 1	df 2	<i>p</i>
Social information	5.577	2	94	0.005
	Coefficient estimate		SE	
“Naïve”	0		0	
“Present before”	0.247		1.056	
“Watched success”	-2.229		0.942	

Data were fitted to a binomial distribution with a logit link. Bird ID was included as a random factor and reference category was set to “naïve”. We excluded all trials that were conducted after the subject’s initial success.

Table A.1.10: List of subjects with information about age, age classification and sex (where known) as well as the number of successful trials and total number of trials in each experiment.

Subject	Age [y]	Age group	Sex	Successful trials / total trials					
				Block-removal		Lid-opening		String-pulling	
B-OY	<1	Juvenile	?	1	1	-	-	-	-
B-Unb_40453	<1	Juvenile	?	-	-	0	1	-	-
B-Unb_40454	<1	Juvenile	?	0	2	-	-	-	-
B-Unb_40456	<1	Juvenile	?	2	4	-	-	-	-
B-Unb_40457	<1	Juvenile	?	0	14	0	5	-	-
B-Unb_4046?	<1	Juvenile	?	2	3	-	-	-	-
B-Unb_40464	<1	Juvenile	?	0	6	-	-	-	-
B-Unb_40465	<1	Juvenile	?	0	9	0	21	-	-
B-Unb_40469	<1	Juvenile	?	56	60	23	38	31	33
B-Unb_40471	<1	Juvenile	?	2	4	-	-	-	-
B-Unb_40472	<1	Juvenile	?	3	8	23	28	38	40
B-Unb_40474	<1	Juvenile	?	-	-	0	1	-	-
B-Unb_40480	<1	Juvenile	?	-	-	-	-	6	6
B-Unb_40489	<1	Juvenile	F	0	20	187	211	75	91
B-Unb_40500	<1	Juvenile	?	0	10	-	-	-	-
B-Unb_40506	<1	Juvenile	?	0	6	-	-	-	-
B-Unb_40518	<1	Juvenile	?	0	2	-	-	-	-
B-Unb_40535	<1	Juvenile	?	4	7	-	-	-	-
Unb-B_405?4	<1	Juvenile	?	-	-	0	3	-	-
Unb-B_40451	<1	Juvenile	?	0	1	-	-	-	-
Unb-B_40455	<1	Juvenile	?	0	1	-	-	9	9
Unb-B_40458	<1	Juvenile	?	-	-	6	39	3	8
Unb-B_40463	<1	Juvenile	?	0	2	-	-	-	-
Unb-B_40534	<1	Juvenile	?	24	26	-	-	-	-
Unb-B_40538	<1	Juvenile	?	2	10	6	31	36	38
Unb-B_43794	<1	Juvenile	?	-	-	29	33	6	7
Unb-B_43798	<1	Juvenile	?	0	1	-	-	-	-
GG-G	1	Subadult	?	0	2	-	-	-	-
G-GM	1	Subadult	?	1	11	0	5	0	1
G-GR	1	Subadult	?	7	27	54	60	85	94
G-MB	1	Subadult	?	0	2	1	6	0	1

Table A.1.10: *Continued.*

Subject	Age [y]	Age group	Sex	Successful trials / total trials					
				Block-removal		Lid-opening		String-pulling	
G-OR	1	Subadult	F	0	25	0	6	1	1
G-YB	1	Subadult	?	0	1	-	-	-	-
KR-G	1	Subadult	?	0	13	0	4	-	-
LG-G	1	Subadult	?	0	4	-	-	-	-
LM-G	1	Subadult	?	0	11	9	28	0	1
RB-G	1	Subadult	?	0	29	-	-	-	-
RM-G	1	Subadult	?	0	10	0	5	-	-
RW-G	1	Subadult	?	0	13	0	9	0	5
YG-G	1	Subadult	?	0	11	0	2	-	-
YP-G	1	Subadult	?	0	3	-	-	-	-
GO-Y	2	Subadult	?	-	-	0	3	-	-
GW-V	2	Subadult	?	-	-	0	5	-	-
Unb-Y	2	Subadult	F	0	30	0	29	59	68
V-KL	2	Subadult	?	0	6	0	1	-	-
V-YW	2	Subadult	F	0	1	0	2	-	-
GL-O	3	Subadult	?	0	2	-	-	-	-
GR-O	3	Subadult	?	-	-	0	1		
KR-Y	3	Subadult	F	0	2	-	-	-	-
KY-O	3	Subadult	?	0	6	0	3	-	-
MO-O	3	Subadult	?	-	-	3	6	-	-
MW-O	3	Subadult	?	1	31	4	48	59	65
O-BO	3	Subadult	?	0	7	0	6		
O-BW	3	Subadult	?	0	7	0	16	25	25
O-GW	3	Subadult	?	0	1	0	8	18	18
OG-Y	3	Subadult	?	-	-	0	1	-	-
O-KL	3	Subadult	?	0	9	-	-	-	-
O-KO	3	Subadult	F	0	15	0	3	-	-
O-LK	3	Subadult	?	0	2	-	-	-	-
O-LM	3	Subadult	?	0	3	-	-	-	-
O-OM	3	Subadult	M	-	-	0	7	0	2
Y-WK	3	Subadult	?	-	-	0	2	-	-
Y-YR	3	Subadult	?	0	5	-	-	-	-

