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Cooperative Cognition in kea

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A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy in Psychology, the University of Auckland, 2016.

ABSTRACT

Kea are a curious and intelligent New Zealand parrot that are relatively understudied. While laboratory studies have shown kea to be capable physical problem solvers, little is known about their social cognition. Given that kea possess many of the traits that are claimed to be prerequisites for advanced social cognition, such as large relative brain size, complex social living, monogamous pair bonding and extractive foraging, they are an ideal candidate for studies of social cognition. By studying social cognition in kea we can compare them with primates and investigate whether kea have evolved similar cognitive mechanisms through the process of convergent evolution. In this thesis, I examine cooperative cognition in kea. I report the findings of three experiments, each designed to explore whether kea possess particular cognitive mechanisms which are claimed to underpin cooperative cognition. These include whether kea understand when they need a partner in a cooperative task and also when they do not, the role that their partner plays in the task and if they preferred to work together or alone on a task. I also examined prosocial behaviour and inequity aversion in kea. I suggest that kea might possess some of the traits that are indicative of advanced cooperative cognition, such as understanding the need for a partner and understanding when a task can be solved alone. The kea's performance on these tasks was on par with the performance of chimpanzees and elephants at similar tasks, and above those of other "intelligent" avian species, such as rooks and African Grey parrots. The results from this thesis indicate that kea may not be intrinsically prosocial but this requires further testing employing different methodologies. Kea did not show any evidence of inequity aversion and our results do not support the hypothesis that inequity aversion evolved in species that are both highly social and cooperative. Overall, this thesis highlights that at least some aspects of cooperative cognition might have evolved convergently in kea.

ACKNOWLEDGEMENTS

Firstly I would like to thank my supervisors, Alex Taylor, Russell Gray and William Hayward. Alex, thank you so much for all of your hard work, patience and support. Thank you also for all of your advice and guidance in regards to running animal cognition experiments. Russell, thank you for your ongoing support, encouragement and belief in me. Thank you to William Hayward for jumping on board. I really appreciate all of your help and support.

A huge thank you to Willowbank for allowing me to work with their wonderful kea. Thanks to the staff in the Natives section and in particular, Nick Ackroyd, for all of your fantastic help and positivity. It was great getting to know you all.

To Teesha Passmore for being a brilliant Research Assistant. I definitely could not have got there without your help. Thank you to my wonderful daughter, Eve, for helping out and being a general dog's body. Thank you for putting up with the cold weather, thieving kea and your stressed mother! To my three other children, Ben, Finn and Tess. Thank you for your support and proud belief that what I was doing was pretty cool. Thank you to Steve Cudby for building all of my contraptions from awful sketches and putting up with me being demanding. Vivian Ward, for your wonderful drawings. Finally, a huge thank you to Stephen Drake, for your invaluable statistics and computer help.

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Chapter Two: Kea perform on par with elephants and chimpanzees on cooperative tasks

Nature of contribution by PhD candidate	Conceived and designed study, collected data, analysed data and wrote the manuscript
Extent of contribution by PhD candidate (%)	70

CO-AUTHORS

Name	Nature of Contribution
Alex Taylor	Contributed to study design, commented on manuscript
Russell Gray	Contributed to study design, commented on manuscript

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The undersigned hereby certify that:

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- that the candidate wrote all or the majority of the text.

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Chapter Three: Examining Prosociality in kea

Nature of contribution by PhD candidate	Conceived and designed study, collected data, analysed data and wrote the manuscript
Extent of contribution by PhD candidate (%)	70

CO-AUTHORS

Name	Nature of Contribution
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Russell Gray	Contributed to study design, commented on manuscript

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Chapter Four: Kea do not show evidence of inequity aversion in a classic token exchange paradigm

Nature of contribution by PhD candidate	Conceived and designed study, collected data, analysed data and wrote the manuscript
Extent of contribution by PhD candidate (%)	80

CO-AUTHORS

Name	Nature of Contribution
Alex Taylor	Contributed to study design, commented on manuscript
Russell Gray	Contributed to study design, commented on manuscript

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Chapter 1

Introduction

"It is not only fine feathers that make fine birds."

(Aesop)

1.1 Comparative psychology and cooperative cognition in animals

What drives the evolution of complex cognition? The "social intelligence" hypothesis claims that increases in social complexity are the main reason for the advanced cognitive abilities seen in humans and some other primate species (Byrne & Whiten, 1988; Dunbar, 1998; Humphrey, 1976; Whiten & Byrne, 1997). This hypothesis is supported by the fact that complex group living is correlated with large relative forebrain size, particularly the necortex (Byrne, 2003; Dunbar, 2003). However, this hypothesis remains controversial. Research has found that the human forebrain is no larger than would be expected to be found in a primate with our brain size (Barton & Venditti, 2013). In addition, it has been discovered that the cerebellum increased more rapidly in size than the forebrain in the evolution of apes and humans (Barton & Venditti, 2014). This finding challenges the "social intelligence" hypothesis. The cerebellum plays an important role in motor control, which suggests that the role of technical intelligence has been at least as important as social intelligence in the evolution of human cognition (Barton & Venditti, 2014). While the "social intelligence" hypothesis relates mainly to the evolution of advanced cognition in primates, in birds it has been suggested that it is the quality, not the quantity of relationships that predicts intelligence (Emery et al., 2007). This comes from the finding that there is no correlation between relative brain size and sociality in birds (Iwanuk & Nelson, 2003). It is claimed that species of birds that form monogamous pair bonds possess more advanced cognition, due to the challenges that arise from having to work together to raise their young (Emery et al., 2007). However, direct comparisons of the analyses of brain size between birds and primates are problematic. The avian analyses have only examined overall relative brain size (Emery et al., 2007), whereas studies with humans and other mammals have focused on the neocortex. An alternative, but not necessarily mutually exclusive hypothesis for the evolution of complex cognition is the "technical intelligence" hypothesis (Byrne, 1997). This theory suggests that natural selection has enhanced cognitive abilities in primate species who face selective pressures of solving problems in their physical environment, especially those that engage in extractive foraging and tool use.

Comparative psychologists test evolutionary hypotheses about how complex cognition evolved by examining the relationship between specific cognitive traits and one or more selective pressures that are hypothesised to drive their evolution (MacLean et al., 2012). By making cross-species comparisons, including between humans and animals, comparative psychologists explore the phylogeny of various behaviours - that is how those behaviours evolved and how they differ between species. Comparisons of only species that are closely related do not allow generalisations to be made about how complex cognition evolved across different species (Povinelli & Giambrone, 1999; MacLean et al., 2012). Convergent evolution is the process whereby distantly related species evolve similar traits due to having to solve similar socioecological problems (Emery & Clayton, 2004). Studying cognition in distantly related species, particularly those that share similar adaptive pressures which are claimed to drive the evolution of complex cognition, increases the likelihood of understanding how complex cognition evolved in primates, including humans. In addition to identifying the selective pressures that led to the evolution of advanced cognition, comparative psychologists seek to identify the cognitive mechanisms that evolved in response to those selective pressures. Identifying the cognitive mechanisms that underpin advanced cognition helps comparative psychologists understand *how* complex cognition evolves, that is, the mechanisms that underpin advanced cognitive abilities, and not just the function that those abilities serve (Vonk & Shackelford, 2013).

Comparative research in social cognition examines how the challenges of social living have led to the evolution of advanced social cognition (Humphrey, 1976; Miklosi et al., 2003). Researchers investigate whether animals possess a range of cognitive mechanisms that are claimed to underpin advanced social cognition in humans. Some of these include, theory of mind (Whiten & Byrne, 1991; Hare, Call & Tomasello, 2001), prosocial behaviour (de Waal et al., 2008; Suchak & de Waal, 2012; Horner et al., 2011), social learning (Byrne, 2002; Huber et al., 2001), joint cooperation in a task (Plotnik et al., 2011; Melis et al., 2006; Drea & Carter, 2013), understanding the role of cooperative partners (Plotnik et al., 2011 ; Melis et al., 2006; Mendres & de Waal, 2000), inequity aversion (Brosnan & de Waal, 2003; Jelbert et al., 2015; Range et al., 2009) and the recognition of conspecifics (Dittrich, 1990).

One area of social cognition that is considered particularly unique in humans is cooperation (Tomasello, 2014; Dean et al., 2011). Cooperative behaviour is defined as an individual acting in a way that benefits another (Mcaullife & Thornton, 2015). Human cooperation occurs in a plethora of forms and contexts. Researchers suggest that this is because human cooperation is underpinned by a number of cognitive mechanisms that have allowed humans to have a more complex understanding of cooperation (Stevens et al., 2005). Some of these mechanisms include understanding the role of the partner (Plotnik et al., 2011), the preference for collaboration (Rekers, Haun & Tomasello, 2011; Bullinger, Melis & Tomasello, 2011), spontaneous prosociality (Horner et al., 2011) and inequity aversion (Brosnan and de Waal, 2003; Brosnan et al., 2010). Examining cooperative cognition in other social and cooperative species enables researchers to test if other species possess cooperative cognition and whether these behavioural traits are prerequisites to social intelligence in general. This allows researchers to compare the cooperative capacities of different species and then draw a map of the phylogenetic distribution of advanced cooperative cognition. The differences between species might reveal the mechanisms that underlie cooperative cognition and also their earliest beginnings in humans. However, it is currently unclear whether any non-human species understand cooperation in the same way that humans do. Cooperative cognition may be uniquely human.

1.1.1 Examining the cognitive mechanisms that underpin cooperation

Human cooperation is claimed to be governed by a "package" of cognitive mechanisms (Stevens et al., 2005). Comparative psychologists, investigating whether non-human species understand cooperation in the same way that humans do, examine whether animals possess particular cognitive mechanisms claimed to underpin cooperative cognition in humans. Some of these include (1) choosing who to cooperate with; (2) coordinating actions with a partner; (3) understanding the need for a partner and the role that the partner plays; (4) a preference for collaboration; (5) prosocial behaviour; (6) inequity aversion.

1.1.1.1. Choosing who to cooperate with

There are several mechanisms that are proposed to explain why animals cooperate and who they choose who to cooperate with. Kin-selection is typically claimed to be the most common reason why a large variety of species preferentially provide help to another individual: doing so maximises their own individual fitness (Mcauliffe & Thornton, 2015; Silk, 2009). Researchers have postulated that a range of mechanisms that do not require cooperative cognition might explain how animals learn to discriminate kin from non-kin (Mcauliffe & Thornton, 2015). For example, nesting birds typically rely on mechanisms such as feeding any animal within their nesting location. Other birds, who have chicks that have fledged, may identify and preferentially assist their own kin by relying on vocalisations that the young learnt from adults while they were still nesting (Mcauliffe & Thornton, 2015).

The most common explanation as to why animals choose to cooperate with unrelated kin, without immediate benefit, is generalised reciprocity (Rutte & Taborsky, 2007). Generalised reciprocity is when an individual chooses to help non-kin based on expected future reciprocity which need not be immediate, due to past cooperative experiences (Cheney, 2011). Evidence of generalised reciprocity in animals is limited but has been found in capuchins (Suchak & de Waal, 2012) and rats (Rutte & Taborsky, 2007). In the capuchin study, capuchins increased their prosocial token preference in a condition in which they alternated taking turns with their partner in choosing between selfish tokens or prosocial tokens, compared to a previous condition in which the subject chose for the entire session. Researchers found that this increase was based on non-contingent reciprocity (Suchak & de Waal, 2012). In rats, Rutte & Taborsky (Rutte & Taborsky, 2007) demonstrated that female rats will cooperate more frequently, by pulling a lever that delivers food to a partner, if they had been helped previously. The identity of the partner did not matter and did not need to be the partner that had previously helped the subject. The authors suggest that this type of generalised reciprocity may have facilitated the evolution of cooperation between nonkin (Rutte & Taborsky, 2007).

Contingent reciprocity involves a tit for tat strategy and requires immediate reciprocity. For example, individual A helps individual B and in the following interaction individual B helps individual A (Warneken & Tomasello, 2013). Contingent reciprocity requires a repertoire of cognitive skills such as skills of memory, temporal discounting and numerical discrimination (Stevens et al., 2005; Stevens & Hauser, 2004). It is claimed that animals do not possess contingent reciprocity, and thus that it is unique to humans (Melis & Semmann, 2010). Evidence that non-human animals lack this package of skills comes from studies with chimpanzees (Brosnan et al., 2009; Yamamoto & Tanaka, 2010) and cotton-top tamarins (Cronin et al., 2010).

1.1.1.2. Coordination of actions

The ability of an individual to coordinate their actions with a conspecific is one of the first requirements for success in a cooperative task (Brosnan et al., 2010). Cooperative hunting in the wild suggests that some non-human animals are capable of acting together to achieve the same goal. Some of the species that are known to hunt together include chimpanzees (Boesch & Boesch, 1989) dolphins (Gazda et al., 2005), Harris hawks (Bednarz, 1988) and mormryid fishes (Arnegard & Carlson, 2005). However, as has been argued in the case of cooperative hunting in chimpanzees, cooperative cognition may not underpin their collaborative hunting. While their behaviour may look cooperative, it is argued that individual chimpanzees are simply pursuing their own individual goals simultaneously (Tomasello & Carpenter, 2007). Within the laboratory, it has been suggested that a variety of species are capable of coordinating their actions with a partner. This has typically been examined by using the ‘loose string’ paradigm which was originally developed by Hirata & Fuwa (2007), to examine cooperation in chimpanzees. In this task, two individuals must coordinate their actions in order to retrieve rewards which are placed out of reach, typically on a tray or platform. A piece of loose string or rope is attached to the platform and one end of the piece of string is available to each member of the dyad. Each member must pull their end of the string at the same time as their partner in order to pull in the platform and retrieve the reward. If one member pulls before the other, the string is pulled from the platform, which does not move, and so the rewards remain inaccessible. Hyaenas (Drea & Carter, 2009), chimpanzees (Melis, Hare & Tomasello, 2006), elephants (Plotnik et al., 2011), rooks (Seed, Clayton & Emery, 2008) and African Grey parrots (Péron et al, 2011) have all been successful at coordinating their actions simultaneously. While the ability to coordinate actions with a partner is an important aspect of cooperation it should be noted that this can be achieved without any awareness of the need for a partner or the role that the partner plays. For example, Seed and colleagues found that while rooks could successfully collaborate to pull a platform in, their failure in a subsequent partner delay condition indicated that this was achieved without cooperative cognition (Seed et al., 2008). Therefore, coordination of action between individuals does not necessarily indicate that they understand how cooperation works.

1.1.1.3. Understanding the need for a partner and the role that the partner plays

Understanding the need for a partner and the role that the partner plays are key aspects of cooperative cognition (Plotnik et al., 2011). Suggestive evidence that non-human species understand the need for a partner comes from research with chimpanzees (Melis et al., 2006), elephants (Plotnik et al., 2011) and coral trout (Vail et al., 2014). In the chimpanzee study, subjects were presented with the ‘loose string’ paradigm. Chimpanzees were first given trials where the arrival of their partner was delayed for increasing periods. Chimpanzees successfully waited for their partner for delay periods of up to 30 seconds. They were also taught how to unlock doors to let a partner enter the room. At test, Melis and colleagues examined whether chimpanzees could discriminate between situations when they needed a partner to collaborate and when they did not. To do this they let subjects enter a room where there was either a solo or a duo platform present, while a potential collaborator waited behind a locked door. The duo platform required a partner to pull in the platform simultaneously with the subject to access the rewards, while the solo platform could be pulled in alone. When presented with the duo platform, the experimenters found that subjects would unlock the door and let the partner enter more often than when presented with the solo platform. This led the authors to conclude that the chimpanzees understood when they needed a partner and when they did not and so altered their behaviour accordingly. The chimpanzees were then given the opportunity to select between two potential collaborators, one who was effective at solving the 'loose string' task with a partner, and one not. After initially showing no preference for either collaborator after a short amount of experience, chimpanzees demonstrated that they were capable of recruiting the most effective collaborator for the task (Melis et al., 2006). The only other species that this has been documented in is coral trout. In naturalistic collaborative hunting coral trout have been shown to understand when they need to recruit a moray eel collaborator, by using gestures to signal the location of prey to the eel. They only recruit a moray eel collaborator when they are required, such as when the prey is hidden in the reef. Also, like chimpanzees, coral trout are capable of selecting the most effective eel to collaborate with (Vail et al., 2014). Elephants have also shown that they are capable of waiting for their partner for delay periods of up to 45 seconds when tested with the 'loose string' paradigm (Plotnik et al., 2011). In a no-rope condition of the same task, in which the partner's rope was coiled up out of reach, subjects pulled their rope less often. This suggests that they understood not only that their partner needed to be present, but also the role that their partner played in the cooperative task. In a similar tasks, dogs were able to wait for their partner for 2 seconds but not 15 seconds (Ostojić & Clayton, 2014).

However, debate still surrounds the extent to which these results demonstrate the use of cooperative cognition, as opposed to associative learning. In the case of the elephant study (Plotnik et al., 2011) it has been suggested that subjects might have been relying on a combination of two associative cues: the presence of a rope in a partner's trunk and a feeling of tautness on the rope (Seed & Jensen, 2011). The results of Vail and colleagues (2014) also highlight that associative learning is a potential hypothesis for the results of Melis and colleagues (2006). The coral trout in Vail and colleagues (2014) were tested in an ecologically valid situation where they could use learnt associations formed during the course of their day-to-day foraging. The coral trout then performed identically to the chimpanzees in Melis and colleagues (2006), who were also given some opportunity to learn how the task worked and how effective their partners were. Thus quick learning, rather than cooperative cognition, could be behind the performances of these chimpanzees.

While cooperative cognition in birds is understudied, studies with rooks found that they could perform the same action in synchronisation with a conspecific, but in a delayed partner arrival task could not wait for the arrival of a conspecific (Seed et al., 2008). They were also not able to discriminate between when they needed to work with a partner or when they could work alone. Similarly, African Grey parrots were not very successful at waiting for the arrival of their partner and did not discriminate between tasks in which they could access a reward alone and when they needed a partner (Péron et al, 2011). Therefore, research examining birds at present does not suggest they understand the need for a partner, the role that their partner plays and when they need a partner and when they don't. This contrasts with work on fish (Vail et al., 2014) and mammals (Melis et al., 2006; Plotnik et al., 2011), where there is suggestive evidence for this type of understanding.

1.1.1.4. A preference for collaboration

A preference for working together, over working alone is also claimed to be one of the cognitive mechanisms that underpins cooperative behaviour in humans. This has been supported by two studies comparing this preference between children and chimpanzees. In one study, chimpanzees showed no preference between collaborating with a partner on the 'loose string' task and working alone. Children, however, had a clear preference for working together (Rekers, et al., 2011). In a similar study researchers found that when given the option between working alone and working together, chimpanzees preferred to work alone. In a subsequent task in which the rewards for choosing to collaborate were doubled, chimpanzees showed a preference for the collaborative option (Bullinger et al., 2011). This suggests that chimpanzees were not intrinsically motivated to collaborate and would only do so if it maximised the rewards they received.

1.1.1.5. Prosocial behaviour

Other research has focused on examining prosocial behaviour in animals. The intrinsic motivation to help others is frequently claimed to be a crucial aspect underpinning human cooperation (Horner et al., 2011; Yamamoto & Takimoto, 2012). Animals demonstrate behaviours indicative of helping in the wild, but the mechanisms that underlie these behaviours are unclear. For example, female baboons regularly groom other females who are lactating. On the surface this may look like prosocial behaviour as it appears to benefit a conspecific without any benefit to oneself. However, grooming actually appears to only take place so that non-lactating females can gain access to the infant of the lactating mother. This is because non-lactating females have a strong intrinsic drive to handle baboon infants (Henzi & Barrett, 2002). Laboratory experiments designed to assess whether animals exhibit the intrinsic motivation to help others have produced mixed findings. Two of the most common paradigms used to assess other regarding preferences in animals are Giving Assistance Tests (GAT) and Prosocial Choice Tests (PCT). In GAT animals must choose between offering instrumental help, such as providing a conspecific with a needed tool so that they can access a reward, or doing nothing (Yamamoto, Humle & Tanaka, 2009). Several GAT studies have found evidence of helping behaviours in chimpanzees (Yamamoto et al., 2009, Yamamoto, Humle & Tanaka, 2012; Melis et al., 2011) and bonobos (Hare & Kwetuenda, 2010). In PCT tests subjects must choose between two options. These options are providing food for both themselves and a partner (prosocial option), or only themselves (selfish option). Earlier PCT studies found no evidence of other regarding preferences in chimpanzees (Silk, 2005; Jensen et al., 2006). A following study conducted by Horner and colleagues addressed some of the methodological pitfalls that were claimed to contribute to the negative prosocial findings in previous PCT studies and adjusted them in their own study. They found that chimpanzees had a clear prosocial preference (Horner et al., 2011). However, Heyes compellingly argued that chimpanzee prosocial choice in this experiment could be explained by associative learning. Heyes suggested that because the rewards were wrapped in a paper that made a rustling sound when opened, the sound eventually became a 'conditioned reinforcer.' By selecting the prosocial token, subjects got to experience hearing the rustling sound more often (Heyes, 2012). Evidence for other regarding preferences has been reported in capuchins (de Waal et al., 2008; Lakshiminarayanan & Santos, 2008; Suchak & de Waal, 2012) and long tailed macaques (Massen et al., 2011). In cotton-top tamarins, Cronin and colleagues (Cronin et al., 2009) and Stevens and colleagues (Stevens et al., 2010) reported that these monkeys did not behave prosocially towards group members.

In avian subjects, Péron and colleagues found that African Grey parrots did not behave prosocially, with the exception of one bird that behaved in a reciprocal manner with a human experimenter (Péron et al., 2013). Similarly, Di Lascio and colleagues found that ravens were indifferent to the gains of a conspecific. A second task designed to examine reciprocity found that subjects also failed to understand the contingencies of this task and thus maximise the rewards they received (Di Lascio et al., 2013). While it is possible that some non-human species such as chimpanzees and capuchins may exhibit prosocial tendencies in certain tasks, at present there is no evidence of this in birds.