Table A.1.10: *Continued.*

Subject	Age [y]	Age group	Sex	Successful trials / total trials					
				Block-removal		Lid-opening		String-pulling	
BG-Y	4	Subadult	?	0	15	0	5	0	3
LK-Y	4	Subadult	?	0	1	-	-	-	-
Y-GL	4	Subadult	M	0	16	31	63	25	30
Y-MK	4	Subadult	?	0	1	-	-	-	-
Y-ML	4	Subadult	M	-	-	-	-	5	5
Y-MW	4	Subadult	?	0	4	0	7	0	1
BB-B	5	Adult	?	-	-	0	2	-	-
B-LY	5	Adult	?	0	2	-	-	-	-
BO-B	5	Adult	F	0	13	-	-	-	-
B-RG	5	Adult	M	0	4	-	-	-	-
B-RW	5	Adult	?	0	2	0	1	0	2
B-WR	5	Adult	M	0	14	0	5	-	-
B-YP	5	Adult	?	0	5	-	-	-	-
KL-B	5	Adult	?	-	-	0	1	-	-
LL-B	5	Adult	?	0	1	0	14	12	12
MP-B	5	Adult	M	-	-	0	3	-	-
YB-B	5	Adult	F	0	2	-	-	-	-
KR-W	6	Adult	F	0	4	-	-	-	-
W-BB	6	Adult	M	0	17	0	9	-	-
W-BR	6	Adult	F	0	5	-	-	-	-
W-MP	6	Adult	F	0	5	0	6	0	1
W-Unb	6	Adult	M	0	2	0	8	5	5
KB-K	7	Adult	F	0	22	-	-	-	-
K-KR	7	Adult	F	0	11	0	39	22	22
RG-S	7	Adult	M	0	4	0	3	-	-
RM-S	7	Adult	M	0	11	2	11	13	14
YY-K	7	Adult	M	0	12	0	6	-	-
L-OP	8	Adult	?	0	1	-	-	-	-
PW-L	8	Adult	F	0	3	0	3	-	-
YK-L	8	Adult	F	0	8	-	-	-	-
YL-L	8	Adult	F	0	10	0	1	-	-
KO-G	9	Adult	F	0	7	0	2	-	-

Table A.1.10: *Continued.*

Subject	Age [y]	Age group	Sex	Successful trials / total trials					
				Block-removal		Lid-opening		String-pulling	
OO-G	9	Adult	M	0	13	0	3	-	-
R-GR	10	Adult	F	0	5	0	3	-	-
BP-P	11	Adult	M	0	3	-	-	-	-
OB-P	11	Adult	M	0	13	0	12	0	4
P-YB	11	Adult	F	0	14	-	-	-	-
P-YR	11	Adult	F	0	11	0	2	-	-
P-WB	12	Adult	M	0	2	0	1	-	-
P-WO	12	Adult	F	0	7	0	1	-	-
RR-P	13	Adult	F	0	8	-	-	-	-

F, female; M, male.

From video footage and test notes we are positive that subjects B-Unb_4046? And Unb-B_405?4 are different individuals from all other subjects included here. E.g. B-Unb_4046? and B-Unb_40469 were present at the test location at the same time, so these two must be different individuals, B-Unb_40465 had a characteristic yellow breast feather, which B-Unb_4046? had not, etc.

A.2 CHAPTER 3: SUPPLEMENT

A.2.1 *Methods*

Subjects

During the 2013/2014 breeding season kaka were banded with a blue cohort band only, either on the right or left leg. For identification of these kaka we relied on the RFID-tag readings and the number imprinted on the cohort band (read with binoculars while in the field) and any distinguishing features in the video records (e.g. yellow breast feathers with the juvenile birds). Unidentifiable individuals were excluded from data analysis.

Statistical Analysis

To assess whether inter-individual variance in kaka's performance across the three different problem-solving tasks could be summarised by a single factor (yielding a single metric for an individual's general problem solving performance) we performed a principal components analysis (PCA) with an unrotated factor solution on the proportion of successful trials for all 24 subjects that participated in all three tasks (from the original full dataset; see Table A.1.10 for individual data). We then used the obtained PC1 scores to test whether this factor was affected by clutch using a GLM with robust estimation. However, it should be noted that this analysis is based on eight subjects only as of the original 24 subjects, only eight were individuals for whom at least one clutch-mate also participated in all three tasks. For these eight subjects we additionally used Fisher's exact tests to investigate whether the distribution of solvers across clutches differed from random.

A.2.2 *Results*

We investigated the variance in problem-solving performance (proportion of successful trials) across our three tasks on the full dataset which included 24 subjects that participated in all tasks (Table A.2.10). Performance in all tasks loaded positively onto the first component extracted from the PCA (Table A.2.11 and Table A.2.12) and this component explained 58.16 % of the total variance. Furthermore, first component scores for the subjects for whom at least one clutch-mate also participated in all three tasks were significantly predicted by clutch (GLM: $\chi^2_3=28.247$, $p<0.000$, $N=8$; Table A.2.13). Intra-class correlation of these first component scores yielded a high, however nonsignificant, intra-class correlation coefficient, likely due to insufficient sample size ($t = 0.650$, $p = 0.084$, $N=4$ pairs).

A.2.3 Supplementary figures

Figure A.2.1: Number of events ($\pm$ SE) kaka were observed without and with siblings from the same clutch at the feeding stations during test sessions ($N=44$).

Figure A.2.2: Number of events ($\pm$ SE) kaka were observed without and with a parent at the feeding stations during test sessions ($N=21$).

A.2.4 *Supplementary tables*

Table A.2.1: List of subjects with information about age, age classification and clutch as well as the number of successful trials and total number of trials in each experiment.

Subject	Age [y]	Age class	Sex	Female Parent	Male Parent	Clutch ID	Sibl. group	Successful trials/total trials					
								BR	LO	SP			
B-Unb_40453	<1	J	?	V-YW	LR-Y	59	59	-	-	0	1	-	-
B-Unb_40454	<1	J	?	P-YR	RG-S	41	41	0	2	-	-	-	-
B-Unb_40456	<1	J	?	P-YR	RG-S	41	41	2	4	-	-	-	-
B-Unb_40457	<1	J	?	P-YR	RG-S	41	41	0	14	0	5	-	-
B-Unb_40464	<1	J	?	BM-Y	B-WR	4	3	0	6	-	-	-	-
B-Unb_40465	<1	J	?	BM-Y	B-WR	4	3	0	9	0	21	-	-
B-Unb_40469	<1	J	?	BY-W	LB-R ?	6	5	56	60	23	38	31	33
B-Unb_40471	<1	J	?	BY-W	LB-R ?	6	5	2	4	-	-	-	-
B-Unb_40472	<1	J	?	BY-W	LB-R ?	6	5	3	8	23	28	38	40
B-Unb_40474	<1	J	?	PW-L	P-WB	-	22	-	-	0	1	-	-
B-Unb_40489	<1	J	F	P-WO	BP-P	-	27	0	20	187	211	75	91
B-Unb_40506	<1	J	?	KO-G	RP-P	-	11	0	6	-	-	-	-
B-Unb_40535	<1	J	?	MG-Y	?	20	20	4	7	-	-	-	-
Unb-B_40451	<1	J	?	V-YW	LR-Y	59	59	0	1	-	-	-	-
Unb-B_40455	<1	J	?	P-YR	RG-S	41	41	0	1	-	-	9	9
Unb-B_40458	<1	J	?	L-KM	OY-G	-	19	-	-	6	39	3	8
Unb-B_40463	<1	J	?	BM-Y	B-WR	4	3	0	2	-	-	-	-
Unb-B_40534	<1	J	?	MG-Y	?	20	20	24	26	-	-	-	-
Unb-B_43794	<1	J	?	KR-W	W-Unb	-	14	-	-	29	33	6	7
G-GM	1	S	?	RR-P	Y-GL	52	52	1	11	0	5	0	1
G-GR	1	S	?	RR-P	Y-GL	52	52	7	27	54	60	85	94
G-MB	1	S	?	PW-L	P-WB	22	22	0	2	1	6	0	1
G-OR	1	S	F	KR-W	?	15	-	0	25	0	6	1	1
G-YB	1	S	?	P-WO	BP-P	-	27	0	1	-	-	-	-
KR-G	1	S	?	PW-L	P-WB	22	22	0	13	0	4	-	-
LM-G	1	S	?	KR-W	?	15	-	0	11	9	28	0	1
RB-G	1	S	?	YL-L	OO-G	-	2	0	29	-	-	-	-
RM-G	1	S	?	BM-Y	B-WR	3	3	0	10	0	5	-	-
RW-G	1	S	?	BM-Y	B-WR	3	3	0	13	0	9	0	5
YG-G	1	S	?	L-KM	OY-G	19	19	0	11	0	2	-	-
YP-G	1	S	?	L-KM	OY-G	19	19	0	3	-	-	-	-
GW-V	2	S	?	P-YR	RG-S	-	41	-	-	0	5	-	-
V-KL	2	S	?	KO-G	RP-P	-	11	0	6	0	1	-	-
V-YW	2	S	F	L-KM	OY-G	-	19	0	1	0	2	-	-
GL-O	3	S	?	KR-W	W-Unb	14	14	0	2	-	-	-	-
GR-O	3	S	?	P-YB	LG-R	-	35	-	-	0	1	-	-
KY-O	3	S	?	BY-W	LB-R	5	5	0	6	0	3	-	-
MO-O	3	S	?	KR-W	W-Unb	14	14	-	-	3	6	-	-