1.1.1.6. Inequity aversion

Inequity aversion is a reaction to unfairness and is hypothesised to have evolved alongside cooperation in order to promote cooperative bonds between nonkin (Brosnan, 2011; Brosnan & de Waal, 2014). In animals it is claimed that inequity aversion may have evolved in species that, like humans, are both highly social and highly cooperative (Brosnan, 2010). Evidence for inequity aversion in animals from experimental studies is mixed. Positive findings have been reported in chimpanzees (Brosnan et al., 2010; Brosnan et al., 2005) and capuchins (Brosnan & de Waal, 2003). However, other studies have failed to find evidence of inequity aversion in chimpanzees (Bräuer et al., 2009) and capuchins (Fontenot et al., 2007; Mcauliffe et al., 2015). Failure to find evidence of inequity aversion has also been reported in studies with bonobos (Bräuer et al., 2009), squirrel monkeys (Talbot et al., 2011), and orangutans (Bräuer et al., 2009; Brosnan et al., 2011). Mcauliffe et al., 2014 (Mcauliffe et al., 2014) tested whether cotton-top tamarins demonstrated inequity averse behaviours when gaining rewards was effortful or effortless. In the effortless condition, subjects could pull a handle and deliver rewards to both themselves and a partner (one piece of food for subject, four for partner). In the effortful condition, weights were added to the handle. The amount of weight added differed between subjects according to the amount of weight they had been willing to pull in order to receive a reward in an assessment task. Overall, subjects showed little sensitivity to inequity when the required task was either effortful or effortless, except for one subject who pulled the handle less often during the effortful condition.

In an experiment examining inequity aversion in dogs, Range and colleagues (Range et al., 2009) found that dogs did not show evidence of inequity aversion when their partner received a high value reward while subjects received a low value reward. However, their performance did decrease in a condition where the subject received no reward for performing a paw shake while their partner received a low value reward, compared to an asocial no reward condition. The authors concluded that dogs might possess a basic form of inequity aversion (Range et al., 2009). In birds, Wascher and Bugnyar investigated inequity aversion in crows and ravens. They found that exchange performance decreased when there was a difference in working effort between subject and partner. That is, when the subject was required to exchange a stone for a reward while the partner received the same reward without having to exchange (Wascher & Bugnyar, 2013). The authors claimed that these birds might be sensitive to inequity in regards to working effort. Performance also declined in the inequity condition compared to equity condition. However, performance rates were even lower in a food control condition compared to the inequity condition. This suggests that birds were reacting to seeing the high vale food reward, the food expectation hypothesis, rather than the fact that their partner received it and they did not. Also, performance was not lower in a no reward condition in which the subject received no reward while their partner received a low value reward, compared to an asocial control condition in which the subject also received no reward. This indicates that observing their partner receive a low value reward while they received nothing was not enough to elicit inequity aversion in crows and ravens. Jelbert and colleagues (Jelbert et al., 2015) examined inequity aversion in New Caledonian crows using two separate tests with two separate groups of birds. In the first test the quantity of rewards that birds received varied from trial to trial and in the second test, the quality of reward was varied. The authors found no evidence of inequity aversion in New Caledonian crows in either condition.

Overall, it is not clear that any non-human species possess inequity aversion. A large amount of research investigating inequity aversion in animals has been criticized for both methodological issues and interpretation of behaviours (Roma et al., 2006; Wynne, 2004). For example, it has been argued that subjects form an expectation that they will receive a high value reward after observing a conspecific consume the same reward type and so have an aversive reaction to being given a low quality food item. This is called the food expectation hypothesis (Bräuer et al., 2006; Dubreuil et al., 2006). Another explanation for the negative reactions observed in inequity aversion tasks is the frustration effect. This is when an animal reacts negatively to receiving a low value food reward because they have previously received a high value food reward, which is independent of what reward their partner received in comparison to themselves (Roma et al., 2006; Silberberg et al., 2009). However, comparative research has shown that species that are both highly social and cooperative, such as chimpanzees and capuchins, are more likely to show evidence of inequity aversion than species that do not possess both of these attributes (Brosnan, 2011; Brosnan & de Waal, 2014).

1.2 Why study cooperative cognition in kea?

As previously discussed, there is very little evidence that other avian species such as rooks (Seed et al., 2008), New Caledonian Crows (Jelbert et al., 2015) and African Grey parrots (Péron et al., 2011) possess cooperative cognition. There are several reasons why it is worthwhile to extend the study of avian cooperative cognition to include kea (*Nestor notabilis*). Firstly, both anecdotal accounts and laboratory research investigating their physical problem solving skills, indicate that kea are an "intelligent" parrot (Werdenich & Huber, 2006; Auersperg, Gajdon & Huber, 2010; Auersperg, Huber & Gajdon, 2011a). Kea also possess many of the attributes that are claimed to underlie advanced social cognition and are excellent candidates to test the "social intelligence" hypothesis. Kea are a highly social species of bird, living in groups of up to 13 birds (Orr-Walker, 2010), and they also have a large relative brain size (Diamond & Bond, 1999; Bond & Diamond, 2003). Their social behaviour shows a number of features that kea share with that of great apes such as chimpanzees, but are not common in other birds. Kea regularly interact with a variety of both related and unrelated kea. This includes complex, frequent and intense play behaviours that are distinctly different from other species of birds (Diamond & Bond, 1999; Bond & Diamond, 2003). Also, there are clear social hierarchies in kea groups that impact an individual's reproductive success. These social interactions require kea, like chimpanzees, to keep track of the relationships of a large number of individuals (Diamond & Bond, 1999; Seed, Emery & Clayton, 2009). Kea also form monogamous pair-bonds, and engage in bi-parental care. Also, young kea have an extended period of dependence on their parents (Diamond & Bond, 1999). Thus, according to the pair bonding hypothesis (Emery et al., 2007), kea should have sophisticated cognition. Also, kea evolved in a challenging physical environment, and are known to engage in intensive extractive foraging (Cuthbert, 2003; Diamond & Bond 1999). This allows us to test the hypothesis that alongside social pressures, selective pressures faced in the physical realm could also contribute to the evolution of advanced social cognition. Therefore, because kea faced similar selective pressures to distantly related species that possess advanced cognition, such as humans and chimpanzees, they are an excellent species to examine whether cooperative cognition can evolve convergently. Finally, the majority of research that has been conducted on kea has taken place overseas at the University of Vienna in Austria. This research presents as an opportunity to study an endemic New Zealand species within New Zealand. In this thesis I sought to explore cooperative cognition in kea by presenting them with a series of experiments designed to test whether kea possess some of the cognitive mechanisms that are claimed to underpin complex cooperation.

In the following sections of this introduction I will provide some general background information about kea, such as their habitat, diet, physiological characteristics, sociality and development and then discuss previous research that has examined the cognitive abilities of kea. Following this, I will describe each experiment that was conducted in this thesis, including a discussion about the different aspects of cooperative cognition that they sought to investigate.

1.3 The kea

1.3.1 Behaviour and ecology

Kea are a remarkable species of parrot that are endemic to alpine and forested areas in the South Island of New Zealand. They are one of 8 surviving species of parrot that are endemic to New Zealand and are the only alpine parrot species in the world (Diamond & Bond, 1999). They were once killed for bounty due to concerns that they were attacking livestock and although they have been a protected species since 1986 their population is estimated to consist of between only 1000 and 5000 individuals (Orr-Walker, 2010). Kea have an omnivorous diet but are predominantly vegetarian feeding on fruit, seeds and roots. On occasion they are known to eat small mammals, chicks, insects and carrion (Schwing, 2010; Cuthbert, 2003).

Kea are a large parrot measuring about 48cm in length and weighing between 0.8-1 kg. In general, males are about 20% heavier and about 10-15% longer than females. The male kea's beak is also considerably longer than that of the female (Diamond & Bond, 1999). Kea have an olive green plumage with a distinctive red/orange colouring under their wings which is visible when they are in flight. Unlike most other parrots, kea's colour pattern changes as they mature. Fledglings and juveniles are identified by bright yellow rings that surround their eyes. The same yellow colouring also marks their cere and lower bill and completely fade by the time they reach adulthood (Diamond &Bond, 1999).

They are an extremely social bird and a clear hierarchy exists within their social structure. However, this hierarchy is non-linear and prone to fluctuations (Diamond & Bond, 1999). In general, adult and juvenile males are the highest ranking individuals while subadults are the lowest. Aggression is common in kea society with subordinates generally deferring to more dominant individuals. Allopreening also plays an important role in kea society and occurs between a range of different individuals in a variety of contexts. The only combinations that never allopreen each other are adult males preening other adult males and females preening other females, regardless of age. Allopreening in kea seems to serve a similar purpose as social grooming does in primates, such as maintaining bonds, conflict resolution and alliance formation (Diamond & Bond, 1999), though in primates grooming occurs between all sexes and ages.

Male kea breed between the ages of 4-5 years and females breed from 3 years of age due to the fact that they reach sexual maturity earlier. Pairs nest in burrows and crevices and the female lays between 3-4 eggs. She is fed by the male while she incubates the eggs and also while the hatched chicks remain in the nest. Once kea leave the nest they develop through a series of stages from fledglings, juveniles, subadults to adults (Diamond & Bond, 1999). Fledglings are poor foragers and are dependent on their fathers for food for 5-6 weeks after leaving the nest. They are highly aggressive and at this stage of development there are no behavioural differences between males and females. Juveniles are birds of about one year of age. They leave their area of birth and travel together with other juveniles. Behaviourally they are very bold and because they are still poor foragers they obtain food by begging or stealing from adults. Juveniles are tolerated by adults who will often share or give up their food. At about 2-3 years of age kea become subadults and at this point they have settled in an area. Unlike fledglings and juveniles, subadults are not tolerated by adults and must find food on their own. Subadults are not yet very proficient foragers and mostly obtain food by stealing it from other kea. At this stage subadults lose their yellow markings and male kea stop playing with other males and females begin to play more with males and never with other females. Physically, they begin to lose their distinctive yellow markings (Diamond & Bond, 1999).

Kea may be described as scavengers (Schwing, 2010). This is most likely because they evolved in an environment that often had limited and fluctuating resources. In order to survive they were required to become dietary generalists as opposed to dietary specialists unlike their close relative, the kaka (Diamond & Bond, 1999). Adult males are the most proficient and dedicated foragers. This is probably because adult males feed their mate during courtship, while she is nesting and also after the chicks have fledged in order to maintain the pair bond. It is also the males who feed the fledglings for quite some time after they leave the nest by regurgitating food for them. Adult males must develop exemplary foraging skills because they are required to provide food for themselves, their mate and their fledglings.

Diamond & Bond (Diamond & Bond, 1999), note two distinctive behavioural characteristics that are exaggerated in kea in comparison to other birds. The first is their insatiable appetite for play and the second is their enhanced social facilitation. The motivation to play in kea is intense and may be unique among birds (Diamond & Bond, 1999; Bond & Diamond, 2004). Kea play in pairs, groups, or with objects by themselves often for extended periods of time. Play with other kea often consists of behaviours such as kicking, beak locking, chasing and wrestling. This type of play is referred to as rough and tumble play. A second type of play is called toss play, which typically occurs between females and males. Toss play typically involves tossing objects in the air, jumping, flapping, locking bills and pushing feet and is claimed to serve the function of courtship and maintaining pair bonds. Kea will also play with a variety of objects from sticks and stones to discarded furniture. Kea will play with objects for extended periods of time, however, the more affordances an object has, that is, the number of different things an object can do, the longer a kea will play with it (Diamond & Bond, 1999; Bond & Diamond, 2004). Play in kea is claimed to be analogous to play in mammals, particularly primates (Diamond & Bond, 1999). Play is serves a variety of functions, from fostering and maintaining bonds between individuals, to more complex manipulations which serve as a social strategy. However, the main function of play is hypothesised to be in maintaining behavioural flexibility (Palagi & Tomasso, 2007; Pellis, Pellis & Himmler, 2014). The ability to adapt to new situations is imperative in species that live in unpredictable environments, or where resources are scarce. Indeed, compared to their close relative the kaka (*Nestor meridionalis*), whose environment has enabled them to become dietary specialists as opposed to generalists like kea, kaka have a smaller period of parental dependence and engage in significantly less play behaviours and in contrast to kea, do not seem to engage in object play (Bond & Diamond, 2004).

The second main predisposition that kea exhibit is social facilitation. That is, kea are drawn to places and objects where other kea are. Kea do not learn through imitation, instead they learn through individual trial and error learning (Diamond & Bond, 1999). Thus social facilitation draws kea to areas and objects where other possibly more skilled foragers are and therefore where better resources are most likely to be accessed. This gives kea the opportunity to learn to become proficient foragers for themselves.

1.3.2 Previous research on cognition in kea

1.3.2.1. Physical cognition in kea

From both anecdotal observation and experimental studies, kea are known to be “intelligent” parrots (Huber et al., 2008). Most cognitive research on kea has been conducted in the kea lab in the Department of Cognitive Biology at the University of Vienna and a large amount of this research has focused on physical cognition. Kea have demonstrated impressive capabilities in the domain of physical intelligence within the laboratory setting. Werdenich and Huber (2006) presented kea with a string pulling task in which a reward was attached to the end of a piece of hanging string. Subjects solved the problem immediately which led researchers to conclude that kea solved the problem through insight as opposed to trial and error learning (but see Taylor and colleagues (Taylor et al., 2010) for an alternative explanation of these type of string pulling performances). Auersperg and colleagues presented kea with a series of tasks using a tube lifting, object inserting paradigm. They found that subjects were able to achieve complex levels of object relationships and could easily solve a second order tool using task (Auersperg et al., 2010). The first innovative use of a tool in kea was reported by Auersperg and colleagues when one subject, Kermit, successfully used a stick tool to gain access to a reward in a multi access box paradigm. This was a particularly interesting finding, given that kea are not natural tool users in the wild (Auersperg et al., 2011a).

Following this study Auersperg and colleagues reported that four out of six subjects could use a stick tool to gain access to a reward after receiving demonstration trials. This was impressive given that subjects had no prior experience with tools and that they are constrained by the shape of their beak which makes it awkward to grasp and direct stick shaped objects. In a following task, subjects were able to use the functional end of a stick tool and aim it at a baited box, which when hit would release rewards while avoiding hitting an unbaited box. This suggests that kea understood the functional properties of the tool as they were able to actively use it to gain a reward while avoiding a negative option (Auersperg et al., 2011b). Gajdon and colleagues presented kea with a mechanical problem solving where they were required to remove a baited tube from two upright poles. The removal of the tube was blocked at one end of one pole but not the other. They found that when kea were able to visually observe which end of the pole would block tube access and which end did not block access they were able to solve the problem and access the tube from the unblocked end. Subjects were then presented with a second apparatus in which one end of the pole had a removable end and the other end was fixed. The main difference between the first and second apparatus was that in the second apparatus the difference between the pole ends was not visible as it had been in the first apparatus. Subjects received an unbaited exploration stage with the second apparatus and during this stage, subjects preferred the pole with the removable end. However, during testing when the tubes were baited they did not push the tubes towards the end of the pole that had a removable end. The researchers concluded that the kea rapidity in solving the problem in task one with the first apparatus was not based on a full causal understanding of the problem. They suggested that a lack of visual functional characteristics had impeded subject's ability to transfer knowledge about what they learnt. Thus, despite their success in task one which still highlights kea's impressive problem solving skills, they failed to transfer their knowledge about what they had learnt in task one to task two (Gajdon et al., 2013).

Another important factor in successful problem solving is behavioural flexibility. O'Hara, Huber and Gajdon examined this in kea by using a reversal learning paradigm. Reversal learning typically requires subjects to learn the rewards that are associated with either solid objects or images on a touchscreen. Once subjects have learnt these contingencies, the contingencies are swapped. The number of trials it takes for subjects to adjust their behaviour are then compared to the results from other species. Kea were presented with a standard reversal learning task using both solid objects and a touchscreen. They found that kea required significantly more trials to reach acquisition and reversal learning using touchscreen compared to solid objects. They concluded that discrimination of solid objects is easier for kea and care must be taken in future studies when comparing results that use two different learning approaches such as comparing the results from a study that uses a touchscreen to another study that uses solid objects (O'Hara, Huber & Gajdon, 2015). Wein, Gajdon & Schwing investigated whether kea demonstrate picture-object recognition in discrimination transfer tasks. They found that kea were successful in these tasks and this occurred when pictures were on a touchscreen or a photograph. Subjects were also able to transfer knowledge back from objects to the original training photograph. The researchers concluded that kea can transfer knowledge between pictures and objects. However they cautioned that this does not provide evidence for kea possessing internal representations as they may not have seen the pictures as representations of objects but may have just recognised similarities between the two such as shape or colour (Wein, Gajdon & Schwing, 2015). Overall, kea performance in the former studies showcase kea's ability to flexibly modify their behaviour according to the contingencies of a task. Importantly, given that they are not a tool using species in the wild, their success in technical problem solving tasks suggests that tool use may not be a prerequisite for technical intelligence (Bird, Emery & Gallistel, 2009).

1.3.2.2. Social cognition in kea

While technical cognition in kea has been examined, very few studies have been conducted examining social cognition in kea. Tebbich, Taborsky & Winkler (Tebbich, Taborsky & Winkler, 1996) examined the behaviour of kea in a cooperative task. They presented kea with a see saw paradigm which required one kea to sit on one end of the see saw, which then lifted the other end up exposing a reward. They found that dominant individuals aggressively harassed subordinate kea into complying to cooperate. Dominant birds never shared rewards and roles never swapped and were fixed. While this study showed the role of harassment in cooperative tasks and demonstrated that kea could "act together' it did not examine what kea actually understood about cooperation.

Huber Taborsky and Rechberger examined social learning in kea. They allowed 5 naïve subjects to observe a trained conspecific opening a large steel box. The lid of the box had several different locks on it and could only be opened once all locks were appropriately dismantled. The researchers compared the behaviour of the 5 naïve observers to 5 naïve non observers and found that although the observers failed to unlock the box in their first attempts, they explored the box more thoroughly and succeeded in unlocking more of the locks than the non-observers. While the subject's behaviour did not match the demonstrating conspecifics in movement or sequence, that is, they did not imitate the conspecific exactly, they did seem to exhibit some kind of emulation learning. This led the authors to conclude that the subjects had reached some sort of understanding of the task through observation (Huber, Taborsky & Rechberger, 2001). However, these results may be interpreted differently. Kea's propensity to social facilitation could have made the subjects more drawn to box as they had observed other kea interacting with it which made them explore the box more thoroughly and open more locks than non-observing kea simply through trial and error learning.

Gajdon and colleagues (Gajdon et al., 2004) examined social learning in a wild kea population in New Zealand. Subjects had to remove a baited tube from an upright pole. One naïve kea was trained to solve the task so it could then demonstrate how to successfully remove the tube to other kea. They found that only 2 of about 15 birds learnt how to remove the tube, suggesting that wild populations do not transmit foraging techniques and social learning did not seem to take place. This supports previous observational findings that kea do not learn by imitation but through individual trial and error learning (Diamond & Bond, 1999).

Overall, there has been very little research examining social cognition in kea and research investigating the cognitive mechanisms that underpin cooperation in kea is non-existent. It is important to examine social cognition in kea because it not only extends the empirical research on social cognition in kea, but birds in general. The aim of this thesis was to begin exploring cooperative cognition in kea by presenting them with a range of experimental tasks designed to examine different aspects of social cognition.

1.4 Examining cooperative cognition in kea

In this thesis I present the results from a series of studies designed to examine whether kea possess aspects of cooperative cognition. These include, the ability to coordinate actions, understanding the need and the role of the partner, a preference for collaboration, prosocial behaviour and inequity aversion. The contents of each chapter are outlined below.

In **Chapter 2** I presented kea with a series of conditions involving a cooperative problem solving task as this has not been studied in this species. I examined whether kea understood the need for a partner in a cooperative task. Suggestive evidence for this ability has been found in chimpanzees (Melis et al., 2006) and elephants (Plotnik et al., 2011) but not in rooks (Seed et al., 2008) and African Greys (Péron et al., 2011). In another task I examined whether they understood the role of their partner in this task as has been claimed in elephants (Plotnik et al., 2011). I also sought to examine whether kea, like chimpanzees, but not other avian species such as rooks (Seed et al., 2008) and African Greys (Péron et al., 2011) could flexibly alter their behaviour during a cooperative task and discriminate between when they needed a partner and when they did not. In the final condition of this experiment I examined whether, when given the choice, kea preferred to collaborate or work alone. Studies examining whether chimpanzees prefer to work alone or work together have found no preference. In contrast, children exhibit a significant preference to work together (Rekers et al., 2011; Bullinger et al., 2012). Therefore, in this experiment we aimed to investigate whether aspects of cooperative cognition, which have not been demonstrated in birds before, may have evolved convergently in kea.

In **Chapter 3,** I examined whether kea exhibit spontaneous prosocial behaviour towards a conspecific and whether this is increased in contexts where direct reciprocity is possible. We presented subjects with a token exchange paradigm whereby they could exchange one of two differently coloured tokens with the experimenter for a reward. One token was designated the prosocial token which when selected, conferred a reward to both the subject and their partner, while the other token was designated the selfish token which rewarded the subject but not their partner. Evidence of prosocial tendencies in animals has been mixed and to date there has been no evidence of such a preference in birds. This experiment allowed us to test whether kea, a social and cooperative species, exhibited prosocial behaviour and if so whether this behaviour was based on non-contingent reciprocity, which is hypothesised to govern reciprocity in animals as opposed to contingent reciprocity, as seen in humans.

In **Chapter 4**, I examined whether kea possess inequity aversion - a sensitivity to the gains and efforts of another compared to oneself (Fehr and Schmidt 1999). It is hypothesised that inequity evolved alongside cooperation in highly social and cooperative species, in order to maximise the benefits from engaging cooperatively and foster cooperative bonds between nonkin (Brosnan 2010; Brosnan; 2011). I tested inequity aversion in kea with a token exchange paradigm that has been used with other species (Brosnan & de Waal, 2003; 2005). Subjects were presented with a series of conditions which varied the quality and quantity of rewards a subject received in comparison to their partner and also the amount of working effort that was required to receive the reward. Whether other species possess inequity aversion remains inconclusive and evidence of inequity aversion in birds has only been reported in one study with crows and ravens which was tentative at best (Wascher & Bugnyar, 2013). (Brosnan, 2010; Wascher & Bugnyar, 2013).

In **Chapter 5**, I conclude this thesis with a discussion of the findings obtained from each experiment with a particular focus on whether kea demonstrated any evidence that they might possess cooperative cognition. I discuss the wider implications of our findings and what they contribute to the study of comparative cognition. Finally, I suggest some worthwhile areas that future research examining cooperative cognition in kea might explore.

Chapter 2

Kea perform similarly to elephants, chimpanzees and humans across a range of cooperative tasks[1]

Abstract

Cooperation between individuals is one of the defining features of our species. While other animals, such as chimpanzees, elephants, coral trout and rooks also exhibit cooperative behaviours, it is not clear if they think about cooperation in the same way as humans do. In this study I presented kea, a parrot endemic to New Zealand, with a series of tasks designed to assess cooperative cognition. I found that kea were capable of working together, even when they had to wait for their partner for up to 65 seconds. Kea also waited for a partner only when a partner was actually needed to gain food. This is the first demonstration that any non-human animal can wait for over a minute for a cooperative partner, and the first conclusive evidence that any bird species can successfully track when a cooperative partner is required, and when not. Kea did not attend to whether their partner could actually access the apparatus themselves, which may have been due to issues with task demands, but one kea did show a clear preference for working together with other individuals, rather than alone. A preference for collaboration has been shown to be present in humans but absent in chimpanzees. Together these results provide the first evidence that birds can perform at a similar level to chimpanzees and humans across a range of collaborative tasks. This raises the possibility that aspects of the cooperative cognition seen in the primate lineage have evolved convergently in birds.

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[1] Heaney, M., Gray, R.D. & Taylor, A.H (2017) Keas perform similarly to chimpanzees and elephants when solving a collaborative task. *PLos ONE* 12 (2): e1069799. doi: 10. 1371/journal.pone.1069799

2.1 Introduction

Humans are uniquely cooperative (Tomasello, 2014). Researchers claim that this is because cooperation in humans is underpinned by cognitive mechanisms that have enabled them to successfully initiate and sustain cooperation in a variety of different ways and contexts (Melis & Semmann, 2011). These cognitive mechanisms encompass abilities such as coordinating actions with a partner, understanding when collaboration is required, identifying and recruiting the best collaborators as partners and understanding the role that the partner plays (Melis et al., 2006). Over the last two decades a large number of studies have been conducted examining cooperative cognition in other species. This has typically been examined by pairing two animals together who must then coordinate their actions in a task to obtain a reward (Noe, 2006). The results from these studies with capuchins (Mendres & de Waal, 2000), cotton-top tamarins (Cronin et al., 2005; Hauser at al., 2003), spotted hyaenas (Drea & Carter, 2009) and dogs (Ostojić & Clayton, 2015) have demonstrated that these species are capable of coordinating their actions with a partner to achieve a common goal. However, what these species actually understand about cooperation remains unclear.

The most compelling evidence that non-human species have an understanding of how cooperation works comes from studies with chimpanzees (Melis et al., 2006), coral trout (Vail et al., 2014) and elephants (Plotnik et al., 2011). Melis and colleagues (Melis et al., 2006) investigated this in chimpanzees using the 'loose string' paradigm designed by Hirarta & Fuwa, (2007). This paradigm requires a pair of animals to pull both ends of a loose piece of string simultaneously to move a platform containing rewards within reach for both subjects. They tested whether chimpanzees would wait for their partner to arrive before pulling their end of a piece of rope. The arrival of the cooperative partner was delayed in increasing increments from 5, 10, 20 and 30 seconds. At any one delay period subjects had to wait for their partner before pulling for two trials in a row before they could move on to the subsequent longer delay period. Subjects made between 0 and 28 errors. In a later condition Melis and colleagues (2006) reported that when allowed access to a room with a duo platform requiring two individuals to pull it in, chimpanzees would unlock a door that allowed a partner in an adjacent room to enter and help to pull the platform in more often than when they were presented with a solo platform that they could pull in alone. Moreover, when given the option between two potential collaborators, subjects preferred to choose the more effective of the two collaborators. These results suggest that 1) chimpanzees understand when a partner is required and when they are not and 2) that they can also judge the efficacy of different individuals as collaborative partners (Melis et al., 2006). It has also been suggested that coral trout understand when they need a partner and when they do not. In naturalistic hunting situations, coral trout collaborate with moray eels to hunt prey that are hiding in reefs (Vail et al., 2014). Coral trout recruit a collaborator only when needed, such as when prey are hiding in the reef. This suggests that they understand when they need a partner and when they don't. Vail and colleagues (Vail et al., 2014) also reported that coral trout recruit eels that are the most effective collaborators based on past hunting history. Plotnik and colleagues tested cooperation in elephants using the 'loose string' paradigm. They found that elephants were able to wait for the arrival of their partner before pulling for up to 45 seconds. In a no rope condition, whereby the partner's rope was coiled up out of reach, subjects pulled significantly less often (Plotnik et al., 2011). This suggests that not only did elephants understand that their partner must be present, but that they also needed access to the rope for task success. However, it has also been argued that the elephants in this study may have been relying on environmental cues, in particular the combination of seeing the rope in their partner's trunk and feeling the tautness of the rope when held by their partner, rather than particular aspects of social cognition (Seed & Jensen, 2011). Nevertheless, these studies do provide suggestive evidence that chimpanzees, coral trout and elephants, understand both when cooperation is required and the role of the partner.

One key difference that has emerged between chimpanzee and human cooperation is the variation in their motivation to cooperate. Rekers and colleagues presented chimpanzees and children with the task of deciding whether they would prefer to solve a task with a partner or alone when the rewards for both choices were the same. While children strongly preferred to collaborate, chimpanzees did not demonstrate any such preference, leading the authors to suggest that the motivation to collaborate is unique to humans (Rekers et al., 2011). In a similar study with chimpanzees, Bullinger and colleagues found that when given the option to work collaboratively or individually, subjects preferred to work alone. In another task they found that this preference only changed when the rewards were greater for the collaborative option. The authors similarly concluded that chimpanzees are not motivated to collaborate and only show such a preference if it maximises their own individual payoffs (Bullinger et al., 2011). These studies suggest that what makes human cooperative cognition different from that of chimpanzees may be their preference towards working together over working alone.

Understanding the cooperative cognition of species distantly related to humans is crucial if we are to understand the selective pressures that lead to the evolution of an understanding of cooperation. It is also critical before making conclusions on whether specific aspects of cooperative cognition, such as the motivation to cooperate, are unique to humans. Birds, particularly parrots and corvids, are an excellent group to study these questions with, given their evolutionary distance from humans and their performance at a number of tasks requiring physical and social cognition (Emery & Clayton, 2004;

Taylor, 2014; Gajdon et al, 2008; Auersperg et al., 2011a). To date, the performances of this group at cooperative tasks has not been particularly impressive. In collaborative tasks similar to those presented to elephants and chimpanzees, rooks and African Grey parrots did not wait for their partner to arrive before they pulled the string, with the exception of one African Grey, who was able to wait 15 seconds (Seed et al., al 2008; Péron et al., 2011). Both species also showed little evidence of an understanding of whether a partner was required for a particular task or not (Seed et al., 2008; Péron et al., 2011). One African Grey did choose correctly between single and duo apparatuses but was not consistent, given that she subsequently chose a solo apparatus when paired with a different partner. The results of these studies therefore suggest that, while both of these avian species can coordinate their actions simultaneously to obtain a reward, they struggle to wait for their partner and to understand when a partner is required in cooperative tasks. A similar result was also found recently in New Caledonian crows using a stone dropping paradigm. Jelbert and colleagues tested New Caledonian crows in a cooperative stone passing task. While these birds were able to produce behaviour that appeared collaborative in a spontaneous stone passing task, they were unable to switch between using an individual apparatus when a partner was not present, and a collaborative apparatus was the partner was present (Jelbert et al., 2015). Therefore, while New Caledonian crows can produce collaborative behaviour, they showed no evidence of an understanding of cooperation.

It is however important to test other species of birds, particularly those that are highly social and demonstrate cooperative behaviours in the wild, as it is these species that are likely to have evolved cooperative cognition. One such species is the iconic New Zealand parrot, the kea (*Nestor notabilis*). Kea live in complex and dynamic social groups, have an extended period of dependence compared to most other birds and show enhanced social facilitation and play behaviours akin to that seen in mammals (Diamond & Bond, 1999; Bond & Diamond, 2003). Kea exhibit cooperative types of behaviours in the wild such as allopreening and bi-parental care. While kea have performed impressively in a variety of experiments designed to assess their technical cognition (Werdenich & Huber, 2006; Auersperg et al., 2011a), there have been limited studies examining their cooperative cognition and in particular examining their understanding of the role that their partner plays. Tebbich and colleagues presented kea with a see saw task in which two kea had to perform different actions in order to obtain a reward. The reward was placed in a covered box under one end of the see saw and could only be accessed if one kea sat on the opposite end which then lifted the lid off the box and made the reward accessible to only kea at the other end. The authors found that dominant individuals forced the cooperation of the more submissive kea by aggression and harassment and that the dominant kea always obtained the reward, which was never shared (Tebbich et al., 1996). While this study suggested that kea may use social manipulation as a mechanism to force cooperation, the structure of the task made it difficult to examine what kea actually understand about cooperation.

Here, we tested kea in a series of conditions based on the 'loose string' paradigm developed by Hirata & Fuwa, (2007). We presented four kea with a series of five conditions, each designed to examine different aspects of their understanding of cooperation. Experiment 1 examined whether kea could coordinate their actions simultaneously on a cooperative task. Experiment 2 tested whether kea could wait for their partner to be present in order to successfully complete the task by delaying the arrival of the partnering kea in increasing increments similar to past work with elephants and chimpanzees (Plotnik et al., 2011; Melis et al., 2006). Experiment 3 tested whether subjects could flexibly alter their behaviour, depending on whether they needed to work with a partner or not. Experiment 4 tested if kea would attend to whether their partner had access to the rope. In the final experiment we tested if kea had a prosocial bias for cooperation, in that they preferred to work with a partner to gain food, rather than work alone, when the reward for both tasks was the same.

2.2 Method

2.2.1 Ethics Statement

This study was conducted under approval from the University of Auckland animal ethics committee (reference no.001416).

2.2.2 Subjects

We tested four male kea (Neo, Zak, Taz and Kati), aged between one and three years. Neo and Zak formed the first pair and were tested first. Taz was then paired with Zak after Zak had completed testing in all conditions with Neo. Zak served as partner while Taz was the subject for the entirety of testing. Once Taz had finished testing he then served as partner to Kati who played the role of subject for all experimental conditions. Pairs were selected based on their preference for one of two apparatuses and whether they would tolerate the other kea inside the other side of the apparatus at the same time without hostility or conflict. Kati was tested last because we were initially unsure whether he would be able to participate, due to his disability. As a fledgling he was found in the wild by a member of the public with his upper beak completely missing, presumably due to being caught in a stoat trap or removed by gun shot. Kati was taken to Willowbank and cared for in their animal hospital was eventually released into the kea aviary at Willowbank where he is a very involved and dynamic member of the flock. Kea were captive bred at Willowbank Wildlife Reserve in Christchurch with the exception of Kati who was born in the wild and came to Willowbank as a fledgling. None of the subjects had participated in an experiment before, nor had they been trained to do anything that was similar to the tasks involved in this study. Subjects share a large outdoor aviary with nine other kea and were free to come and go from the apparatus at any time. Food and water were available ad libitum within the aviary.

2.2.3 Apparatus and general set up initial training

Subjects were trained and tested in a wooden apparatus (150cm x 50cm x 100 cm). The apparatus had a wooden frame covered in chicken wire enabling subjects to see each other but not interfere with their partner's behaviour. The top of the apparatus was not covered so that subjects did not feel trapped or restricted and could exit the apparatus at any point. The apparatus could be entered at two separate entry points at opposite ends of the apparatus. Once inside neither kea could gain access to the other kea side as the apparatus was divided down the middle with a permanent wire partition. Platforms with rewards were placed just outside the wire partition in the middle of the apparatus. Rewards could be retrieved by pulling both ends of a piece of rope attached to a platform. Platforms would then slide under a small gap at the bottom of the apparatus.

Platforms (20 cm x 15 cm) were made of wood and had a bottle top glued to each side in which rewards could be placed for each kea. A piece of rope (45 cm) was threaded through two loopholes on the back left and right hand corner of the platforms. A knot was tied 10 cm from the end of each end of rope so that if one kea pulled one end of the rope, the platform would get jammed. Platforms were placed between two small pieces of wood attached to the apparatus. This meant that if a kea only pulled one end of the rope, the platform would get stuck and could not be pulled in. It also meant that the kea could not pull the piece of rope out of the platform and leave the apparatus with it. To keep birds out of the apparatus when the experimenter was setting up or for experimental purposes, a wooden partition was placed just in front of each entry point of the apparatus. Kea would wait on perches behind each partition and partitions were inserted and removed by simply sliding them horizontally in and out. Kea received between half to one piece of Hills a Science Diet during each training and experimental trial. For experiments 1 - 3 only one side of the apparatus was used. The apparatus was enlarged and modified for Experiments 4 - 6 as they required subjects to choose between two platforms on either side of the apparatus. For this, the apparatus was simply doubled in size with the new side mirroring the existing side. Data was coded from a Panasonic 3MOs camera which was attached to a tripod overlooking the apparatuses beside the experimenter. Data was also manually recorded at the time of testing by an experimenter or research assistant who was not involved in testing at that time.

2.2.4 General Procedure

2.2.4.1. Familiarization and training

Kea were first habituated to entering the apparatus, walking to the end and receiving a reward from the experimenter under the small gap that the platform was placed behind. Each bird was then trained to pull both ends of the rope attached to the platform so that an individual bird could pull in the platform alone (solo apparatus). Training to pull the platform in individually involved four stages. In the first stage both ends of rope overlapped, in the second stage they were placed 1 cm apart and in the third and fourth stages they were placed 3 cm and 6 cm apart respectively, as in past studies (Seed et al., 2008). Once subjects achieved 3 successful trials in a row they moved on to the next stage. Three errors at one stage meant that birds moved back to the previous stage. Training ended once each bird successfully completed stage four. The solo platform used for Kati differed slightly in that he could pull in both ends of rope tied together. Due to him missing his upper mandible he was not able to gather up two pieces of separated rope. After birds completed stage four they were then trained to wait on a perch attached to the apparatus behind a wooden partition while their partner waited behind a partition on the other end of the apparatus. Once the partition was removed, subjects could enter the apparatus. Once both birds waited behind the apparatus for 5 trials in a row they moved on to testing.

2.2.5 Specific Procedure

2.2.5.1. Experiment 1: Simultaneous release.

Following familiarization and training, both dyads were tested in a cooperation test. This experiment examined whether kea can work together by performing the same action simultaneously. The platform was placed out of reach of both subjects with one end of the rope available to each bird. The ends of the rope were 30cm apart and subjects had to wait to be released behind the wooden partitions. Partitions were removed and both birds were released into the apparatus simultaneously. Pairs received up to two sessions a day consisting of 20 trials in each session. Testing continued until each pair successfully pulled in the platform in 90% or more of trials in one session (18/20 trials).

2.2.5.2. Experiment 2: delayed partner arrival.

Experiment 2 was identical to Experiment 1 except that the arrival of the partner was delayed. This experiment assessed whether kea understood that their partner had to be present to successfully complete the task. This experiment had two conditions:

Condition A: Partner arrival started out being delayed between one and two seconds. Once birds had individually succeeded in waiting for this delay period for three successive trials the delay period was increased to 5 seconds. This increased by 5 second increments until each bird was successful at waiting for their partner for 25s for three successive trials. This shaping procedure was similar to that used in similar tasks with elephants (Plotnik et al., 2011) and chimpanzees (Melis et al., 2006). Three successive failures at a given delay period meant that birds regressed back to the previous shorter delay period. Each bird was tested in sessions consisting of blocks of 10 trials as the focal bird for up to 5 sessions a day. Testing ended once a subject completed three successive trials at 25 seconds.

Condition B: Following this the same subjects were tested in 6 randomized partner delay sessions consisting of 10 trials per session. This procedure was similar to the one used by Plotnik et al., (2011) with elephants, except that we extended the maximum partner delay time by 20 seconds. Each block of ten trials included three trials of partner delays ranging between 0 - 25 seconds, three trials consisting of previously unexperienced delays ranging between 26 - 45 seconds and 4 trials of unexperienced delays ranging between 46-¬65 seconds.

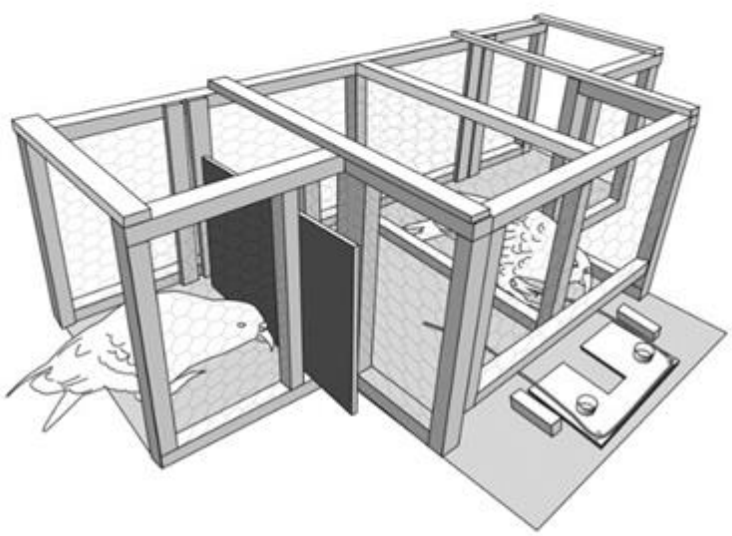

Figure 2.1: Drawing showing experimental setup for the delayed partner arrival conditions. Subject is presented with the duo platform. One end of the string is on the subject's side and the other end is on the partner's side. This can only be pulled in with the help of their partner. Drawing by Vivian Ward.

2.2.5.3. Experiment 3: Discriminating between solo and duo platforms

As pointed out by previous research on animals using the loose string paradigm (Plotnik et al., 2011; Seed et al., 2008), success at the simultaneous release task can be explained by individual action scaffolded by the structure of the task itself, while success at the delay tasks can be explained by the learning of a combination of cues, such as seeing a partner while feeling tension on the rope (Seed & Jensen, 2011). To date, only one study has shown that an animal is able to flexibly alter is behaviour depending on whether cooperation is necessary or not. Melis et al (2006) showed chimpanzees would choose to allow a partner to enter a testing room more often when presented with an apparatus that required two individuals to solve it compared to when they could solve it by themselves (Melis et al., 2006). In contrast studies with rooks (Seed et al., 2008) and African Grey parrots (Péron et al., 2011) have shown that birds typically fail to behave flexibly when presented with situations where cooperation either is, or is not required. In Experiment 3 we created a similar situation to Melis and colleagues (2006): we presented either the duo or solo apparatus to subjects in a randomised order, and looked to see whether they would flexibly alter whether they waited for a partner to arrive before pulling the string, depending on trial type. Experiment 3 was comprised of an assessment phase and a test phase, as described below:

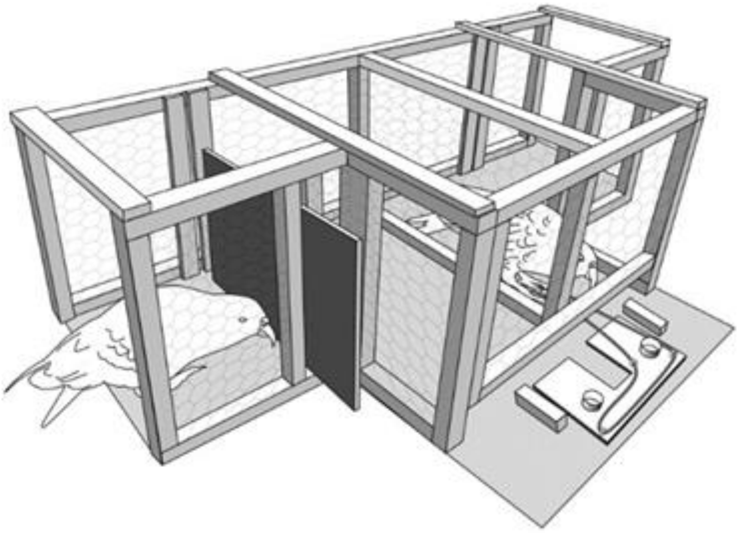

Figure 2.2: Drawing of solo condition that was presented to subjects in randomized order with the duo condition (Figure 2.1**Error! Reference source not found.**) in experiment 3. In the solo condition, both ends of the string were available to the subject allowing the platform to be pulled in without the help of a partner. Drawing by Vivian Ward.

Assessment task: In order to run Experiment 3 we needed a delay period for the arrival of the partner that was sufficient for each bird to solve the solo condition, but not too long as to lead to the task becoming a test of inhibitory control, rather than cooperative cognition. We therefore set the delay period for each individual based on their performance at two assessment tasks. The first assessment task examined how long it took each bird to solve the solo condition. We gave birds 5 trials of the solo rope pulling condition, where the rope ends were placed 1cm apart without a partner present in the apparatus and recorded the average time taken to solve the task for each kea. The second assessment task checked each kea could inhibit pulling the string consistently when a partner took the time to solve the solo condition plus 3 additional second. Subjects therefore received 5 delay trials where they had to wait for their partner for the average time it took them to solve the solo condition and an additional three seconds. If subjects did not solve these two tasks in their first 5 trials, testing continued until each kea successfully pulled the platform in for 5 consecutive trials of each condition.