Table A.2.1: *Continued.*

Subject	Age [y]	Age class	Sex	Female Parent	Male Parent	Clutch ID	Sibl. group	Successful/total trials					
								BR	LO	SP			
MW-O	3	S	?	R-GR	OB-P	-	50	1	31	4	48	59	65
O-BO	3	S	?	BY-W	LB-R	5	5	0	7	0	6	-	-
O-BW	3	S	?	P-YR	RG-S	-	41	0	7	0	16	25	25
O-GW	3	S	?	BY-W	LB-R	5	5	0	1	0	8	18	18
O-KL	3	S	?	PW-L	G-GK	23	23	0	9	-	-	-	-
O-LK	3	S	?	P-YB	LG-R	-	35	0	2	-	-	-	-
O-OM	3	S	M	PW-L	G-GK	23	23	-	-	0	7	0	2
BG-Y	4	S	?	YL-L	OO-G	2	2	0	15	0	5	0	3
Y-MK	4	S	?	P-YR	R-P	42	42	0	1	-	-	-	-
Y-ML	4	S	M	P-YR	R-P	42	42	-	-	-	-	5	5
Y-MW	4	S	?	YL-L	OO-G	2	2	0	4	0	7	0	1
BB-B	5	A	?	P-WO	BP-P	-	27	-	-	0	2	-	-
BO-B	5	A	F	G-OK	G-LO	7	7	0	13	-	-	-	-
B-RW	5	A	?	?YL-L	?OO-G	10	2	0	2	0	1	0	2
B-YP	5	A	?	?YL-L	?OO-G	10	2	0	5	-	-	-	-
KL-B	5	A	?	P-YB	LG-R	-	35	-	-	0	1	-	-
LL-B	5	A	?	R-GR	?OB-P	-	50	0	1	0	14	12	12
MP-B	5	A	M	G-OK	G-LO	7	7	-	-	0	3	-	-
KR-W	6	A	F	P-WO	BP-P	-	27	0	4	-	-	-	-
W-BB	6	A	M	UNB/ L-KM	OY-G	55	-	0	17	0	9	-	-
W-BR	6	A	F	UNB/ L-KM	OY-G	55	-	0	5	-	-	-	-
KB-K	7	A	F	P-WO	BP-P	27	27	0	22	-	-	-	-
K-KR	7	A	F	P-WO	BP-P	27	27	0	11	0	39	22	22
RG-S	7	A	M	20053	B640	1	1	0	4	0	3	-	-
RM-S	7	A	M	20053	B640	1	1	0	11	2	11	13	14
YY-K	7	A	M	P-YB	LG-R	-	35	0	12	0	6	-	-
PW-L	8	A	F	P-YR	R-P	-	42	0	3	0	3	-	-
YK-L	8	A	F	P-YB	LG-R	35	35	0	8	-	-	-	-
YL-L	8	A	F	P-YB	LG-R	35	35	0	10	0	1	-	-
KO-G	9	A	F	P-WO	BP-P	-	27	0	7	0	2	-	-
P-YB	11	A	F	P-WY	RP-P	34	34	0	14	-	-	-	-
P-YR	11	A	F	P-WY	RP-P	34	34	0	11	0	2	-	-
P-WB	12	A	M	KA0285	970051	8	8	0	2	0	1	-	-
P-WO	12	A	F	KA0285	970051	8	8	0	7	0	1	-	-

F, female; M, male.