Test: Kea were presented with the same platform used in previous experiments. However, the platform was presented as either the solo condition (both ropes available to focal kea) (Fig.2.2) or the duo condition (one piece of rope available to the focal kea and their partner) (Fig.2.1). The arrival of the partnering kea was delayed in every trial. The delay time was determined by ascertaining how long on average it took each subject to successfully solve the solo condition with an added 3s. Thus, kea had to choose between pulling the rope available immediately and waiting for their partner. Subjects received 10 trials a day for two days as the focal bird. The presentation order of the solo and duo platform conditions was pseudo-randomized across trials.

2.2.5.4. Experiment 4: No rope control.

I presented the kea with the choice of pulling an apparatus where their partner had access to a rope on the other side of the loose string apparatus, or one where the rope on the partner's side was coiled and therefore out of reach, as in (Plotnik et al., 2011).

Training: A training stage was necessary before beginning Experiment 4 as it required subjects to learn to open a Perspex door. Stage one involved the kea individually entering the apparatus and retrieving a reward that was placed under the gap where the platform was usually accessed on either their left or their right hand side. The sides that the rewards were on were randomised. Kea moved to stage two once they had chosen the correct side for four trials in a row. Stage 2 was the same as stage one except that Perspex doors were placed on both sides of the apparatus. Kea had choose the correct door to slide open and access the reward. Birds moved on to testing after completing four successful trials in a row.

Test: Testing began with both kea waiting behind the wooden partitions. The focal kea was let in first. A platform with ropes available to both kea was placed on one side of the apparatus. An identical platform was placed on the other side of the apparatus except that while the focal kea's rope was accessible the partnering kea's rope was coiled up and out of reach. To access either of the platforms the focal kea had to open a Perspex door. There were no Perspex doors on the partnering kea's side. Once the focal kea had made a choice by beginning to open a door, the partnering kea was let in. The partnering kea was let in after the subject to prevent the partnering kea from cuing the subject towards the platform with the partner's rope available. The rationale behind having the subject open the Perspex doors was that it was a way to clearly signal which platform the subject had chosen so that the experimenter could then let the partner in. The sides that each platform was presented on was randomised and counterbalanced as was the position of the two experimenters. Kea were not able to access the other platform once they had made their choice. Subjects received two sessions consisting of 10 trials each as the focal bird.

2.2.5.5. Experiment 5: Solo vs. Duo preference test.

Past work has shown that human children, but not chimpanzees are motivated to work together, rather than work alone for the same rewards (Rekers et al., 2011). We presented kea with a task that examined if they had a similar preference for working together.

Training: Kea received a brief pre training stage to preclude a possible side bias that may have developed for some subjects in Experiment 4. Two Perspex doors were set up on both the left and right hand side of the apparatus. Only one door had a reward behind it. Subjects were required to enter the apparatus and choose to slide a door on either their left or the right hand side. Training was done with a partner present. The side that the rewards were on were randomised and during half of the trials both the subject and partners rewards were on the same side and on the other half of trials rewards were on opposite side of their partner. This was done to rule out not only a bias to always choosing one side but also to rule out a bias towards going to the same or opposing side as their partner. Training stopped for each kea once they completed a minimum of 9/10 successful trials in a row.

Test: Experiment 5 was based on a study conducted by (Rekers et al., 2011) with chimpanzees. It tested whether kea preferred to work alone (solo platform) or with a partner (duo platform) when rewards for both kea were the same on both platforms. Subjects had to choose between two platforms presented on opposite sides of the apparatus. One was a solo platform that could be pulled in individually on the focal kea's side and the other was a duo platform that required the cooperation of a partner. The partnering kea was let into the apparatus first. To encourage the partnering kea to stand in front of the duo platform a wooden partition was placed over the partnering kea side that the solo platform was on so that the rewards contained on the solo platform were not visible to this kea. Both rewards were of course visible to the focal kea. While the solo platform and rewards no were not visible to the partnering kea, if the focal kea chose to pull in the solo platform the partnering kea still received the reward through a gap between the bottom of the apparatus and the partition. When the partner was standing in front of the duo platform the focal kea was let in. Once the focal kea had chosen a platform and both kea had accessed the reward the partitions at the entry points of the apparatus were put in to prevent subjects from accessing the other platform. Both the focal kea and partner received equal rewards from both platforms. Each subject received one block of 10 trials for 2 days and they did not alternate roles until testing for the first kea was completed.

2.3 Results

See Appendix 1 for video example trials from experiments.

2.3.1 Results from each experiment

2.3.1.1. Training to pull in the solo apparatus

It took Neo four sessions (each session consisted of 20 trials) to complete stage four of training. Zak reached criterion after 7 sessions, Taz after 5 sessions and Kati after 9.

2.3.1.2. Experiment 1: Simultaneous Release

Neo and Zak reached the desired criterion on their first session of 20 trials, making only two errors. Taz and Zak scored 20/20 in session two, making a total of 5 errors in 40 trials. Kati and Taz reached criterion after three sessions, making a total of 8 errors over 60 trials.

2.3.1.3. Experiment 2: Delayed partner arrival

All 4 kea learnt to wait for their partner in the delayed partner arrival condition (Condition A) (Mean ± SD number of trials to reach criterion across all subjects = 97.25 trials ± 35.49). Subjects made between 13 and 49 errors during this condition ($\bar{x}$ =38, *SE* = 16.79). In comparison, elephants made between 3-12 errors and chimpanzees made between 0-28 errors in a similar task. The performance of Neo at this task is therefore particularly impressive as he made only 13 errors, well within the range seen for chimpanzees and only just outside of that seen in elephants. For individual performance data see Appendix 2: Table A.1.

When presented with randomized partner delays of between 1-65secs (Condition B), subjects were successful between 75% and 92% of the time ($\bar{x}$ = 84, *SE* 7.41%) (Fig.2.3). For the previously unexperienced delay periods ranging from between 26-65s all subjects were very successful at waiting for their partner's arrival. This ranged from a success rate between 74% to 91 % ($\bar{x}$ = 83, *SD* = 7.10%) (Fig 2.3). Elephants were successful at waiting for their partner across the 60 trials in the randomised condition between 88% and 97% of the time, though elephants only had to wait up to 45 seconds ($\bar{x}$ = 93.33, *SD* = 3.72%). For individual performance data see Appendix 2: Table A.2 and A.3.

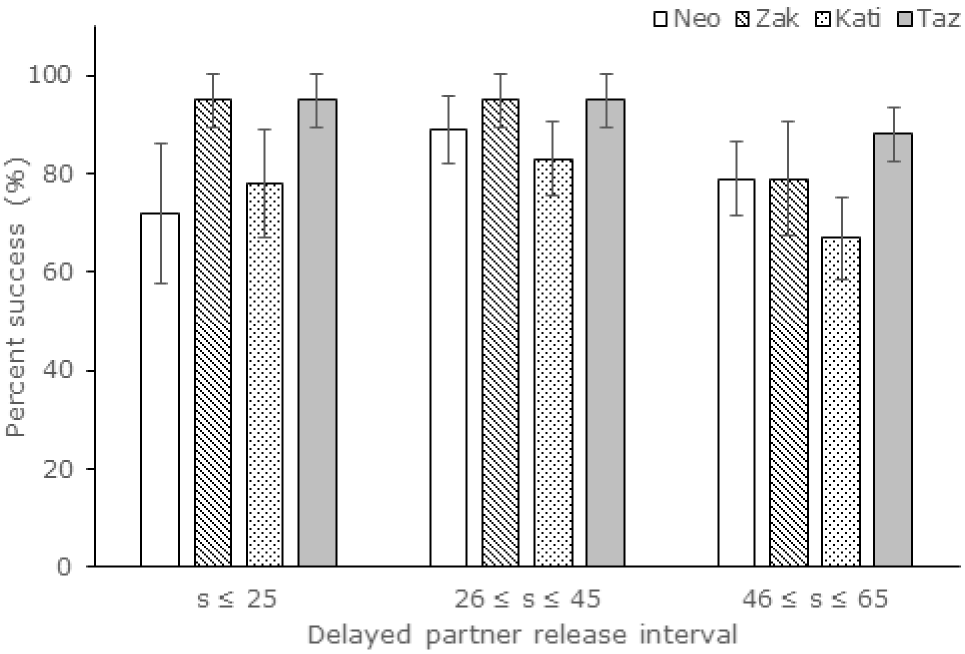

Figure 2.3: Bar graph depicting success rates of subjects in the randomised condition for previously experienced partner delay intervals (≤ 25s) and unexperienced intervals (26 ≤ s ≤45 and 46 ≤ s ≤ 65). Error bars represent ± SEM.

2.3.1.4. Experiment 3: Discriminating between solo and duo platforms

In training Taz was successful in his first block of 10 assessment trials. Kati took two blocks, Zak three blocks and Neo four blocks. Kea made the correct choice between 100% and 70% of the time (Fig.2.4). Individually, three out of four subjects successfully demonstrated that they could discriminate between the solo and duo platforms at a significant level. Taz (Binomial choice 20/20 trials $p = < 0.001$), Kati (15/20 trials $p = 0.044$) and Zac (15/20 trials $p = 0.044$). The only kea not to show a significant performance across both blocks, Neo (Binomial choice 14/20 trials $p = 0.116$), chose correctly in 5 out of 10 trials in block one and then 9/10 trials in block two. All four subjects selected the correct course of action on the first trial of their first session. The performance of Taz in particular is of note as selected the correct course of action in 20 out of 20 trials. For individual performance data see Appendix 2: Tables A.4 and A.5.

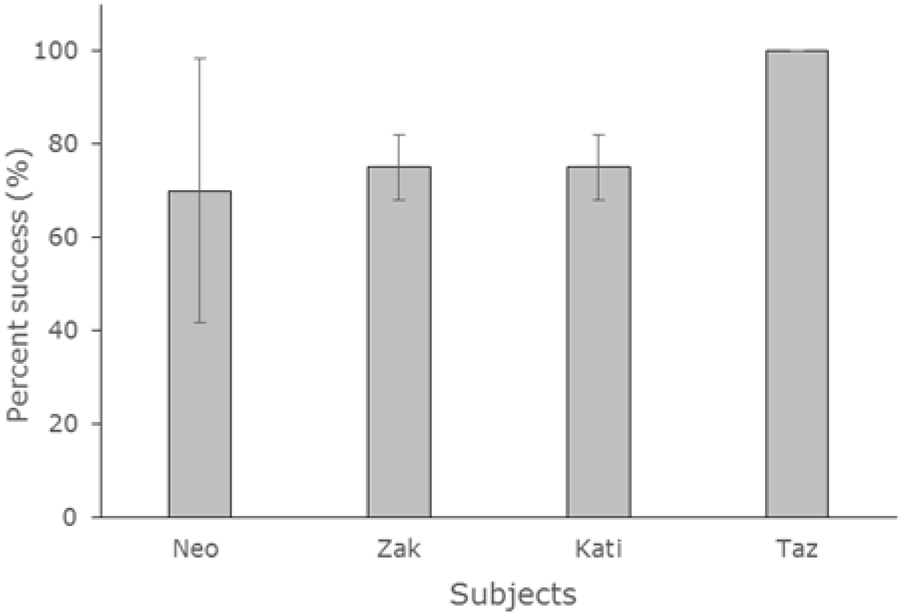

Figure 2.4: Bar graph representing subject's success at discriminating between the solo and duo platforms across both sessions. Error bars represent ± SEM.

2.3.1.5. Experiment 4: No rope control

No subject was successful at discriminating between a duo platform with both ends of rope available to both kea and a duo platform with the partner's rope coiled out of (Neo, binomial choice 9/20 trials p = 0.826; Zak, binomial choice 9/20 trials *p* = 0.826; Kati, binomial choice 10/20 trials, *p* = 0.5 and Taz, binomial choice 14/20 trials *p* = 0.116). Success at this task ranged between 45% and 70% ($\bar{x}$ = 53, *SD* = 11.90). This suggests that subjects either did not attend to their partner needing access to the rope, or that they did not understand the requirements of the task. It should be noted that while Taz's performance in this condition was not significant, he did outperform the other kea as he did in Experiment 3. For individual performance data see Appendix 2: Tables A.6 and A.7.

2.3.1.6. Experiment 5: Solo vs. Duo preference test

Individually, only one kea, Neo, showed a significant preference for the duo apparatus (Binomial choice 16/20 trials *p*= 0.014). We tested Neo again with a different partner to see if this preference was stable and he again showed a significant preference to work together for food, rather than alone (Binomial choice 16/20 trials *p* =0.014).Subjects selected the duo platform between 35% and 80% of trials ($\bar{x}$ = 56, *SD* = 18.43%). For individual performance data see Appendix 2: Tables A.8 and A.9.

2.3.2 Discussion of possible order effects

For dyad 1 (Neo and Zak), for all experiments, except Experiment 1 in which both kea served as subjects simultaneously, one kea played the role of subject and one played the role of partner until testing was finished for that experiment. The roles were then reversed. We assessed whether there were any order effects present due to the kea who went second as the subject in this dyad learning from observing the naive kea who played the role of subject in the experiment first. We found no evidence of any order effects. In Experiment 2, Neo served as subject first and reached criterion after 45 trials while his partner Zak reached criterion after 108 trials. For Experiment 3 Neo served as subject first and was successful in 70% of trials while Zak was successful in 75% of trials. No subject chose the correct platform in a significant amount of trials in Experiment 4 and in Experiment 5, Neo, who was the only subject who had a significant preference for collaboration served as subject second in both dyads.

2.4 Discussion

All subjects could coordinate their actions simultaneously with their partner to access the reward. In the delay condition all subjects reached the 25s delayed partner arrival criterion, with one subject performing on par with some elephants and chimpanzees (Plotnik et al., 2011; Melis et al., 2006). In the randomised delay condition all subjects were able to wait for delay periods of up to 65s. This is the longest delay period that any known non-human species has demonstrated that they are capable of waiting for the arrival of a cooperative partner. In the solo/duo platform discrimination condition all subjects were successful in differentiating between when they needed to wait for their partner to pull, and when they did not have to wait for their partner because they could pull in the solo platform by themselves. Therefore, kea performed similarly to chimpanzees who were also able to differentiate between when they needed a partner and when they did not (Melis et al., 2006). In the no rope condition, no subject had a preference for the platform in which their partner's rope was within reach. Finally, in the solo/duo apparatus choice condition only one subject demonstrated a significant preference for collaboration over working alone, while all other subjects had no preference for either option. Overall, kea outperformed other species of birds such as African Greys and rooks who were unsuccessful at waiting for their partner in delayed partner arrival conditions and did not seem capable of differentiating between solo and duo apparatuses (Seed et al., 2008; Péron et al., 2011).

As has been suggested in the past, simultaneously pulling the string, as in Experiment 1 may have occurred simply because subjects were released at the same time. However, the small number of errors made by kea in the shaping session of Experiment 2, particularly by Neo who made only 13 errors, is not only comparable to the number of errors made by chimpanzees and elephants, but also suggests that kea may have had some understanding of the task, given that they learnt so quickly to wait. The ability of kea to transfer to waiting for up to 65 seconds is highly impressive. This delay period is 20s longer than the longest delay period tested with elephants, and 35 second longer than that presented to chimpanzees. Clearly, kea have excellent inhibitory control, despite their small absolute brain size.

In Experiment 2 kea had been rewarded for waiting until a partner had arrived before pulling the string. If they were using only associative learning to solve this task, they should have formed such as “only pull when a partner is present”, or “pull when a partner is present and there is tension on the rope” (Seed & Jensen, 2011). Experiment 3 directly tested this possibility by examining how kea reacted when they had to choose between waiting for a partner and immediately pulling the string, depending on the set-up of the apparatus. Kea clearly did not use the above associative rules: they pulled, rather than waited, when there was no partner, and no tension on the rope in the solo condition but did wait when there was no partner, and no tension on the rope, in the duo condition. The ability to flexibly alter cooperative behaviour depending on two factors, the presence of a partner and whether cooperation is required, is critical for effective cooperation. Only chimpanzees, and coral trout (in natural foraging situation) have been shown to flexibly alter their behaviours in this way (Melis et al., 2006; Vail et al., 2014). Birds such as African Grey parrots (Péron et al., 2011) and rooks (Seed et al., 2008) have typically failed at these tasks. While kea had had experience with both the solo and duo apparatus before, they had not been presented with a choice between waiting for a partner and pulling the rope. To find kea flexibly alter their behaviour on a trial by trial basis strongly suggests they had an understanding of how each apparatus worked and thus of when they did and did not need a partner. However, as with work on chimpanzees and elephants, the use of associative rules remains a possibility. For example, kea might have been relying on a learnt rule such as “two strings on own side pull, one string wait and pull when partition is removed”. It is possible that they were able to implement this rule, even after long testing periods with only the duo platform, because of their ability to learn associative cues rapidly.

In Experiment 4 (the no rope condition) kea did not have a preference for either the platform where their partner’s rope was within reach or the platform where it was coiled up out of reach. One interpretation of this result, is that while the kea did have an understanding of when they needed a partner (as seen in Experiment 2), they did not have a clear idea of the role their partner played, in terms of interacting with the rope. However, the kea failure to differentiate between platforms in this condition may be due to other factors such as limitations or difficulties in shifting their attention to their partner’s string, or a lack of understanding and attentiveness to the connectivity of the string. Without a comprehension of connectivity or attention towards their partner’s string, they may have assumed that their partner’s string was accessible to them even when it was out of reach. This task was also rather complicated, as it required subjects to learn new behaviours such as opening Perspex doors and then choosing between two platforms placed on opposite sides of the apparatus. This complexity also could have hindered performance. Finally, it is not yet clear if any animal has passed the no rope condition due to an understanding of connectivity. While Plotnik and colleagues (Plotnik et al., 2011) demonstrated that elephants would pull the rope less often if their partner’s rope was out of reach, in their experiment, the subject and partner were released simultaneously. It is possible that elephant subjects pulled less in the no rope condition because they were cued by their partner’s behaviour, such as a delay or reluctance to approach the platform, or their partner’s reaction once they reached the platform. Similarly, elephants may have been relying on other cues such as a feeling of tautness on the rope before pulling or seeing the rope in their partner’s trunk rather than paying attention to whether their partner had access to it (Seed & Jensen, 2011). These issues highlight that the performance of kea in this condition should be interpreted with caution.

In Experiment 5 (solo/duo apparatus choice condition), three out of four kea did not have a preference for working alone or together with a partner. This is consistent with similar studies conducted with chimpanzees (Rekers et al 2011; Bullinger et al 2012). However, in a highly surprising result, one kea, Neo, did prefer to work with both a related and un-related kea, rather than solve a task on his own, despite receiving no additional material benefit from cooperating. Neo’s behaviour suggests that at least one non-human animal might have an intrinsic motivation to cooperative.

I did not deliberately examine whether kea could use information about the effectiveness of individual kea as partners, as has been done with chimps, however I did note some interesting behaviours in this regard. In particular, a kea called Taz was paired with Kati. As discussed, Kati lost his upper mandible in an accident as a fledgling and his performance in tasks was significantly slower than other kea and it would often take him some time to pick the rope up and then to pull it in. While the other pair would rapidly pick up their respective ends of the string, and pull when the partner was present without any apparent observation of their partner, Kati’s partner Taz would wait for Kati to pick up the string and then wait for him to start pulling before he started. Indeed, Taz outperformed other kea in the randomised delay task and the solo/duo apparatus choice test. Interestingly, although he did not perform at a significant level of performance in the no rope condition, he did outperform the other kea reaching a success rate of 70%. Taz’s behaviour highlights that investigating if at least some kea are sensitive to the abilities and weaknesses of others might be an area worth exploring in further experiments. There was also considerable variation between the individual performances of the kea. As noted, Neo outperformed the other kea in the first delay condition of Experiment 2. He was also the only kea to show a significant preference for working together over working alone in Experiment 5. Similarly, Taz outperformed the other subjects in the randomised delay condition in Experiment 2, Experiment 3 and Experiment 4. This suggests that particular individuals may attend to different aspects of cooperative tasks, possess a greater aptitude for tasks that require mechanisms such as inhibitory control, or be more highly motivated to solve tasks in a social setting.

Before kea are deemed superior to other avian species in regards to their performance, it is important to note that the success of kea in the first delay condition required a learning phase, as it did to varying degrees with elephants and chimpanzees. Studies with rooks (Seed et al., 2008) and African Grey parrots (Péron et al., 2011) did not employ a shaping procedure and it would be worthwhile testing these species again using this procedure before they are deemed incapable of understanding the need of having their partner present. Overall, these findings suggest that it is possible that aspects of cooperative cognition, possessed by humans and other species such as chimpanzees, may have evolved convergently in kea. However, further research is required to confirm this.

Chapter 3

Testing prosociality in kea

Abstract

Kea (Nestor notabilis) were presented with a series of conditions designed to examine whether they exhibit prosocial tendencies and in particular, reciprocity. Two out of four kea had an initial preference for the prosocial token which rewarded both themselves and a partner. While prosocial token preference did increase for three out of four kea when they alternated taking turns with a partner, it did not decrease in a subsequent control condition in which the experimenter replicated the token choice made by the partner in the previous alternating trials. Finally, prosocial token choice only decreased for two kea and actually increased for one in an asocial control condition where no partner was present. I found no evidence of reciprocity in kea and at present, it remains unclear whether two of the four kea exhibited spontaneous prosocial choice in condition 1, or if this preference was attributable to other factors. Due to our small subject pool and subject's prior inexperience with token exchange paradigms, further research needs to be undertaken before conclusions can be made about whether the selective pressures faced by kea facilitated the evolution of prosociality in this species.