Table A.2.2: Number and percentage of individuals that were successful out of the total number of individuals tested in each of the three experiments and the number of clutches they originate from.

Age group	Block-Removal				Lid-Opening				String-Pulling				Total	
	S	T	%	Cl	S	T	%	Cl	S	T	%	Cl	Ind	Cl
Juveniles	6	12	50	4	2	2	100	1	2	2	100	1	12	4
Subadults	2	15	13.3	7	3	13	23.1	6	2	6	33.3	3	15	7
Adults	0	14	0	7	1	4	25	2	-	-	-	-	14	7
Total	8	41	19.5	18	6	19	31.6	9	4	8	50	4	41	18

J = juveniles, S = subadults, A = adults, S = solvers, T = total, Cl = clutches, Ind = individuals.
 This table is based on the subset of individuals of whom we tested at least one sibling from the same clutch in the same experiment.

Table A.2.3: Solving events across clutches. Data of individual kaka is pooled to show the total number of successfully and unsuccessfully completed tasks each clutch participated in.

Clutch ID	Solved	Unsolved	# of individuals
6	7	0	3
20	2	0	2
1	2	3	2
5	1	6	3
14	1	1	2
15	2	4	2
22	1	4	2
27	1	3	2
41	2	4	4
42	1	1	2
52	4	2	2
2	0	6	2
3	0	5	2
4	0	4	3
7	0	2	2
8	0	4	2
10	0	4	2
19	0	3	2
23	0	3	2
34	0	3	2
35	0	3	2
55	0	3	2
59	0	2	2

Fisher's exact test: $p = 0.00016$

Table A.2.4: Distribution of solvers and nonsolvers across clutches in the block-removal task ($N=36$).

Clutch ID	Solvers	Nonsolvers
1	0	2
2	0	2
3	0	2
4	0	2
5	0	2
6	2	0
8	0	2
10	0	2
15	0	2
19	0	2
20	2	0
22	0	2
27	0	2
34	0	2
35	0	2
41	1	1
52	2	0
55	0	2

Fisher's exact test: $p = 0.003$ Table A.2.5: Distribution of solvers and nonsolvers in the string-pulling task across groups of siblings from different clutches ($N=16$).

Sibling group	Solvers	Nonsolvers
5	3	0
27	2	0
41	2	0
50	2	0
15	1	1
52	1	1
2	0	3

Fisher's exact test: $p = 0.049$

Table A.2.6: Microchipped subjects with information about age, age classification and clutch as well as the number of events they were detected with and without a sibling from the same clutch at the feeders and the number of tasks they solved and participated in.

Subject	Age [y]	Age class	Clutch ID	Without CM	With CM	Tasks solved
BG-Y	4	S	2	1146	180	0/3
Y-MW	4	S	2	357	180	0/3
RM-G	1	S	3	469	30	0/2
RW-G	1	S	3	443	30	0/3
Unb-B_40463	<1	J	4	117	39	0/1
B-Unb_40464	<1	J	4	89	34	0/1
B-Unb_40465	<1	J	4	572	62	0/2
KY-O	3	S	5	76	13	0/2
O-BO	3	S	5	409	43	0/2
O-GW	3	S	5	174	46	1/3
B-Unb_40469	<1	J	6	478	34	3/3
B-Unb_40471	<1	J	6	3	0	1/1
B-Unb_40472	<1	J	6	168	34	3/3
BO-B	5	A	7	7	0	0/1
MP-B	5	A	7	4	0	0/1
B-RW	5	A	10	86	15	0/3
B-YP	5	A	10	179	15	0/1
G-OR	1	S	15	352	21	1/3
LM-G	1	S	15	610	21	1/3
YG-G	1	S	19	24	1	0/2
YP-G	1	S	19	12	1	0/1
Unb-B_40534	<1	J	20	63	7	1/1
B-Unb_40535	<1	J	20	121	7	1/1
G-MB	1	S	22	19	2	1/3
KR-G	1	S	22	113	2	0/2
O-KL	3	S	23	68	2	0/1
O-OM	3	S	23	73	2	0/2
B-Unb_40454	<1	J	41	19	2	0/1
Unb-B_40455	<1	J	41	22	0	1/2
B-Unb_40456	<1	J	41	35	0	1/1
B-Unb_40457	<1	J	41	582	2	0/2
Y-MK	4	S	42	10	0	0/1
Y-ML	4	S	42	36	0	1/1
G-GM	1	S	52	319	36	1/3
G-GR	1	S	52	741	36	3/3
Unb-B_40451	<1	J	59	49	0	0/1
B-Unb_40453	<1	J	59	41	0	0/1

CM = clutch-mate

Table A.2.7: Association between solvers, task-dependent solvers and nonsolvers and whether they were recorded together with their siblings from the same clutch at least once.