3.1 Introduction

Prosocial behaviour, whereby an individual confers benefits to another at no cost to themselves is ubiquitous in humans and is likely to have played a role in the evolution of human cooperative behaviour (Amici et al., 2014; Horner et al., 2011). Animals also demonstrate behaviours indicative of prosocial tendencies in naturalistic settings, such as mutual grooming, sharing food, assistance in conflict and cooperative hunting (de Waal et al., 1997; Koyama et al., 2006; Schino, 2007). Prosociality in animals has typically been examined using two different paradigms, the Giving Assistance Test (GAT) and the Prosocial Choice Test (PCT). In the GAT subjects must decide between giving instrumental help to another and doing nothing. GAT studies with chimpanzees have demonstrated that chimpanzees were willing to provide assistance to a conspecific by giving a conspecific a tool they required to access a reward (Yamamoto et al., 2009; Yamamoto et al., 2012), unlocking a door that prevented a partner from accessing a food reward (Warneken et al., 2007), releasing food so it could be reached by a conspecific (Melis et al., 2011) and pulling a handle that helped the conspecific access the reward (Greenberg et al., 2012).

In PCT tasks subjects must choose between two options, a selfish option (1/0) which only yields a reward for the subject and a prosocial option (1/1) that yields a reward for both subject and partner. For the most, PCT tasks have examined prosociality in animals using tokens or platforms (Amici et al., 2014). In platform tasks, subjects can choose between either a prosocial platform containing rewards for both subject and partner or a selfish platform which only contains rewards for the subject (Amici et al., 2014). Similarly, token tasks typically require subjects to choose between two tokens, one selfish and one prosocial. Selection of the selfish token only confers a reward to the subject, whereas selection of the prosocial token confers a reward to both subject and their partner. Prosociality studies with chimpanzees using platform tasks have found little evidence of other regarding preferences in chimpanzees (Silk, 2005; Jensen et al., 2006; Vonk et al., 2008). In similar platform tasks, Cronin et al., (2009) and Stevens (2010) reported that cottontop tamarins did not behave prosocially towards group members, including long-term mates. In contrast, platform studies with long tailed macaques (Massen et al., 2011) and capuchin monkeys (Lakshiminarayanan et al., 2008; Takimoto, Kuroshima & Fujita, 2010) reported that these species were sensitive to the outcomes received by others.

One of the first token exchange paradigms examining prosocial behaviour in animals was conducted by de Waal and colleagues (de Waal et al., 2008) in capuchins. They found that capuchins had a significant preference for the prosocial token and concluded that capuchins possessed other regarding preferences. However, this study was subsequently criticized for a number of reasons (House, et al., 2014; Jensen et al., 2006; Amici et al., 2014). Firstly, subjects were only required to choose between one of two tokens and so it was argued that the presence of only two possible choices might create a bias for a particular token. Furthermore, this study did not have any control conditions such as a partner absent condition. This made it impossible to discern whether the capuchin's preference for the prosocial token was motivated by a prosocial preference or simply a preference for the token that conferred more visible rewards (Amici et al., 2014). Finally, rewards were always visible to both participants which may have masked prosocial tendencies and fostered competitive and selfish attitudes by subjects towards partners (Horner et al., 2011; Amici et al., 2014).

Horner et al., (2011) examined prosociality in chimpanzees with a token exchange experiment designed to avoid some of methodological pitfalls present in the capuchin study by de Waal et al., (2008) and other prosociality experiments (Massen et al., 2010). Rather than presenting chimpanzees with only two tokens at a time to choose from, Horner et al., (2011) presented subjects with 30 tokens in a bucket, 15 of each colour and did not make rewards were visible to both subject and partner. This study also presented subjects with partner-absent control conditions. Chimpanzees chose the prosocial token significantly more than the selfish token suggesting that, similar to the results found in previous GAT studies, chimpanzees may have other regarding preferences.

Based on the study conducted by Horner and colleagues (Horner et al., 2011), Suchak and de Waal investigated prosociality in capuchin monkeys. Previous studies with capuchins have already suggested that they possess prosocial tendencies (de Waal et al., 2008; Lakshiminarayanan et al., 2008; Takimoto et al., 2010) and the authors sought to investigate if this increased when subjects took turns and whether this increase might be based on contingent, or non-contingent reciprocity (Suchak & de Waal, 2012). Their study included two new conditions, an alternating turns condition and a yoked control condition, which was designed to assess whether an increase in prosocial preference in the alternating turns condition was due to prosocial behaviour or simply due to the rewards conferred by the prosocial token. These conditions allowed researchers to directly test whether capuchins, like humans, demonstrate contingent reciprocity, which requires a repertoire of cognitive skills such as skills of memory, temporal discounting and numerical discrimination (Stevens et al., 2005; Stevens & Hauser, 2004). Suchak and de Waal found that the capuchins prosocial tendencies increased significantly when they alternated taking turns with their partner. However, token choice was not contingent upon the choice that their partner had made in the previous trial, suggesting subject's choices were not based on some sort of tit for tat mental scorekeeping scenario like contingent reciprocity. The authors suggested that situations that involve joint action enhance prosociality in capuchins and that subjects could produce outcomes similar to that produced by contingent reciprocity through non-contingent reciprocity, without possessing the complex cognitive mechanisms required for contingent reciprocity (Suchak & de Waal, 2012).

While most research on prosociality in other species has been conducted in primates, it is also important to study prosociality in distantly related species as it allows us to examine whether prosociality can evolve through convergent cognition in unrelated species and so discover what selective pressures might be responsible for its evolution (Smith et al., 2003). That is, by examining the similarities and differences between the prosocial behaviour of distantly related species comparative psychologist can test hypotheses about the selective pressures that may lead to its emergence. In turn, this may bring us closer to understanding the emergence of prosociality in humans.

Birds, particularly parrots and corvids, are excellent distantly related species to examine whether they exhibit prosocial tendencies. They both live in social groups, have extended periods of parental dependence and have large forebrains relative to their size (Emery, 2005; Bond & Diamond, 2003). At present, there is a paucity of studies exploring prosociality in avian subjects and the limited number that have been conducted have found little evidence of other regarding preferences in birds. Péron et al., (2013) examined sharing and reciprocity in two African Grey parrots over two Experiments. In Experiment 1 subjects were presented with four differently coloured cups, a sharing cup which contained a reward for both subject and partner, a giving cup which contained a reward that was given to the partner not the subject, a null cup which contained no reward for both subject and partner, and a selfish cup which contained only a reward for the subject. Birds alternated taking turns at choosing a cup. If subjects understood reciprocity then it would be expected that they would choose the sharing cup considerably more often as this would maximise rewards for both birds. However, the authors found that subjects had no preference for the sharing cup and therefore did not seem to understand reciprocity. In Experiment 2 subjects were paired with 3 different human experimenters. One experimenter always chose the selfish cup, one always chose the giving cup and one copied the choice that had previously been made by the subject. This experiment examined whether a partner acting consistently in a given way (giving or selfish) might in turn shape the choices made by the subject. It also sought to examine whether birds were capable of understanding whether their partner was copying or mirroring their previous choice and would adjust their behaviour accordingly. While subject 1 did not behave consistently in any of the sessions, bird 2 demonstrated a trend for choosing the sharing cup when paired with an experimenter that always chose the giving cup. The authors suggest that this behaviour might be based on ensuring that he could both reward his partner for giving while receiving the maximum number of rewards himself. Therefore, this subject may have an understanding of sharing and reciprocity. However, this finding needs to be interpreted cautiously as the results from this part of the study were not statistically analysed due to their being only two subjects. Results were discussed in the context of trends that emerged as opposed to statistical findings.

Di Lascio and colleagues, examined other regarding preferences in 5 ravens. In the first task, subjects were presented with two boxes, one which when opened contained a reward for both themselves and a conspecific and the other that once opened only rewarded the subject. Researchers found no evidence of other regarding preferences in ravens using this classic paradigm. In a second task, the ravens played a no-cost cooperation game with the experimenter. The set up was the same as the first task in that ravens had access to the same two boxes, except that the experimenter also had access to two identical boxes on their side of the apparatus, a selfish box that when opened rewarded only themselves and a prosocial box which rewarded both themselves and the raven subject. In this task the experimenter matched the choice made by the subject. Thus, by selecting the prosocial option, subjects could maximise their rewards as the experimenter would also be required to select the prosocial box on their turn. Subjects failed to understand the contingencies of this task and therefore did not demonstrate both other-regarding preferences and reciprocity (Di Lascio et al., 2013).

Given that there are very few studies examining prosociality in birds, further research needs to be conducted with avian subjects before any conclusions can be made concerning whether birds possess other regarding preferences or not. Kea (*Nestor notabilis*) are an exceptionally suitable species to study prosociality in birds. Kea are endemic parrots to the South Island of New Zealand. They live in complex social groups, form monogamous pair bonds and have an extended period of dependence compared to other birds. They also demonstrate a varied and intense array of play behaviours and enhanced social facilitation (Diamond & Bond, 1999; Bond & Diamond, 1993). In both observational and experimental studies, kea have been successful at solving problems in the domains of both technical and social cognition (Huber & Gajdon 2006; Auersperg et al., 2010; Auersperg et al., 2011a; Diamond and Bond 1999; Tebbich et al., 1996).

Here, I examined prosociality in kea in four different conditions using the same paradigm as Suchak and de Waal (Suchak & de Waal, 2012). Condition 1 simply examined whether kea exhibited spontaneous prosocial choice, and so preferred to choose a prosocial token over a selfish one. In Condition 2 kea took alternating turns choosing a token with a partner. This condition examined whether turn taking might elicit reciprocity in kea. Condition 3 was a yoked control condition in which the focal kea was the only one to select a token and the experimenter replicated the choice of the partner from previous trials in condition 2. This tests whether kea were responding to the choices their partner made in Condition 2 or the rewards they were receiving. If they were responding to their partner's choices prosocial choices would be expected to decrease in condition 3 as the experimenter, rather than the partner was choosing, despite the rewards being received within each condition being identical. Finally, subjects were tested in a partner absent condition. This assessed whether they had simply developed a strong preference for a particular token that was independent of whether a partner was actually present.

3.2 Method

3.2.1 Subjects

I tested four male Kea, aged between one and three years. Subject one (Neo), two (Zak), three (Taz) and subject four (Kati). Kea were captive bred at Willowbank Wildlife Reserve in Christchurch with the exception of Kati who was born in the wild and came to Willowbank as a fledgling. Subjects share a large outdoor aviary with nine other kea. Subjects were tested in pairs within their aviary and were free to come and go from the testing apparatuses at any time. Pairs were selected on the basis of birds that had previous experience with the apparatus and had demonstrated a tolerance for being inside the apparatus with their partner on the other side. For round two of the experiment I changed the existing dyads around so that the more dominant member of the pair remained on the same apparatus while their partner moved to the second apparatus. This was done by only rewarding the kea that formed the new pair for entering the apparatus and not rewarding kea that did not form part of the new dyad. Food and water were available ad libitum within the aviary.

3.2.2 Ethics statement

This study was conducted under approval from the University of Auckland animal ethics committee (reference no. 001416).

3.2.3 Apparatus

Subjects were trained and tested either individually or in pairs in a wooden apparatus (150cm x 50cm x 100 cm) (Figure 3.1) The apparatus had a wooden frame covered in chicken wire enabling subjects to see each other but not interfere with their partner's behaviour. The top of the apparatus was not covered so that subjects did not feel trapped or restricted and could exit the apparatus at any point. The apparatus could be entered at two separate entry points at opposite ends of each other. Before each trial both subjects had to wait on a perch attached to the apparatus behind a wooden partition. Once the experimenter removed the partition subjects could enter the apparatus. This was to prevent kea from entering the apparatus before their partner. This did not require a training stage as it was a behaviour that they had learnt in a previous experiment. Once inside neither kea could gain access to the other kea side as the apparatus was divided down the middle with a permanent wire partition. Pieces of wooden dowel (5cm x 3cm) dyed with food colouring were used as tokens for subjects to exchange with the exception of Kati's tokens which were not as wide (5cm x 1.5cm) due to him missing his upper mandible. During testing tokens were placed in plastic containers (20cm x 17cm x 10cm) which were attached at the rear of the interior of the apparatus.

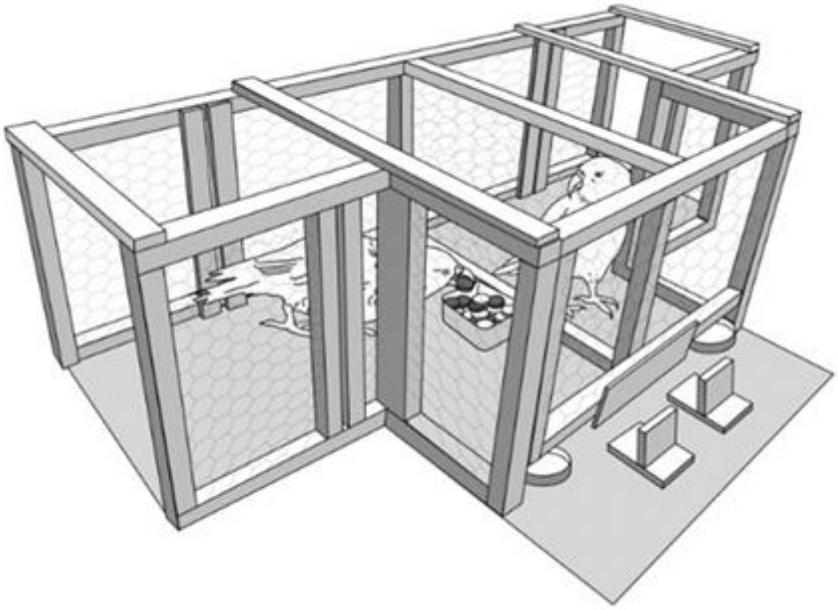

Figure 3.1: Experimental set up and apparatus. One kea selects either a prosocial or selfish token and places it in the small dish on their side. The experimenter takes the token and places it in front of both kea. The experimenter then retrieves the corresponding reward from behind the screen on the white platform and places it on the side of the platform closest to the kea. A reward for subject, or rewards for both subject and partner are then delivered to the kea by sliding the platforms underneath the gap in the apparatus. Drawing by Vivian Ward.

3.2.4 Preliminary tasks and familiarisation

3.2.4.1. Token exchange training

In stage 1 kea learnt to exchange tokens. All subjects were naïve at token exchange paradigms therefore stage 1 of training was necessary before subjects could move on to learning the values of different coloured tokens later on in training. Tokens for this stage were a natural coloured piece of dowel measuring 5 x 3 cm. Kea were required to enter the apparatus. Inside the apparatus, in front of the experimenter was one token. Kea had to learn to put the token in a small tray just beside the token which was accessible to both the subject and the experimenter. Following this, the experimenter retrieved the token and immediately rewarded the kea. Training continued until kea placed the token in the tray 10 times in a row.

3.2.4.2. Token preference test

Following token exchange training, subjects were given a token preference test similar to that designed by de Waal and colleagues (de Waal et al., 2008) to make sure that they did not have a significant preference for a certain colour. Subjects were presented with 2 differently coloured tokens side by side for 10 trials and subjects had to choose one token to trade with the experimenter for a reward, gaining one piece of Hills Science Diet for each token. If any subjects had a preference for one token in 8 or more of the 10 trials, both tokens would be replaced with new colours and neither colour would be used during testing. The average initial preference for any token colour was 52.5 ± 13.89% and no token needed to be replaced. Subjects were tested with 6 different colours (Purple/ green, blue/pink and orange/black).

3.2.4.3. Training on token values

Stage 2 of training was designed to begin to familiarise kea on different token values. Three different tokens were used in stage two of training. These were a no reward token (0/0), in which neither the subject or partner received a reward if it was selected, a prosocial token (1/1), whereby both subject and partner received a reward and a selfish token (1/0), in which only the subject received a reward. In any one trial only two tokens were used. The no reward token was used in every trial and was paired with either the selfish token or the prosocial token. Kea received trials (no reward 0/0 with selfish 0/1 or no reward 0/0 with prosocial 1/1) in randomized order and had to learn to discriminate between the two tokens. Rewards were placed out of subjects view behind a screen. There were two identical platforms, one in front of the subject and one in front of the partner. Once the subject placed a token in the tray, the experimenter either retrieved a reward from behind either both screens if the prosocial token was returned, or only the subjects screen if the selfish token was returned, or no reward if the no reward token was selected. Rewards were held up so that they were now visible to both kea, placed on one or both platforms in front of the screen and then slid towards either both subject and partner or just the subject. Ten successful trials of choosing the selfish token over the no reward token and the prosocial token over no reward token moved kea on to stage 3.

Stage 3 of training was designed to teach the kea they were now required to select tokens from a plastic container at the back of the apparatus and place it in the tray in front of the experimenter. Kea were presented with token combinations of either (0/0 or 0/1) or (0/0 and 1/1) jumbled in a container containing 6 tokens, 3 of each option, in randomised order. Kea had to select either the (0/1) token over the (0/0) token and the (1/1) token over the (0/0) token in 10 trials in a row. Ten successful trials moved subjects on to stage 4 of training.

Stage 4 was designed to further test that the kea had learnt the value of each token. Previous PCT experiments using token exchange paradigms have used subjects that had extensive previous experience with token exchange paradigms. Given that our subjects had limited experience with token exchange paradigms I wanted to ensure that they had been given enough opportunity to learn to discriminate between the selfish and the prosocial tokens. Subjects were given randomised trials where they either had to take a selfish token (forced choice selfish trials, 10 given in total), choose between a no reward and selfish token (5 trials) or choose between a no reward and prosocial token (5 trials). Ten successful exchanges in trials that included the no reward tokens moved subjects on to testing. For stage 4 subjects received between two and three sessions of 30 trials per day and took between one and three days to complete training.

3.2.5 General procedure

3.2.5.1. Description of conditions

The experiment consisted of four different conditions which were identical to that used by Suchak and de Waal (Suchak & de Waal, 2012):

1) Unilateral condition: this condition tested whether kea demonstrated spontaneous prosocial choice when one kea was selecting tokens for all of the sessions.

2) Alternating turns condition: this condition assessed prosocial preference when kea took alternating turns at selecting a token with a partner. This condition tested whether prosociality might be enhanced in kea in situations in which reciprocity is possible.

3) Yoked control condition: in this condition, the subject selected a token. However, instead of the partner selecting a token on the next trial, the experimenter selected the token that the partner had chosen in the corresponding alternating session. This condition is designed to test whether an observed increase in prosocial token preference in condition 2 is due to kea responding to what their partner actually chose in condition 2 or simply the rewards conferred by their partner’s choices.

Prosocial choice between conditions 2 and 3 would be expected to decrease if kea were responding to their partner's choices and behaviour rather than just the outcomes of their partner's token choice.

4) Partner absent condition: this condition was designed to assess whether an observed prosocial preference in kea is due to them possessing other regarding preferences, or whether it is based on them having developed a strong preference for the prosocial token. This condition was exactly the same as condition 1 except that the partnering kea was absent.

3.2.5.2. Testing

There were 2 rounds of testing. In round one, subjects were paired with the same partner and completed all four conditions. In round two they were then paired with a new partner and different coloured tokens and tested again in all four conditions. Training and testing were identical for both rounds and one kea acted as the subject from stage 2 of training until the end of condition 1. Then, the other kea underwent all the training stages and completed condition 1. Then subjects were paired up again and given round two of testing. Subjects completed two rounds of testing so that if in round one our results indicated that one or more kea might be prosocial, I could test this again with a new partner and new tokens and compare their performance between rounds. Also, given that this was the first time that subjects had exchanged tokens, another round of testing gave subjects more opportunity to understand the contingencies of the task. In each condition subjects had to choose one token from a container filled with 10 tokens, 5 prosocial tokens (1/1) and 5 selfish tokens (1/0). After selecting a token subjects were required to place it in a tray in front of the experimenter. The experimenter then retrieved the token and placed it in front of both kea. Rewards were retrieved from behind the screen attached to the platform, held up for both kea to observe, placed on the platform and delivered to subjects. The actor always received their reward first, followed by their partner if the prosocial token was selected. Tokens were replaced and jumbled after every trial. Rewards were one piece of Hills science diet for each kea. Kea received 3 sessions of 20 trials per condition and subjects received between one and two sessions a day (Fig 3.1).

During round 2, session 2 of the alternating turns condition, one subject (Neo) began to enter the apparatus, take a token and then leave the apparatus with it and disperse it throughout the aviary. This happened numerous times and it eventually became disruptive. His partner, Zak also began to mimic this behaviour. To continue testing I attached one end of a piece of string (40cm) to each token and to the top of the apparatus. The string was long enough so that it did not get tangled when subjects were selecting a token and the experimenter was still able to jumble the tokens after each trial. I tested both subjects like this for one session (Session 2, round 2), after which I resumed testing without the strings attached. While this was not ideal, it did not affect token preference as Neo exclusively chose the prosocial token in all three sessions and Zak chose the prosocial token in 5 out of 10 trials of each session.

3.3 Results

See Appendix 1 for example trials from experiments

Paired samples t tests were conducted to examine whether there was any significant difference in overall prosocial token preference in each condition between round one and round two. There was no significant difference in prosocial token preference between round one ($\bar{x}$ =31.75, *SD*=19.24) and round two ($\bar{x}$=35.75, *SD*=13.40) of condition one (*t* (3) =0.8627, *p*=0.4518) and round one ($\bar{x}$=24.25, *SD*=6.24) and round two ($\bar{x}$ =20.25, *SD*=7.80) of condition two (*t* (3) =0.6532, *p*=0.*5602*). There was also no significant difference between round one ($\bar{x}$ =24.50, *SD*=6.45) and round two ($\bar{x}$= 21.00, *SD*= 7.35) of condition 3 (*t* (3) =1.2852, *p*=0.2890) or between round one ($\bar{x}$ = 45.75, *SD*=12.63) and round two ($\bar{x}$ = 36.00, *SD*=20.02) of condition 4 (*t (*3) =2.4984, *p*=0.0878).

In condition 1 prosocial token preference ranged from 42 to 75% across subjects (mean ± standard deviation: 56 ± 14.6%) I examined whether there was a significant change in prosocial token preference between sessions in condition one and found no significant difference between sessions (repeated-measures ANOVA, *F* 3,2 =575, *p*= .65) suggesting that subjects had learnt the values of the tokens during training.

Individually, in condition 1, Neo and Zak did not exhibit a significant preference for the prosocial token overall (Neo, binomial test *p* = 0.787; Zak, *p* = 0.0836), while Kati and Taz did (Kati, *p* = 0.036; Taz, *p* = < 0.001). For individual performance data see Appendix 3: Tables A.10 and A.11.

In condition 2, all subjects except Zak (binomial testing, *p* = 0.900) had a significant preference for the prosocial token. (Neo, binomial testing *p* = < 0.001; Kati, *p* = 0.007; Taz, p = < 0.001). All subjects increased their prosocial preference between condition 1 and 2 (40% for Neo, 52% for Zak, 8% for Kati and 13% for Taz). This is comparative to capuchin monkeys which increased their prosocial preference by 10% from condition 1 to 2 (Suchak & de Waal, 2012). For individual performance data see Appendix 3: Tables A.10 and A.11.

While Suchak and de Waal (Suchak & de Waal, 2012) found no contingency between the choices that a subject made and the choice that had previously been made by their partner, I found evidence of a significant contingency between actor's choices and that made by their partner (Pearson's Chi, X^2= 5.771, *p*=.016). I used the results of a Pearson's r to analyse the strength of the correlation between these two variables (r= -.17, n=4, *p* = .010). Our r value indicates that the strength of the correlation is small and the relationship between the two variables is negatively correlated, suggesting that actor's selfish token choices were more likely to follow after their partner's prosocial token selection. Thus kea were more likely than capuchins to choose a selfish token choice following their partner's prosocial token choice (86% of selfish choices compared to 77%).

In condition 3, yoked control, all kea except Zak (binomial testing *p* = 0.052) had a significant preference (Neo, *p* = < 0.001; Kati, *p* = 0.001 and Taz, *p* = 0.000) for the prosocial token. Prosocial token preference between conditions 2 and 3 increased for all subjects (Neo 5 %, Zak, 11% and Kati 4%) except Taz who had a 15% decrease. Overall, capuchins decreased their prosocial preference between conditions 2 and 3 by 9% (Suchak 7 de Waal., 2012). Prosocial token preference in condition 4 remained significant for all subjects (normal binomial testing, Neo, *p* = < 0.001; Zak, *p* = 0.000 and Taz, *p*= 0.000) except Kati (*p* = 0.171). Prosocial preference declined by 17% between conditions 3 and 4 for Neo, 15% for Kati and 3% for Taz. Zak was the only kea to increase their preference, which he did by 7%. Overall I found no significant differences in prosocial token preference across all conditions (repeated-measures ANOVA, *F*, (3, 1) = .639, *p* = .703).

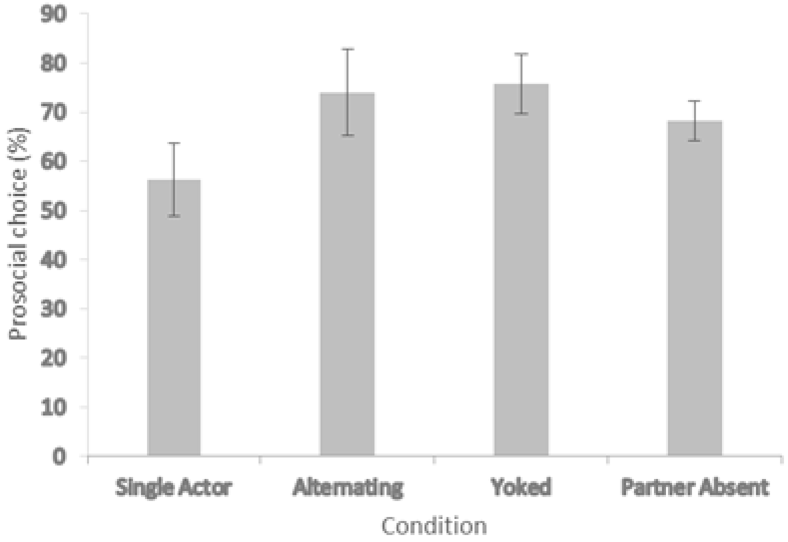

Figure 3.2: Comparison of prosocial choices across conditions. The mean (+ SEM) percent of prosocial choices are illustrated.

For individual performance data see Appendix 3: Tables A.10 and A.11.

3.4 Discussion

We found that only two out of four subjects demonstrated a prosocial preference in condition 1. This indicates that unlike capuchins, kea may not exhibit a spontaneous prosocial preference. In condition 2, three out of four kea had a significant preference for the prosocial token. However, this remained the same in condition 3 indicating that, unlike capuchins, kea were not demonstrating reciprocity in situations such as turn taking. The most likely explanation for this finding is that the prosocial token was associated with the visible delivery of two lots of rewards in this condition. This is supported by the finding that in condition 4, three out of four subjects still had a significant preference for the prosocial token. If kea were behaving prosocially in condition 1, it would be expected that prosocial preference would be lower in condition 4 than it was in condition 1. Instead, it is likely that kea developed a strong preference for the prosocial token across subsequent conditions due to its greater association with rewards in conditions 2 and 3.

Most studies which test animals using token exchange paradigms only select subjects with extensive previous experience exchanging tokens (Suchak & de Waal, 2012). Subjects in this study had limited experience with token exchange paradigms and this may have effected their performance. However, it is hard to see how a lack of experience can account for the performances of kea in conditions 3 and 4, particularly given that I carried out two rounds of testing. One kea, Taz, did demonstrate a pattern of preferences similar to that of capuchins. Like capuchins, he had a significant preference for the prosocial token in condition 1 which increased in condition 2. Taz decreased his prosocial preference between conditions 2 and 3 which decreased further in condition 4. While no strong interpretations can be drawn from these observations, it does indicate that it might be worth further analysing the performance of individual birds.

At present, it does not seem the kea are prosocial. However, further testing examining prosocial behaviour in kea is clearly needed with a significantly larger subject pool than the present study. It is also worth considering the environment that kea evolved in and whether it is reasonable to expect that prosocial behaviour is likely to have evolved in kea. As discussed in **Chapter 1**, kea evolved in an extremely harsh and unpredictable ecological environment whereby locating food was particularly challenging. This required kea to become extremely skilled and adaptive scavengers. Male kea in particular are required to provide food for not only their mate but also for their offspring for extended periods (Diamond & Bond, 1999). In addition, the significant amount of time and energy required by kea to locate very limited resources raises the question as to whether prosociality would have been an important or even helpful adaptive behaviour in kea. In such a harsh and unforgiving environment, prosocial behaviour in kea, particularly related to food may not been beneficial to survival in kea. Future studies examining whether prosocial behaviour evolved in kea could employ a GAT paradigm. In chimpanzees, GAT studies have reported findings of other regarding preferences (Warneken et al., 2007; Yamamoto et al., 2009; Yamamoto et al., 2012) whereas PCT tasks have not (Silk, 2005; Jensen et al., 2006; Vonk et al., 2008). GAT studies in kea could examine whether kea behave prosocially in contexts that are not food related, such as providing help for a conspecific that has been separated from the rest of the flock. For example, a kea could choose whether to provide assistance for a conspecific to unlock a door that is separating them from the rest of the flock as opposed to doing nothing. Also, prosociality is claimed to have evolved in order to maintain cooperation between unrelated kin (Horner et al., 2011). Therefore, it would also be worthwhile testing prosociality in kea in the context of a cooperative task. Future studies will focus on these directions.

Chapter 4

Kea do not show evidence of inequity aversion in a classic token exchange paradigm[2]

Abstract

It is claimed that inequity aversion is a mechanism that evolved to maximize the payoffs from engaging in cooperative tasks and to foster long term cooperative relationships between unrelated individuals. While evidence of negative responses to inequitable outcomes in species other than humans remains controversial, evidence of inequity aversion has typically been found in species that, like humans, live in complex social groups and demonstrate cooperative type behaviours. I examined inequity aversion in kea (Nestor notabilis) using a classic token exchange paradigm. I compared the number of successful exchanges and the number of abandoned trials in each condition and found no evidence of an aversion to inequitable outcomes when there was a difference between reward quality or working effort required between actor and partner. No evidence of inequity aversion was also found when the subject received no reward while their partner received a low value reward. While more tests are required to confirm these findings, our results do not support the hypothesis that inequity aversion is a mechanism that evolved in species that are both social and cooperative.

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[2] Heaney, M., Gray, R.D. & Taylor, A.H (2017) Kea show no evidence of inequity aversion. *Royal Society Open Science* 4(3). doi: 10.1098/rsos.

4.1 Introduction

Inequity aversion may be defined as a sensitivity to others efforts and payoffs compared to one's own costs and gains (Fehr & Schmidt, 1999; Range et al., 2008; Brosnan, 2011). It is a behaviour that is claimed to have evolved alongside cooperation and served the purpose of maximizing payoffs from engaging cooperatively and fostering long term bonds between unrelated individuals (Brosnan, 2011). In the laboratory, inequity aversion has been tested in humans using games such as the ultimatum game. In the ultimatum game the first player receives a sum of money and proposes how to divide it between themselves and a second player. The second player must then choose whether to accept or reject the proposal (Brosnan & de Waal, 2014). Human participants in laboratory studies will turn down a proposal in which they still make a gain if the other player receives more because they deem it unfair (Brosnan, 2011).

At present it remains controversial whether inequity aversion is a mechanism that is possessed by non-human species, particularly those which have experienced selective pressures thought key to its emergence, such as complex social living and cooperative behaviour (Brosnan et al., 2011; Jelbert et al., 2015). The first reports of inequity aversion in animals were reported by Brosnan & de Waal. Using a token exchange procedure in which capuchin monkeys had to trade a token with the experimenter in order to receive a reward, they found that capuchins would reject a food that they had previously accepted when they witnessed another monkey receive food of higher value. They suggested that capuchins possessed inequity aversion in the same way that humans do (Brosnan & de Waal, 2003). However, Brosnan and de Waal's (2003) interpretation of their findings have been questioned by other researchers. Wynne (2004) highlighted the similarities in refusal rates between the inequity condition and an asocial food control condition where the high value reward was visible but no partner was present. This suggested that subjects were not responding to inequity but rather to the mere visibility of the high value food reward. Brosnan & de Waal responded to these criticisms by pointing out that although the refusal rates between the inequity and food control conditions were similar and that visibility of the high reward food did indeed effect subject's performance, the capuchins reactions differed between these two conditions. That is, in the inequity condition refusal rates increased across trials while in the food control condition refusals decreased across trials, indicating that subjects could discriminate between conditions (Brosnan & de Waal, 2004). Following this, other researchers have proposed alternative explanations for behaviours that look indicative of inequity aversion (Roma et al., 2006; Silberberg et al., 2009; Bräuer et al., 2006; Dubreuil et al., 2006). One explanation for these behaviours is the frustration effect. This is when an animal responds negatively to receiving a low value reward after they have previously received a high value reward, independent of the social context it is in (Roma et al., 2006; Silberberg et al., 2009). Another explanation is the food expectation hypothesis, where seeing a conspecific receive and consume a high value food reward creates the expectation that an animal will receive the same reward themselves (Bräuer et al., 2006).

Subsequent research examining inequity aversion in animals, most of which employ methodologies similar to Brosnan & de Waal, (Brosnan & de Waal, 2003) have produced mixed findings. While some studies with chimpanzees have suggested that they might be sensitive to inequity (Brosnan et al., 2010; Brosnan et al., 2005), others have failed to replicate these findings (Bräuer et al., 2009). Negative findings have been reported in capuchins (Fontenot et al., 2007; Mcauliffe et al., 2015), bonobos (Bräuer et al., 2009), squirrel monkeys (Talbot et al., 2011) and orangutans (Bräuer et al., 2009; Brosnan et al., 2011). Mcauliffe and colleagues reported that cotton-top tamarins showed little sensitivity to inequity when the required task was either effortful or effortless. However, one individual was less likely to pull in a reward tray in which the outcomes were inequitable to that of their partner when doing so was effortful to due to a weight being attached to the actor's lever. In contrast, this subject's pulling rate did not decrease in a weighted asocial control condition and a non-weighted inequity condition (Mcauliffe et al., 2014).

Dogs are the first non-primates that have been reported to exhibit inequity aversion. Range and colleagues found that dogs exhibited evidence of inequity aversion when their partner received a low value reward and they received nothing. However, inequity aversion was not observed when their partner received a high value reward while subjects received a reward of lower value. Based on these results, they suggested that dogs possess a basic version of inequity aversion (Range et al., 2009). There have been limited studies investigating inequity aversion in birds. In one study, inequity aversion was investigated in crows and ravens over a series of conditions in which subjects were required to exchange a stone with the experimenter (Wascher & Bugnayar., 2013). They found that crows and ravens exchange performance decreased when their partner received a reward as a gift while they were still required to exchange the stone, compared to the baseline equity condition. This suggests that these birds might be sensitive to inequity in regards to working effort. They also found that subject's performance exchanging stones and acceptance of reward declined in the inequity condition compared to equity condition. However, in line with the food expectation hypothesis, performance rates were even lower in the partner absent food control condition in which the actor saw the high value food reward but received the low value reward. This suggests that subjects were sensitive to the reward quality, rather than inequity. This conclusion was also supported by the finding that subjects did not react with decreased exchanges when they saw a partner receive a reward while receiving nothing themselves, compared to a control where an exchange occurred and no partner was present.

In another study, Jelbert and colleagues examined inequity aversion in New Caledonian crows using a novel stone dropping task. Subjects were required to pass a stone to their partner who would then drop it down a hole to collapse a platform containing rewards for both birds. Inequity aversion was examined using two separate tests with two separate groups. In the first test the quantity of rewards that birds received varied from trial to trial. In the second test, the quality of reward that birds received was varied. Researchers found no evidence in either condition that crows were sensitive to inequity (Jelbert et al., 2015). Overall, the results from inequity aversion research in animals has been controversial due to concerns over methodology and results appearing to provide support for both the inequity aversion hypothesis and the food expectation hypothesis (Roma et al., 2006; Wynne, 2004).

As stated, it is hypothesised that inequity aversion evolved alongside cooperation in humans so that individuals could form stable cooperative partnerships. Advocates of this hypothesis suggest that inequity aversion is likely to be found in non-human species that, like humans, are also highly social and cooperative (Brosnan, 2006; Brosnan, 2011; Brosnan & de Waal, 2012). As support, they highlight comparative studies which have found evidence of inequity aversion in species that are both cooperative and social, such as capuchins (Brosnan & de Waal, 2003) and chimpanzees (Brosnan et al., 2010; Brosnan et al., 2005), but not in solitary species such as orangutans (Bräuer et al., 2009; Brosnan et al., 2011), or in highly social yet non-cooperative species such as squirrel monkeys (Talbot et al., 2011). Kea are excellent candidates to test the hypothesis that inequity aversion might evolve through the process of convergent evolution in species that are both highly social and engage in cooperative behaviours.

Kea (*Nestor notabilis*) are endemic parrots to the South Island of New Zealand. They live in complex social groups, engage in bi-parental care, extensive allopreening and a variety of play behaviours akin to that seen in mammals (Diamond & Bond, 1999; Bond & Diamond, 2003). They also engage in extractive foraging and demonstrate enhanced social facilitation (Diamond & Bond, 1999; Cuthbert, 2003). In both observational and experimental studies, kea have exhibited an aptitude for solving problems within the domains of both technical and social cognition (Huber & Gajdon 2006; Gajdon et al., 2004; Gajdon et al.,2013; Auersperg et al., 2011a; Diamond & Bond, 1999; O'Hara et al., 2015; Tebbich et al., 1996). We aimed to investigate inequity aversion in kea using a token exchange methodology similar to that used by Brosnan & de Waal (2003) and Brosnan and colleagues (Brosnan et al., 2005). Here, we tested kea in series of conditions designed to assess whether they were sensitive to inequity in both reward quality and working effort. We also investigated whether the absence of reward might induce inequity aversion in kea by including two no reward conditions, one in which subjects received no reward while their partner received a low value reward for exchanging, and a no reward asocial control condition where the partner was not present. By comparing subject's performance between these two no reward conditions we are able to explore whether kea might be sensitive to inequity in the context of receiving no reward while their partner receives a low value reward, or whether a decline in performance is simply attributable to the fact that subjects were not receiving a reward themselves, irrespective of whether their partner was rewarded.

4.2 Method

4.2.1 Ethics statement

All aspects of this study were conducted under approval from the University of Auckland ethics committee (reference no.001416).

4.2.2 Subjects

I tested four male Kea, aged between one and three years (Neo, Zak, Taz and Kati). Kea were captive bred at Willowbank Wildlife Reserve in Christchurch except for Kati who was born in the wild and came to Willowbank as a fledgling. Subjects shared a large outdoor aviary with nine other kea. Subjects were tested in pairs within their aviary and were free to come and go from the apparatus at any time. Food and water were available ad libitum within the aviary.

4.2.3 Materials

Subjects were trained and tested either individually or in pairs in a wooden apparatus (150cm x 50cm x 100cm cm) (Fig 4.1). The apparatus had a wooden frame covered in chicken wire enabling subjects to see each other but not interfere with their partner's behaviour. The top of the apparatus was not covered so that subjects did not feel trapped or restricted and could exit the apparatus at any point. The apparatus could be entered at two separate entry points at opposite ends of the apparatus. Once inside, neither kea could gain access to the other kea side as the apparatus was divided down the middle with a permanent wire partition. Pieces of wooden dowel (5cm x1cm) were used as tokens for subjects to exchange. Tokens were attached to a thin piece of string (40cm long) which was held by the experimenter. This was to prevent subjects from leaving the apparatus with the token and dispersing it throughout the aviary at Willowbank.

4.2.4 Procedure

4.2.4.1. Training and familiarisation

Subjects were required to exchange a token for a reward, a behaviour they had been taught in previous experiments. Here, subjects were required to take a token offered to them by the experimenter and then return it to the experimenters open hand in exchange for a reward. The experimenter's hand was open over a small tray which had been used in previous token exchange experiments. Once subjects had returned the token it was held up by the experimenter and placed in sight of the subject. The experimenter then delivered a reward to the subject. Training ended once each subject successfully exchanged the token for 10 trials in a row.

4.2.4.2. Food preference test

Stage 1: This stage was to confirm that Hills Science Diet was the preferred reward over a piece of peanut and could be used as the high value reward while the peanut could be used as the low value reward. Subjects received two sessions of 10 trials where they had to choose between a piece of Hills Science Diet and a piece of peanut. The side that each reward was presented on was randomized to control for a possible side bias. Once a subject chose a reward the other reward was immediately removed. Subjects had to choose the Hills Science Diet in 80% of trials for it to be used as the high value reward. All subjects passed the food preference test.

Stage 2: the next condition was designed to check that even though Hills Science Diet was the preferred reward subjects would still accept and consume the peanut in the absence of Hills Science Diet. To pass this stage subjects needed to accept the peanut for 10 trials in a row. Following this, subjects moved on to testing. All subjects passed this stage and no subject refused to consume the peanut on any trial.

4.2.4.3. Trial methodology

For testing, both types of rewards were always visible to subjects. Rewards were placed on circular, white trays in front of both kea and both rewards remained visible to both subjects throughout the entire session (Fig 4.1) To start a trial, the experimenter passed the token to a kea, the kea had to then take the token and put it in the experimenter’s hand which was open over a small dish. The experimenter then took the token, held it up and placed it in front of both kea. Following this the experimenter then retrieved the appropriate reward from one of the trays, held it up so it was visible to both kea and then delivered it to the exchanging bird. Partners always exchanged with the experimenter before the actor and birds only knew which type of reward they were receiving after they had exchanged the token.

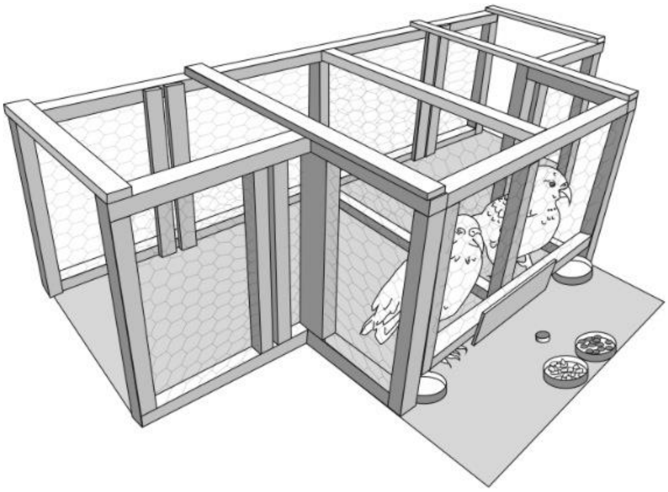


Figure 4.1: Experimental setup and apparatus used. Rewards were placed in circular trays in front of subjects. The experimenter offered the subject a token under the gap towards the midline of the apparatus. Subjects were required to take the token and then return it to the experimenter's hand which was outstretched over the empty circular dishes towards the outside of the apparatus. The experimenter took the token, held it up and placed it down so that both birds could see it. They then took the appropriate reward from the dishes, held it up so that it was visible to both birds and handed it to the bird that had just exchanged (except for trials in which the partner received a reward without having to exchange). Drawing by Vivian Ward.