	Tasks solved		
	All	Some	None
Foraged without clutch-mate	3	1	5
Foraged with clutch-mate	5	5	18

Table A.2.8: Association between overall solvers, task-dependent solvers and nonsolvers and whether they were recorded together with their siblings from the same clutch on more than 10 occasions.

	Tasks solved		
	All	Some	None
Foraged with clutch-mate < 10x	5	2	12
Foraged with clutch-mate > 10x	3	4	11

Table A.2.9: Association between overall solvers, task-dependent solvers and nonsolvers and whether they were recorded together with their siblings from the same clutch on more than 30 occasions.

	Tasks solved		
	All	Some	None
Foraged with clutch-mate < 30x	5	4	15
Foraged with clutch-mate > 30x	3	2	8

Table A.2.10: Subjects that participated in all three experiments with information about age, age classification and clutch ID as well as the proportion of successful trials in each experiment.

Subject	Age [y]	Age class	Sex	Female Parent	Male Parent	Clutch ID	Sibl. group	Prop. of successful trials		
								BR	LO	SP
B-Unb_40469	<1	J		BY-W	LB-R ?	6	5	0.933	0.605	0.939
B-Unb_40472	<1	J		BY-W	LB-R ?	6	5	0.375	0.821	0.950
B-Unb_40489	<1	J	F	P-WO	BP-P		27	0.000	0.886	0.824
Unb-B_40538	<1	J		UNB	V-PG			0.200	0.194	0.947
G-GM	1	S		RR-P	Y-GL	52	52	0.091	0.000	0.000
G-GR	1	S		RR-P	Y-GL	52	52	0.259	0.900	0.904
G-MB	1	S		PW-L	P-WB	22	22	0.000	0.167	0.000
G-OR	1	S	F	KR-W		15		0.000	0.000	1.000
LM-G	1	S		KR-W		15		0.000	0.321	0.000
RW-G	1	S		BM-Y	B-WR	3	3	0.000	0.000	0.000
Unb-Y	2	S	F					0.000	0.000	0.868
MW-O	3	S		R-GR	OB-P		50	0.032	0.083	0.908
O-BW	3	S		P-YR	RG-S		41	0.000	0.000	1.000
O-GW	3	S		BY-W	LB-R	5	5	0.000	0.000	1.000
BG-Y	4	S		YL-L	OO-G	2	2	0.000	0.000	0.000
Y-GL	4	S	M					0.000	0.492	0.833
Y-MW	4	S		YL-L	OO-G	2	2	0.000	0.000	0.000
B-RW	5	A		?YL-L	?OO-G	10	2	0.000	0.000	0.000
LL-B	5	A		R-GR	?OB-P		50	0.000	0.000	1.000
W-MP	6	A	F	KO-G	LY-R			0.000	0.000	0.000
W-Unb	6	A	M	UNB	LB-R			0.000	0.000	1.000
K-KR	7	A	F	P-WO	BP-P	27	27	0.000	0.000	1.000
RM-S	7	A	M	20053	B640	1	1	0.000	0.182	0.929
OB-P	11	A	M					0.000	0.000	0.000

Table A.2.11: The loadings and percentage of variance explained of components with an eigenvalue >1 extracted by the unrotated PCA ($N=24$).

	PC1
Block-removal	0.814
Lid-opening	0.835
String-pulling	0.621
Eigenvalue	1.745
% variance explained	58.16

Table A.2.12: Correlation matrix of the PCA

		Block-removal	Lid-opening
Lid-opening	r	0.534	
	p	0.004	
String-pulling	r	0.259	0.301
	p	0.111	0.076

Table A.2.13: Clutches that participated in all three experiments with information about age, age classification and clutch ID as well as the proportion of successful trials in each experiment.

Subject	Age [y]	Age class	Sex	Female Parent	Male Parent	Clutch ID	Proportion of successful trials		
							BR	LO	SP
B-Unb_40469	<1	J		BY-W	LB-R ?	6	0.933	0.605	0.939
B-Unb_40472	<1	J		BY-W	LB-R ?	6	0.375	0.821	0.950
G-GM	1	S		RR-P	Y-GL	52	0.091	0.000	0.000
G-GR	1	S		RR-P	Y-GL	52	0.259	0.900	0.904
G-OR	1	S	F	KR-W		15	0.000	0.000	1.000
LM-G	1	S		KR-W		15	0.000	0.321	0.000
BG-Y	4	S		YL-L	OO-G	2	0.000	0.000	0.000
Y-MW	4	S		YL-L	OO-G	2	0.000	0.000	0.000

Dotted lines separate clutches.

A.3 CHAPTER 4: SUPPLEMENT

A.3.1 *Results*

There was no difference in the proportion of successful trials between subadult and adult kaka (GLMM: Age group: $F_{1,33} = 1.549$, $p = 0.222$; Blocked options: $F_{1,35} = 1.186$, $p = 0.284$; Age group* Blocked options: $F_{2,31} = 0.002$, $p = 0.998$).

Subadult and adult kaka did not differ in the time required to find a first or alternative solutions to the MAB (Figure A.3.1; GLMM: Age group: $F_{1,31} = 0.056$, $p = 0.814$; Phase: $F_{2,32} = 0.282$, $p = 0.756$; Age group* Phase: $F_{2,29} = 0.198$, $p = 0.822$).

Our analyses of the individual variation in behavioural measures between subadults and adults are consistent with those showing the differences between 1- to 2-year-olds and kaka older than two. Subadults and adults did not differ in their latency from landing on the platform to touching the MAB (Mann-Whitney U test: $U = 46.5$, $N_S = 12$, $N_A = 8$, $p = 0.910$). Subadults showed overall greater exploratory diversity than the adults (Figure A.3.2; Mann-Whitney U test: $U = 8.5$, $N_S = 10$, $N_A = 5$, $p = 0.040$), however, they did not contact all three target panels faster (Figure A.3.3; Mann-Whitney U test: $U = 22$, $N_S = 10$, $N_A = 5$, $p = 0.768$). On average, subadults spent more time trying to find a solution to the problem than adults, however, this difference in individual persistence only approached significance (Figure A.3.4; Mann-Whitney U test: $U = 9$, $N_S = 10$, $N_A = 5$, $p = 0.055$).

A.3.2 Supplementary figures

Figure A.3.1: Mean latency $\pm$ SE to successfully use a first option in Phase 1 and an alternative version after blocking of the previous one in Phases 2 and 3 for subadults and adults. The number of subjects is given at the base of the bars.

Figure A.3.2: Mean $\pm$ SE of the number of exploratory actions at different parts of the MAB for subadult ($N=10$) and adult ($N=5$) kaka.

Figure A.3.3: Mean $\pm$ SE of the latency to touch all three target panels with the beak for subadult ($N=10$) and adult ($N=5$) kaka.

Figure A.3.4: Mean $\pm$ SE of the time a kaka spent trying to find a solution to the problem before 'giving up' for subadult ($N=10$) and adult ($N=5$) kaka.

A.3.3 *Supplementary tables*

Table A.3.1: Definitions of the exploratory behaviours the kaka exhibited in each trial in their efforts to access the food, as well as the parts of the apparatus an individual explored.

Behaviour	Part of the MAB	Definition
Contacts MAB		Touches any of the parts of the MAB with the beak.
Nibbles		Nibbles softly with beak or uses the tongue to explore one of the following structures of the MAB:
	Aluminium bar	One of the aluminium corner bars.
	Board	The handle of the wooden food board.
	Base	The wooden base of the MAB.
	Door bolt	The little round white plastic bolt at the edge of the door that keeps the door from opening on its own.
	Door edge	The slit between the closed door and the panel.
	Door hole	The rim of the door hole.
	Hinges	One of the hinges on the door panel.
	Opening edge	The opening edge of the Board panel.
	Side panel	The Perspex surface on any of the panels.
	Screw	One of the 4 screw nuts that hold the top panel in place.
	SD edge	One of the side edges of the sliding door without moving it.
	SD handle	The handle on the sliding door.
	SD rail	One of the rails that hold the sliding door.
	Stick	The wooden stick.
	Top panel	The edge of the top panel.
Bites/ Breaks		Forcefully biting down on one of the parts of the MAB or trying to use the beak as a lever to break parts off of the MAB.
	Aluminium bar	Biting one of the aluminium corner bars.
	Base	Excavating the wooden base of the MAB.
	Door at edge	Trying to break the door open by hooking the beak into the slit between door and panel.
	Door hole	Biting the rim of the door hole.
	Edge btw back panel and aluminium bar	Trying to hook the beak into the slit between the back panel and the aluminium corner bar.
	Hinge	Trying to break one of the hinges off.