Each condition consisted of two testing sessions, each consisting of 25 trials. For each trial, the partner exchanged first, or in the case of the effort control condition received a reward, followed by the actor. One kea remained as actor for the entirety of both sessions of a condition, apart from conditions such as the equity and food control condition which both kea performed the same action and received the same reward. In this case both birds were functionally playing the role of actor. For these conditions it was randomly decided which bird started session 1 which meant that the other bird in the dyad started session 2. The order of conditions that subjects were tested in were randomized except that no subject started with the inequity or no reward condition, nor did subjects receive two no reward conditions in a row. Before each trial, subjects received 5 warm up trials where they exchanged the token for a low value reward. Each bird was tested in six different conditions (Table 4.1). For all of these conditions I examined the actor's responses to the token and the food and actors could choose to accept or refuse both the token and the food. Refusal behaviours, or behaviours indicative of inequity aversion were scored if they met one out of several criteria (Brosnan et al., 2010) (Table 4.2). If actors did not complete an exchange within the required timeframe of 40 seconds (10 seconds to take the token and 30 seconds to return) they did not receive a reward. Because kea were free to come and go from the apparatus, a session was terminated if a bird left the apparatus without returning for 2 minutes. The six experimental conditions were as follows:

1. **Equity condition (EC)** - Baseline condition. Focal and partner both exchanged a token for a low value food reward.
2. **Inequity condition (IC)** - Focal and partner both exchanged, however the focal received a low value reward and the partner received a high value reward.
3. **Food control (FC)** - both kea exchanged and took turns as the actor. Both subjects saw the high value reward which was held up in front of subjects to gain their attention. The high value food was then placed back into the container it came from. The actor was then required to exchange the token. After a successful exchange they then received the low value reward. The same method was then repeated with the other kea which served as actor. This condition measured whether inequity aversion is elicited because of the mere presence of the high value reward or whether it is due to seeing the partner actually consume it. Results from this session can be compared to the results in condition 2. It examines whether signs of inequity aversion in condition 2 are the result of individual expectation (what the subject expects to receive) or social expectation (that is inequity aversion in condition 2 was the result of comparing what they saw their partner receive). Signs of inequity aversion would be higher in condition 2 than 3 if their responses were based upon social expectations rather than individual expectation.
4. **Free Gift (FG)** - Focal kea exchanged and received a low value reward while partner did not exchange but received a low value reward as a gift. This condition controls for the role of “working effort” which is another form of inequity aversion. If kea are sensitive to the working effort of their partner we can compare the results of condition 1 (Equity condition) with this condition and would expect signs of inequity aversion to increase in this condition compared to condition 1. If kea are not sensitive to working effort inequity then it would be expected that exchange and food acceptance rates would be similar to condition 1.
5. **No reward inequity condition (NRIC)** - both kea exchanged however the focal kea received nothing while their partner received a low value reward. This condition was designed to examine whether receiving no reward while their partner receives a low value reward might induce inequity aversion in kea.
6. **No reward partner absent (NRPA)** - Only the actor was present in this condition. The actor had to exchange the token but received no reward. On alternate turns, the experimenter held up a piece of peanut and moved it towards the empty side of the apparatus where the partnering kea would normally be. The peanut was then returned to the tray. This condition also controlled for the movement of food in condition 5. This condition was designed to assess whether any evidence of inequity aversion in condition 5 were due to subjects seeing their

partner receive a reward while they received nothing, or, whether a decrease in performance was because subjects simply didn't receive a reward.

Table 4.1: Description of experimental conditions

Abbreviation	Condition name	Exchange	Food	Description	Purpose of Condition
EC	Equity Condition	Both exchange	Both low value (piece of peanut)	Both actor and partner exchanged of a low value reward	Baseline condition measuring responses when both working effort and rewards were equal.
IC	Inequity Condition	Both exchange	Partner receives high value food (Hills Science Diet) and actor receives low value (piece of peanut).	Partner exchanged for high value reward and actor exchanged for low value reward	This condition measured actor's responses when rewards differed in quality. If kea were averse to differences in reward quality we would expect a decline in exchange performance between this condition and the equity condition
FC	Food control	Both exchange	Both see high value before exchange (Hills Science Diet). Both receive low value (Piece of peanut)	Before exchange experimenter holds up a piece of high value food in front of exchanger and then places it back in dish. After successfully completing exchange actor receives low value reward.	Control condition designed to assess whether a decline in performance between the equity condition and the inequity condition was because actor's witnessed their partner receiving a high value reward, not because the high value reward was simply visible
FG	Free Gift	Only actor exchanges	Both receive low value (piece of peanut)	Partner receives a low value reward for "free" without exchanging. Actor receives low value reward after completing successful exchange	This condition assessed whether kea may be sensitive to the working effort of their partner. That is do they demonstrate behaviours indicative of inequity aversion when their partner receives a reward for free without effort while they must complete an "effortful" task for a reward.
NRIC	No reward/ Inequity condition	Both exchange	Partner receives low value reward (piece of peanut). Actor receives nothing, partner receives low value	Partner exchanges for low value food reward and actor exchanges but receives nothing.	Assesses whether receiving no reward while their partner receives a low value reward might induce inequity aversion in kea.

NRPA	No reward/Partner absent	Only actor/ partner absent	Actor receives nothing	Partner is absent. To control for the movement of food, before exchange experimenter holds up a piece of low value reward and then moves it towards the partner's empty side of the apparatus. The experimenter then places the reward back into the dish. After completing a successful exchange the actor receives nothing.	An asocial control condition designed to assess whether a decline in performance between the equity condition and the no reward inequity condition is because the actor witnessed their partner receive a reward while they received no reward or whether it is simply be due to actor's not receiving a reward themselves.

Table 4.2: Classification of aversion responses

Ignore	Experimenter offered token to actor but subject did not take token out of experimenters hand within 10 seconds
Refusal	Actor took token but did not return it to the experimenter within 30 seconds
Push back	Actor took token but pushed it back to experimenter
Food ignore	Actor did not take food offered by experimenter within 10s
Food refusal	Actor took food but did not consume within 30s

4.3 Results

See Appendix 1 for example trials from experiments

A repeated measures ANOVA was conducted to examine whether there were any differences in the percentage of successful exchanges between the four conditions in which actors always received a reward (EC, IC FC and FG). There was no significant differences between conditions (ANOVA =.5 *F* (2, 2) =1.0 *P* =.5). This indicates that subjects may not be sensitive inequity in regards to reward quality or working effort of their partner. Zak was the only kea that did not successfully exchange the token in all trials in the inequity condition (35/50 trials). Taz was the only kea that did not complete all trials in the free gift condition. It is difficult to ascertain whether Zak may be sensitive to a difference in reward quality or whether Taz may be sensitive to differences in working effort. This is due to the open nature of the apparatus, whereby subjects were free to come and go. It is not possible to determine whether subjects left the apparatus because they were sensitive to inequity or whether they were distracted by something in the aviary. However, Taz did not make any refusals before leaving the apparatus and Zak only made one on his last trial. This suggests that their decreased performance in these conditions might not due to a build-up frustrations due to being inequity averse, but rather that their departure from the apparatus was more likely due to other reasons.

A repeated measures ANOVA was then conducted to examine whether there was a difference between the baseline equity test and the two no reward conditions (Partner absent and partner present). A significant difference was found between these conditions (*Λ*= 007 F (2, 2) = 137.64 *P* =.007), suggesting that performance dropped significantly between the baseline equity test and one or both of the no reward conditions (Fig. 4.2). To analyse whether subjects decrease in performance was due to a response to inequity in regards to witnessing their partner receive a reward while they received nothing or whether it was simply due to the fact that they themselves did not receive a reward a paired samples t-test was conducted to measure the differences in performance between these two conditions (NRPA and NRIC). No significant difference between the number of successful exchanges was found (*t* (3) =.46 *p*=.68). There were also no aversion behaviours exhibited by any birds in any of these four conditions in which the actor received a reward (EC, IC, FC and FG). Therefore, the fact that subjects did not receive a reward themselves, regardless of whether they witnessed their partner receive a reward was probably the reason that performance dropped so significantly in these conditions. For individual performance data see Appendix 4: Table A.12.

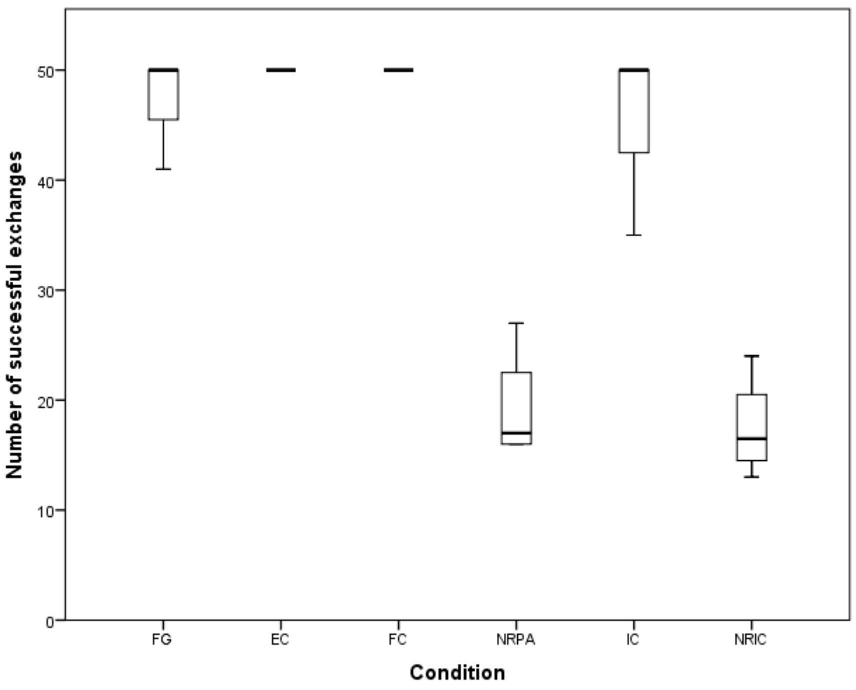


Figure 4.2: Box plots showing average number of time actors successfully exchanged token with the experimenter in each condition (out of a maximum of 50 trials). Boxes represent the interquartile range, lines within boxes represent median values and whiskers represent the 5th and 95th percentiles.

In the analyses above I examined the number of successful trials completed in each condition. In the following set of analyses I analysed the total number of trials that kea abandoned in each condition (Fig 4.3). A repeated measures ANOVA revealed that there were no significant differences in the number of abandoned trials between the four reward conditions (EC, IC, FC, FG) (A =.5 *F* (2,2)=1.0 *p*=.5). In the two no reward conditions, subjects abandoned more trials in the partner present no reward condition (x̅ =29.25 out of 50 possible trials *SD*=5.50), compared to the no reward, partner absent condition (x̅ =24.00 *SD* =7.07). However, a paired samples t -test revealed that there was not a significant difference between the number of abandoned trials between these two conditions (*t* (3) = 2.414 *p*=.095). Refusal type behaviours also increased in the no reward partner inequity condition (n=27) compared to the no reward partner absent condition (n=13) but this is may be due to the fact that subjects completed more trials in the no reward, partner absent condition. Comparing the percentage of aversion behaviours as a function of the number of trials completed I found no significant difference between the two no reward conditions (*t* (3) = -1.036, *p*=.38). For individual performance data see Appendix 4: Tables A.13 and A.14.

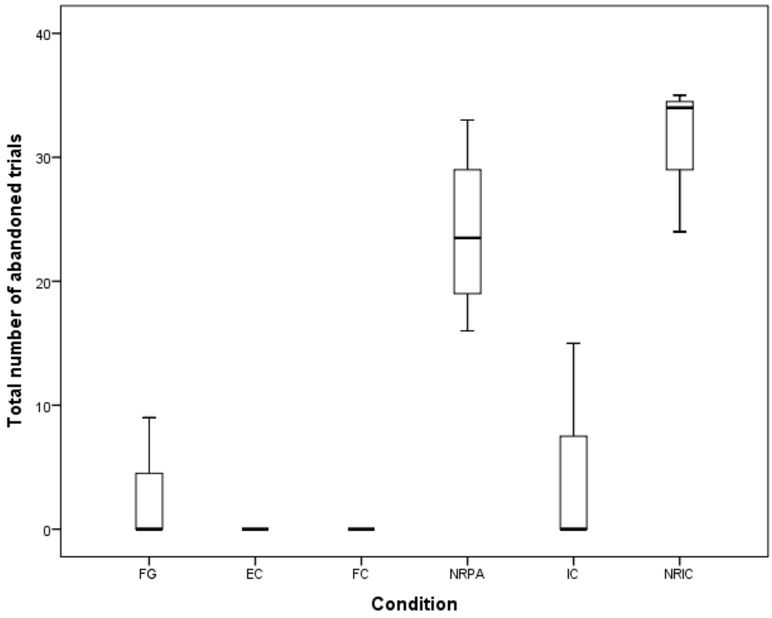


Figure 4.3: Box plots showing the number of abandoned trials for each condition. Boxes represent the interquartile range, lines within boxes represent median values and whiskers represent the 5th and 95th percentiles.

4.4 Discussion

Keas did not seem sensitive to inequity in regards to differences in reward quality. Differences in working effort required by their partner also did not seem to effect kea's responses. However, in the inequity condition Zak was the only kea that did not complete all trials and Taz was the only kea in the free gift condition that did not complete all trials. However, both kea left the apparatus abruptly in these conditions and did not demonstrate refusal behaviours indicative of frustration as they did in the two no reward conditions. This suggests that their differences in performance from other kea in these conditions is more likely to be due to an unknown factor as opposed to a sensitivity in inequity. These discrepancies in individual performances do however indicate that it is important that future studies investigate whether particular individuals may possess aspects of inequity aversion.

Clearly, all subject's behaviour was affected by not receiving a reward as performance rates decreased dramatically in both no reward conditions. There were no significant differences in performance between the partner present and partner absent no reward conditions suggesting that subjects decrease in performance was due to not receiving a reward themselves as opposed to witnessing their partner receive a reward.

There are several possible reasons why keas might not have shown evidence of sensitivity to inequity in this study. The most likely scenario is that keas are simply not sensitive to inequity and do not compare their efforts or outcomes to that of their partner. That is, unlike humans and possibly other species such as chimpanzees and capuchins, inequity aversion is not a mechanism that evolved in keas. Given that kea are both highly social and cooperative, our findings question the hypothesis that inequity aversion evolved in highly social and cooperative species to maintain cooperative bonds between unrelated individuals (Brosnan, 2006; Brosnan, 2011; Brosnan & de Waal, 2012). Alternatively, it may be that the intensity and frequency of kea sociality and cooperation are not quite enough to have facilitated the evolution of inequity aversion in this species. It is also possible that there are other selective pressures that have not yet been identified that are required for the evolution of inequity aversion. Another possible reason as to why I did not find evidence of inequity aversion in kea might be due to the selection of our low value food reward. While Hills Science Diet was preferred over peanuts, peanuts may have still been quite desirable and not deemed worth rejecting. There might be a fine line between finding a low value reward that subjects will accept in the absence of a high value reward, but is not too close to the value of the high value reward. It may be that considerable tweaking of the high and low value rewards might be required before inequity aversion is elicited.

Finally, recent studies examining responses to inequity in different societies have produced some intriguing results that suggest that culture may play a larger role in the expression of inequity aversion than had been previously assumed. Henrich and colleagues compared the responses of 15 non-western small scale societies' to versions of economic games to the responses of student populations from Western societies, or those from societies which are strongly influenced by Western thoughts and ideals. The authors found that their results differed greatly from studies that used student populations. Some of these small scale societies rarely rejected an offer, unfair or not while other societies rejected offers frequently, both unfair and hyper fair (Henrich et al., 2005). In another study, Blake and colleagues measured the responses of children from 7 different societies to both disadvantageous inequity (partner gets more than subject) and advantageous inequity (subject gets more than partner). They found that while all societies demonstrated disadvantageous inequity by the time they reached middle childhood, only 3 exhibited advantageous inequity which only emerged when they reached preadolescence. The 3 societies that demonstrated advantageous inequity, USA, Canada and Uganda, were the societies in this study that have been the most exposed to Western culture. While Uganda is a non-Western country, the children from Uganda that participated in this study were from schools with Western teachers and researchers. Together with that fact that advantageous inequity only emerged in these 3 cultures much later than the emergence of disadvantageous inequity, which was apparent in all 7 societies, the researchers suggested that the children from these 3 societies may have been influenced by Western cultural ideals of equality and fairness and that culture may play a greater role in the development of fairness than has originally assumed (Blake et al., 2015).

In regards to how this might apply to studies that have previously examined inequity aversion in animals, it is important to note that all of these studies have been conducted with captive populations. Considering the findings in humans that suggest that culture may influence the expression of inequity aversion, it is also feasible to suggest that positive findings of inequity aversion in non-human species may also have been influenced by these species captive environments and the type of exposure and interactions that they have had with humans. Many of the species examined, while all being captive bred, would vary greatly in how much interaction they have had with humans. For example, I found no evidence of inequity aversion in kea. While our population was captive bred and interacted with humans on some level every day, the level of interaction was no greater than their keepers delivering food to them daily and members of the public walking through their enclosure. The studies conducted in this thesis were the first time that the kea at Willowbank had intensive, regular, one on one contact with a human, engaging in a variety of tasks and activities. In contrast, it might be argued that other species that show evidence of inequity aversion, such as some captive chimpanzee populations (Brosnan et al., 2005; Brosnan et al., 2010), have had significant amounts of interaction with humans, regularly engaging with their keepers and experimenters, serving as experimental subjects for studies a large period of their lives and often performing tasks designed by humans for rewards. It possible that their social experiences with humans may have influenced the expression of inequity aversion in these particular populations. It would be of great interest to find a way to measure inequity aversion in these primate species in naturalistic as opposed to laboratory settings.

This is the first test of inequity aversion in kea with a small and naïve subject pool and further extensive research is required before any firm conclusions can be made. In particular, as was tested by Brosnan and colleagues (Brosnan et al., 2011), it would be of interest to include a condition whereby the subject is required to complete a task in exchange for a low value reward and their partner receives a high value reward for free, without effort. This would directly test whether the presence of a task induces inequity aversion in keas if the rewards are unequal (Brosnan et al., 2011). Also, as discussed, while our results were not significant, subjects had more abandoned trials in the no reward condition in which their partner was present compared to the asocial control condition. Therefore, it would be worthwhile to specifically examine whether the absence of rewards might induce inequity aversion in kea. Finally, given that inequity aversion is hypothesised to have evolved alongside cooperation in humans it would seem that inequity eversion would be more likely to be elicited in a cooperative context. Rather than test inequity aversion in keas while they complete a task independently, future research might examine whether inequity aversion is elicited when subjects are engaging in a cooperative task.

Overall, our findings suggest that kea are not sensitive to other's efforts and gains in comparison to themselves. Given that kea are a highly social species that also engages in cooperative type behaviours in the wild, our findings challenge the hypothesis that inequity aversion evolved in highly social and highly cooperative species to maximise the benefits of cooperating with non-kin. Our findings are supported by recent research that failed to find evidence of inequity aversion in primate species (Mcaullife et al., 2014; Mcauliffe et al., 2015). Finally, research has shown that culture plays a significant role in the expression of inequity averse behaviours in humans, particularly advantageous inequity (Blake et al., 2015). Therefore, this study contributes to the growing dialogue as to whether it is reasonable to assume that other non-human species who possess aspects of advanced social cognition should demonstrate inequity aversion akin to that seen in humans.

Chapter 5

Concluding remarks

Without question, kea are a unique, intelligent and fascinating bird. While the cognition of kea is relatively understudied, there is particularly a lack of research examining cooperative cognition in this spirited parrot. As outlined in **Chapter 1**, the aim of this thesis was to examine cooperative cognition in kea. By examining whether kea possess some of the cognitive mechanisms claimed to underpin cooperative cognition, I sought to explore whether aspects of cooperative cognition can evolve convergently in kea and other species, such as humans and chimpanzees, and then try to pinpoint what the selective pressures might be that facilitate the emergence of these traits.

In this thesis, I reported the results from three experimental studies, each of which was designed to assess whether kea possessed particular aspects of cooperative cognition. In this chapter, I will summarise the main findings from each experiment, what these findings might imply about cooperative cognition in kea overall and then suggest directions for future research examining social cognition in kea.

5.1 Summary of the main findings

In **Chapter 2** I examined cooperative cognition in kea using a classic string pulling paradigm designed by Hirata and Fuwa (Hirata & Fuwa, 2007). I examined whether kea understood the need for a partner in a cooperative task, whether they could discriminate between when they required the help of a cooperative partner to access a reward and when they could access the reward alone and whether they understood the role of their partner. In the final experiment I examined whether kea had a preference for working together or working alone. All of these attributes are considered necessary requirements for a deeper understanding of cooperation. I found that kea performed on par with some chimpanzees, elephants and humans on a range of cooperative tasks and outperformed other species of birds such as rooks (Seed et al., 2008) and African Greys (Péron et al., 2011). Kea were able to successfully wait for the arrival of their partner in delayed partner arrival conditions, which suggests they might understand the role of their partner. I also provided the first demonstration that any non-human animal is capable of waiting for over a minute for the arrival of a cooperative partner. This finding also demonstrated that kea possess impressive inhibitory control, which many species struggle with (Seed et al., 2008). Kea were also able to differentiate between when they were able to access the reward by themselves, when presented with the solo apparatus, and when they were required to wait for a partner (duo apparatus). In a no rope condition, kea did not attend to whether their partner had access to the rope to pull in the apparatus but this may have been due to problems with task demands. In the final condition, one kea showed a significant preference for collaboration over working alone. Given that the intrinsic motivation to collaborate is considered to be unique to humans, this finding indicates that this is an area that is worthy of further investigation.