Behaviour	Part of the MAB	Definition
Moves	Opening edge	Biting or trying to break the Board panel at the edge of the opening.
	Opening edge by wedging beak underneath	Placing the tip of the beak onto the wooden base underneath the opening edge of the Board panel and levering upwards.
	SD rail	Biting or trying to break off one of the rails that hold the sliding door.
	Sliding Door	Hooking the beak into the space between the sliding door and the panel and trying to use it as a lever break the sliding door.
	Stick	Shredding the wooden stick.
	Top panel	Biting or trying to lift off the top panel.
		Moving one of the following without fully opening or using one of the options:
	Board	Moving or lifting the wooden food board.
	Door	Partially opening or closing the door.
	MAB	Pushing or pulling the MAB.
	Sliding Door	Partially opening or closing the sliding door.
	Stick	Nudging, lifting or throwing the stick off the platform.
	Sits on MAB	Hopping onto the top panel and looks down into the MAB.
	Picks up stick and holds it in foot	Picking up the stick with the beak and transferring it into one foot (sometimes in order to then further manipulate it with the beak).
	Tries to reach through slot	Trying to reach the food board with the beak by pushing it as far as possible through the opening in the Board panel.
	Lifts MAB	Hooking the beak underneath the base of the MAB and using it as a lever to lift the MAB or slightly lifting the MAB off the platform by grabbing the lid or sliding door rail without fully tilting it.
	Tilts MAB	Tilting the MAB by lifting one side of it at the top panel.
	Throws MAB (almost) off	Pushing the MAB until it (almost) falls off the platform.

Table A.3.2: Techniques used in the door (D) and sliding door (SD) options.

Option	Technique	Definition
D	Walk around	Standing behind the door (at the hinges) and pulling it towards oneself, then walking around.
D	Walk around + push door	Standing behind the door (at the hinges) and pulling it towards oneself a ways, then walking or bending around the door and pushing it the rest of the way (with the beak against the inside of the door or by grabbing the door hole or by grabbing the edge).
D	Turn MAB around	Standing behind the door (at the hinges) and pulling it towards oneself and continuing to pull at the door so that the MAB turns around.
D	Pull door	Standing at the hole side of the door and pulling it away from oneself as far as the neck stretches.
D	Swing door open	Strongly pulling the door so that it swings open away from bird
D	Pull + push door	Standing at the hole side of the door and pulling it away from oneself a ways, then pushing the door the rest of the way (with the beak against the inside of the door or by grabbing the door hole or by grabbing the edge).
D	Continuous	Pulling the door away from oneself and going over to pushing the door in one continuous motion never letting go of door only adjusting the position of the beak.
D	Middle pull + push	Sitting right in front of the door and pulling the door past oneself (mostly having to lean backwards in doing so), then bending around the door to push it the rest of the way (with the beak against the inside of the door or by grabbing the door hole).
D	Middle continuous	Sitting right in front of the door and pulling the door past oneself leaning backwards in doing so and going over to pushing the door in one continuous motion never letting go of door only adjusting the position of the beak.
SD	Left, pull, handle	Pulling the SD to the left by grabbing the handle with the beak.
SD	Left, pull, edge	Pulling the SD to the left by grabbing the edge with the beak.
SD	Left, push, handle	Pushing the SD to the left by grabbing the handle with the beak.
SD	Left, push, beak against handle	Pushing the SD to the left by pushing the beak against the handle
SD	Right, pull, handle	Pulling the SD to the right by grabbing the handle with the beak.
SD	Right, pull, edge	Pulling the SD to the right by grabbing the edge with the beak.
SD	Right, push, handle	Pushing the SD to the right by grabbing the handle with the beak.
SD	Right, push, edge	Pushing the SD to the right by grabbing the edge with the beak.
SD	Right, push, beak against handle	Pushing the SD to the right by pushing the beak against the handle

Table A.3.3: GLMM analysis of the overall problem-solving success (successful out of total number of trials) with age group and number of blocked options included as fixed factors in the model.

	F	df 1	df 2	<i>p</i>
Age group	3.932	1	33	0.056
# of blocked options	3.512	2	33	0.041
	Coefficient estimate		SE	
Unblocked	0			
1 option blocked (B or SD)	-1.436		0.719	
2 options blocked (B and SD)	-2.052		0.898	

Data were fitted to a binomial distribution with logit link. $N_{\text{Unblocked}} = 15$, $N_{\text{1blocked}} = 12$, $N_{\text{2blocked}} = 10$.