In **Chapter 3**, I examined prosociality in kea. Spontaneous prosocial behaviour towards conspecifics is another cognitive mechanism that is claimed to underpin advanced cooperative cognition (de Waal et al., 2008). This experiment was designed to examine firstly, if kea exhibited a spontaneous prosocial preference and secondly, if they increased prosociality and reciprocity in situations such as turn taking. In species such as capuchins (Suchak & de Waal., 2012), which have been shown to previously exhibit prosocial tendencies towards conspecifics, prosociality increases in situations such as turn taking. It has been claimed that these species understand the benefits of behaving prosocially in situations in which reciprocity is possible as such behaviour maximises their own rewards. I found that two out of four kea exhibited a preference for the prosocial token in condition 1 and three out of four kea had a prosocial token preference in conditions 2, 3 and 4. I suggest that for those kea that had a prosocial token preference in conditions 1 and 2, this was not because they were choosing to behave prosocially. It is more likely that kea had developed a preference for the prosocial token through associative learning because of the rewards it conferred. Further testing with a larger subject pool with previous token exchange experience is required to examine whether kea are intrinsically prosocial and whether, like capuchins, prosociality increases in situations such as turn taking when reciprocity is possible

In **Chapter 4** I examined whether kea might possess inequity aversion. That is, are they sensitive to the efforts and gains of a conspecific in comparison to themselves? Inequity aversion is claimed to have evolved alongside cooperation in order to allow individuals to maximise the benefits from engaging in a cooperative task (Brosnan, 2011; Brosnan & de Waal, 2014). I examined whether kea were sensitive to inequity when there were differences in reward quality, in working effort required to obtain the same reward and also when their partner received a reward while the subject received nothing for exchanging. I found no evidence of inequity in any of these conditions. Our findings that kea failed to exhibit inequity aversion in any of the conditions are in line with previous studies that found no evidence of inequity aversion in chimpanzees (Mcauliffe et al., 2015; Bräuer et al., 2009), capuchins (Mcauliffe et al., 2015), bonobos (Bräuer et al., 2009), orangutans (Bräuer et al., 2009; Brosnan et al., 2011) and cotton-top tamarins (Mcauliffe et al., 2014). Our results are also similar to those found in other avian species such as New Caledonian crows which also failed to exhibit signs of inequity aversion (Jelbert et al., 2015). Finally, our findings do not support the hypothesis that inequity aversion evolved in species that are both highly social and cooperative (Brosnan, 2011; Brosnan & de Waal, 2014).

5.2 Cooperative cognition in kea and implications for comparative psychology

The results reported in this thesis produced some interesting findings about cooperative cognition in kea that have broader implications for comparative psychology. Importantly, I found that kea performed on par with species such as chimpanzees and elephants on a range of cooperative tasks (**Chapter 2**). Taken together, our findings suggest that aspects of cooperative cognition, such as understanding the need for a partner in a cooperative task, might have evolved convergently in kea. However, further research is required to rule out alternative explanations for the behaviour of kea on these tasks, such as the use of associative rules. If it is found that kea do share aspects of cooperative cognition with humans and some non-human species, given that kea are a highly social species, our results support the hypothesis that advanced cognition evolves due to the problems posed by complex group living (Byrne & Whiten, 1988). Kea are an exceptionally social species that engage in a variety of social behaviours with a variety of different individuals from their flock (Diamond & Bond, 1999). This includes a vast repertoire of play behaviours that are typically not seen in other avian species, at least in variety and duration (Diamond & Bond, 1993). Play not only gives kea more shared experiences engaging with conspecifics, it also serves the function of maintaining behavioural flexibility, which kea clearly demonstrated in some of these tasks. By learning when and when not to initiate play with conspecifics, kea may also learn inhibitory control in the presence of a conspecific, another ability they demonstrated in our experiments. Kea also exhibit enhanced social facilitation which makes them attracted to other kea and what other kea are doing. This increases the amount of interaction and engagement with both related and unrelated conspecifics and also the likelihood that kea will learn about engaging with conspecifics (Diamond & Bond, 1999). Alongside, high levels of sociality, kea also form monogamous pair bonds and engage in bi-parental care of their young. In birds, this is hypothesised to be a better predictor of advanced cognition rather than high sociality (Emery et al., 2007). If further tests do reveal that kea do indeed possess aspects of cooperative cognition, it might be that in birds, advanced cooperative cognition might be found in species who have high quality relationships within their small family groups, and who also frequently play with other unrelated individuals. This would suggest that future research investigating cooperative cognition in birds should examine species that are both monogamous and exhibit high sociality with unrelated group members.

The harsh alpine environment that kea evolved in most likely required enhanced extractive foraging abilities. Kea engage in intensive extractive foraging (Huber & Gajdon, 2006) and there are typically a number of different individuals present at foraging sites (Diamond & Bond, 1999). As noted by Sterelny (Sterelny, 2007), through joint foraging individuals can learn a lot of information about other members of the group, such as temperament, emotional liability, task effectiveness, as a by-product. Kea are also one of only two species of parrot, along with the Antipodes Island Parakeet (*Cyanoramphus unicolor*), that are actively known to hunt and kill vertebrates such as mice (Greer, Gajdon & Nelson, 2015). Kea are also known to predate on Hutton's shearwater chicks by digging them out of their burrows (Cuthbert, 2003) (Fig 5.1). Anecdotal evidence suggests kea may actually hunt collaboratively when extracting shearwater chicks from nests. Sterelny (2007) argued that while the ecological environment that humans evolved in created extensive selective pressures, it is the way in which humans acted on these ecological pressures socially that propelled the development of human cognition. Therefore, ecological and social factors became merged in humans through a two-way positive feedback loop (the "social intelligence – ecological complexity" hypothesis). In kea, it may be that a rudimentary form of this feedback loop has also formed in this species, and so led to an understanding of cooperation. However, further work is clearly required to explore this hypothesis further.

Figure 5.1: Photo of kea hunting Hutton's shearwater chicks in their burrows. Photo credit: Rod Morris

The second finding that has broad implications for comparative psychology are the results of **Chapter 4**. Inequity aversion has not been documented with great consistency in any non-human species, even those that have demonstrated aspects of advanced social cognition such as chimpanzees (Bräuer et al., 2006; Bräuer et al, .2009). Our findings are not in line with the hypothesis that inequity aversion evolved in highly social and cooperative species to maximise the benefits from engaging cooperatively (Brosnan 2011; Brosnan & de Waal 2014). I also discussed another reason why kea and perhaps other species fail to exhibit inequity aversion. Inequity aversion has typically been assumed to be a cognitive mechanism that evolved alongside cooperation in humans and is therefore a mechanism that would be expected to be found in species that possess advanced social cognition. However, there is growing evidence that supports the idea that the expression of inequity averse behaviour in humans might be significantly influenced by societal norms and values (Henrich et al., 2005; Blake et al., 2015). These studies, alongside recent failures to find evidence of inequity aversion in primate species (Mcaullife et al., 2015) question whether it is reasonable to assume that inequity aversion is a cognitive mechanism that should be found in animals that possess advanced social cognition. However, it is also possible that kea sociality and cooperation is not intense or frequent enough to have facilitated inequity aversion in this species or, that there is another unknown factor that is required for the evolution of inequity aversion. Further research is therefore required to confirm whether kea are really not averse to inequity.

It is important to note that there was considerable variation in individual patterns of performance. In particular two kea, Neo and Taz, generated some interesting results. In **Chapter 2,** Neo outperformed other kea in the first condition of Experiment 2, performing on par with other species such as elephants and chimps. He was also the only kea that demonstrated a significant preference for working together over working alone in Experiment 5 of **Chapter 2**. Similarly, Taz outperformed other kea in the randomised delay condition of Experiment 2 of **Chapter 2** and was the only kea that selected the correct course of action in all trials of Experiment 3 in **Chapter 2**. In **Chapter 3**, although it is hard to make any strong inferences, Taz's pattern of performance was the most similar to that observed in species such as capuchins, that have been found to exhibit spontaneous prosocial preferences which are enhanced in situations such as turn-taking. These differences in individual performance between the four kea raise the possibility that certain individuals may either possess different aptitudes, such as better inhibitory control than others, or, attend to different aspects of a social task. Similarly, some individual kea may be more strongly motivated when tasks are in a social setting. It would be worthwhile investigating whether these differences might be related to factors such as an individual's ranking within the social group or some currently unspecified factor.

The research in this thesis also has implications for future research examining cooperative cognition in birds. Other species of birds, such as rooks (Seed et al., 2008) and African Greys (Péron et al., 2011) did not demonstrate evidence of cooperative cognition on tasks such as the 'loose string' task. However, kea were tested using a shaping procedure that was also employed with chimpanzees (Melis et al., 2008) and elephants (Plotnik et al., 2011). Kea are the first species of bird that has been tested using this shaping procedure and the first species of bird that has demonstrated evidence of cooperative cognition. It is important that other species of birds are tested using the same shaping procedures before it is concluded that they do not possess cooperative cognition.

5.3 Future directions

Future research investigating cooperative cognition in kea might be improved upon in several ways. First, further research requires experiments with a larger number of subjects than that which participated in our experiments. Second, given that all of our subjects were aged between 1 and 2 years, it would be beneficial to include subjects with greater variation in ages. Third, apparatus complexity may have also caused unintended issues, particularly in Experiment 4 of **Chapter 2**.

Perhaps the most significant improvement that could be made in Experiment 1 would be to simplify the task demands and apparatus design in both the no rope condition and the collaboration versus solo preference condition. Unintended task complexity in these conditions may have created a performance bias in which the observed results were due to task complexity. Thus it is unclear if kea did not attend to whether their partner could actually access the rope or not. An experiment could be designed that is similar to that conducted with chimpanzees by Melis and colleagues (Melis et al., 2006) in which kea could be trained to open doors to let a conspecific enter. In the experimental conditions, kea would be presented with the solo or duo platform. Rather than the experimenter remove the partition to allow entry for the partner like the experiments in this thesis, like chimpanzees, subjects would be required to unlock or open the door for their partner in the duo platform condition which they would not be required to do when the solo platform is presented. Comparing the number of times that kea opened the door to allow entry to their partner when the solo and duo platforms were presented might help show whether kea understand that they need a partner and when this is required.

The finding in **Chapter 2** that one kea had a preference for working together over working alone was exciting and this requires further investigation. Once again, apparatus and task complexity may have impeded other kea in the experiment from understanding the task. In our experiment, there was not a great distance between the solo and duo platforms and therefore where the partnering kea was waiting. This may not have made it entirely obvious which side they could go to if the subject chose to collaborate or work alone. One modification that could be made is to extend the distance between the two platforms and then completely block the partnering kea’s access to the side of the solo apparatus, by a partition which is removed so that the partner can also access the reward once the subject had pulled in the solo platform. The placement of the partnering kea and increased distance between the two platforms would make the differences between the two choices much more obvious.

Another issue stems from token experience In Experiment 2 (**Chapter 3**): subjects had only limited experience with token exchange paradigms. In token exchange paradigms with other species, subjects are typically selected who have extensive experience in token exchange and thus an understanding that different tokens represent different values or outcomes. Clearly it would be preferable to work with subjects in future studies that had previous experience with this paradigm as the results from this experiment may have been effected by subject’s lack of experience. Also, most prosociality experiments in animals do not test subjects within the context of engaging in a cooperative task. Token designs have very little naturalistic validity as it is not a situation that birds would be presented with in the wild. In **Chapter 3**, I suggested that it is important to test whether kea, or other species demonstrate prosocial behaviour when engaging in a cooperative task. This would allow subjects to visually track the effects that their actions have on their partner from moment to moment rather than having to make a symbolic choice. It would also be beneficial if the partnering kea could “signal” to the actor by trying to reach and grab at the inaccessible reward with his beak. Proponents of the signalling hypothesis argue that helping behaviour may require obvious cues and signals from the partner (Warneken & Tomasello 2006; Warneken et al., 2007). That is, subjects are able to “infer the recipient’s goals” through actions such as an outstretched arm, making loud noises and other signals to gain the attention of the actor. Researchers who support this theory argue that signalling from the recipient may be a critical requirement for helping or prosocial behaviour because animals may be unable to infer the needs and wants of their partner without obvious cues (Call et al., 2004). This could be tested in kea by using a modified version of the platforms and apparatus used in the experiments in **Chapter 2.** Kea would be required to enter the apparatus simultaneously with a partner. A platform with strings attached to it would be used to distribute rewards. This would be the same platform that was used in previous experiments, except that it would be slightly longer. A second, unattached, much smaller platform would fit within the larger platform. This would not have any strings but would have a wooden rod attached on its right side (the subject’s side). Platform one could be set up in the duo condition (as in the cooperative string pulling experiments), however, rather than have rewards on one side it would only have rewards on the actor’s side (Figure 5.2). Platform 2 (the smaller platform) would only have a reward available on the partnering kea’s side. Subject and partner would be required to pull both strings simultaneously which would move platform one towards the kea so that the actor can access the reward. Because platform two is underneath, nestled within platform one,

Figure 5.2: Example of proposed platform set up that could be used to examine prosociality in kea without the use of tokens.

pulling platform one also brings platform 2 closer so that the wooden rod is now in reach of the actor. If the actor chooses to pull the rod, this will bring platform 2 within reach of both kea and the partner will now receive a reward. There is no reward for the actor on platform 2. This, is therefore the test of their prosociality. Because the reward for the partner will be visible and just out of reach, the partnering kea will be able to “signal” to actor by trying to reach and grab at the inaccessible reward with his beak. This experiment would also include an asocial control condition where no partner would be present but the apparatus would be baited as before. This would test whether kea were pulling in the second platform to reward their partner or because they think they might be able to access to the rewards. This design does also not require subjects to exchange tokens, which was a possible confounding factor in the prosociality experiment in this thesis.

Finally, further research in inequity aversion (**Chapter 4**) in kea may benefit from experimenting with a wider variety of foods to use as the high and low value food rewards. In our Experiment, while Hills Science Diet was preferred by all subjects over peanuts, peanuts may not have been a low enough food reward to elicit inequity aversion. Also, has been claimed, inequity aversion evolved alongside cooperation so that individuals could maximise the benefits of engaging in a cooperative task, further research in kea should test whether inequity aversion is elicited in the context of a cooperative task. Our experiment and most other experiments examining inequity aversion in other species do not test their subject’s responses to inequity when they are engaging cooperatively.

Kea’s impressive performance on tasks designed to assess the understanding for the need of a partner do suggest that it is possible that kea possess aspects of cooperative cognition similar to that possessed by humans and other species such as elephants and chimpanzees. However, this has only been investigated in one experiment with a small subject pool and it is possible that alternative explanations such as associative learning might explain kea’s performance. It is therefore important to examine whether kea really do understand the need for a partner with further research.

5.4 Final remarks

The finding that kea performed on par with species such as chimpanzees and elephants in tasks designed to assess aspects of cooperative cognition is exciting and suggests that kea may possess aspects of advanced cooperative cognition. While kea did demonstrate a preference for spontaneous prosocial behaviour, I found no evidence of reciprocity in kea. Overall the results from our experiments examining prosociality in kea are inconclusive due to the possibility that the results obtained were solely due to associative learning. I found no evidence of inequity aversion in kea and my findings do not support the hypothesis that inequity aversion evolved in species that are both highly social and cooperative. Overall, this thesis provides the first insights into the cognition underpinning cooperation in kea. Without question, kea are an intriguing, capable and exciting species to study and this research is only the beginning of understanding the “social mind” of this truly remarkable parrot.

Appendices

Appendix 1 – List of online supplementary materials

Supplementary figures, methods and small data tables have been reproduced in later appendices. Videos of example trials can be found at the following online locations:

Chapter 2

Experiment 1: Simultaneous release

https://onedrive.live.com/redir?resid=FFF9877574C90024!411&authkey=!ANIMJ4NPkELx2l4&ithint=video%2cts

Experiment 2: 15 second delay example

https://onedrive.live.com/redir?resid=FFF9877574C90024!430&authkey=!AAW1zTJViBgTwhw&ithint=video%2cts

Experiment 2: 65 s delay example

https://onedrive.live.com/redir?resid=FFF9877574C90024!272&authkey=!ABKxQ4e5f2pLpYY&ithint=video%2cMTS

Experiment 3: Example of a solo and duo platform presentation

https://onedrive.live.com/redir?resid=FFF9877574C90024!443&authkey=!AHACNaVJ6AQNwF0&ithint=folder%2c

Experiment 5: Example of choosing to collaborate

https://onedrive.live.com/redir?resid=FFF9877574C90024!406&authkey=!AIuT7srxsv5mYh4&ithint=video%2cts

Chapter 3

Example of a prosocial and selfish token choice

https://onedrive.live.com/redir?resid=FFF9877574C90024!436&authkey=!AG0FcEdzMfUu1gs&ithint=folder%2c

Chapter 4

Example of inequity trials

https://onedrive.live.com/redir?resid=FFF9877574C90024!440&authkey=!AKtALijQPlud9LM&ithint=folder%2c

Appendix 2 – Supplementary Figures for Chapter 2

Kea perform similarly to elephants, chimpanzees and humans across a range of cooperative tasks

Experiment 2: Delayed partner release

Table A.1: Number of trials and errors it took each bird to reach 25s waiting criterion

Subject	Number of trials/errors
Neo	25/13
Zak	108/44
Taz	112/46
Kati	124/49

Table A.2: Performance of each bird in the randomised delay condition 0-65s

Subject	Successful trials out of 60
Neo	49
Zak	53
Taz	55
Kati	45

Table A.3: Performance of each bird in the randomised delay condition 26-65s

Subject	Successful trials out of 42
Neo	35
Zak	36
Taz	38
Kati	31

Experiment 3: solo/duo apparatus discrimination

Table A.4: Performance of each bird in Experiment 3

Subject	Successful trials out of 20
Neo	14
Zak	15
Taz	20
Kati	15

Table A.5: Trial by trial performance in Experiment 3

Subject	Neo	Zak	Kati	Taz
1	🟩	🟩	🟩	🟩
2	🟥	🟩	🟩	🟩
3	🟩	🟥	🟩	🟩
4	🟥	🟩	🟥	🟩
5	🟥	🟩	🟩	🟩
6	🟩	🟥	🟥	🟩
7	🟥	🟩	🟩	🟩
8	🟩	🟩	🟩	🟩
9	🟩	🟩	🟩	🟩
10	🟥	🟩	🟥	🟩

11	🟩	🟩	🟩	🟩
12	🟩	🟥	🟩	🟩
13	🟩	🟩	🟩	🟩
14	🟩	🟩	🟩	🟩
15	🟥	🟥	🟥	🟩
16	🟩	🟥	🟩	🟩
17	🟩	🟩	🟩	🟩
18	🟩	🟩	🟥	🟩
19	🟩	🟩	🟩	🟩
20	🟩	🟩	🟩	🟩

Experiment 4: no rope control

Table A.6: Performance of each bird in Experiment 4

Subject	Successful trials out of 20
Neo	9
Zak	9
Taz	14
Kati	10

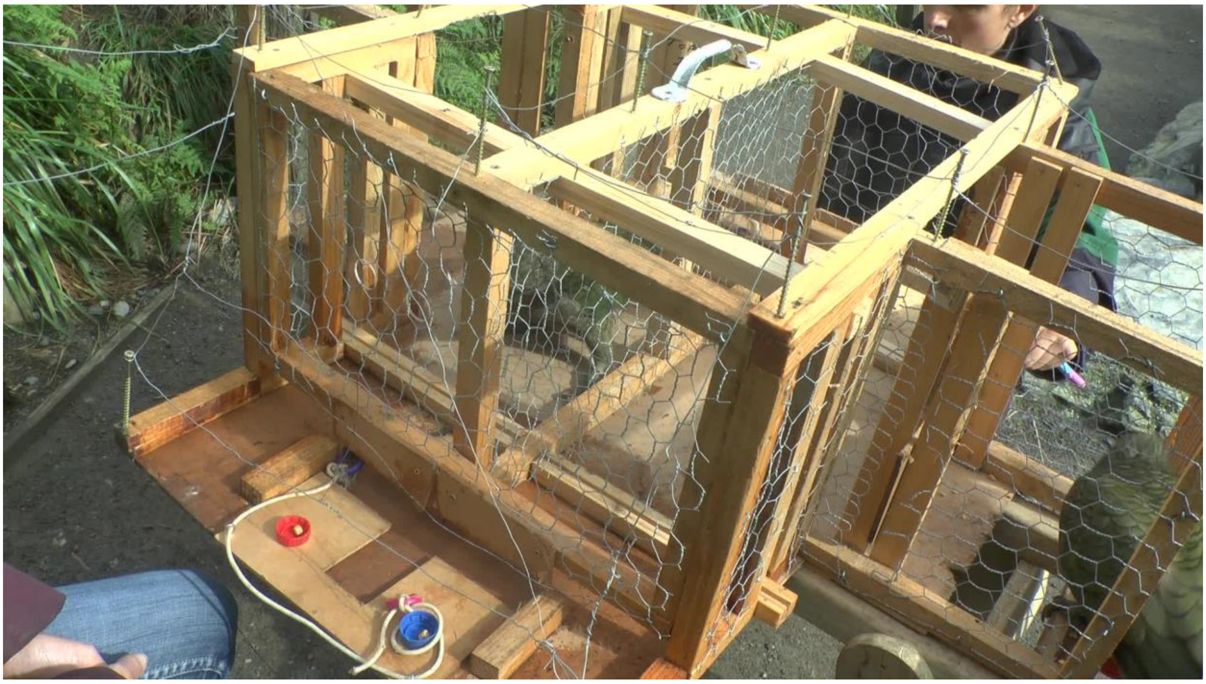


Figure A.1: Set-up for no rope condition (Experiment 4).

Table A.7: Trial by trial performance in no rope condition (Red= Chose no rope platform, Green= chose duo)

Subject	Neo	Zak	Kati	Taz
1	🟥	🟥	🟩	🟩
2	🟩	🟩	🟩	🟩
3	🟥	🟥	🟩	🟥
4	🟩	🟥	🟥	🟩
5	🟥	🟩	🟥	🟩
6	🟩	🟥	🟩	🟩
7	🟥	🟩	🟩	🟩
8	🟥	🟥	🟥	🟩
9	🟩	🟥	🟩	🟩
10	🟥	🟩	🟥	🟥
11	🟩	🟩	🟩	🟩
12	🟩	🟥	🟥	🟥
13	🟥	🟩	🟩	🟩

14	🟥	🟥	🟥	🟥
15	🟩	🟥	🟥	🟩
16	🟥	🟩	🟩	🟥
17	🟩	🟥	🟥	🟥
18	🟥	🟩	🟩	🟩
19	🟩	🟩	🟩	🟩
20	🟥	🟥	🟩	🟩

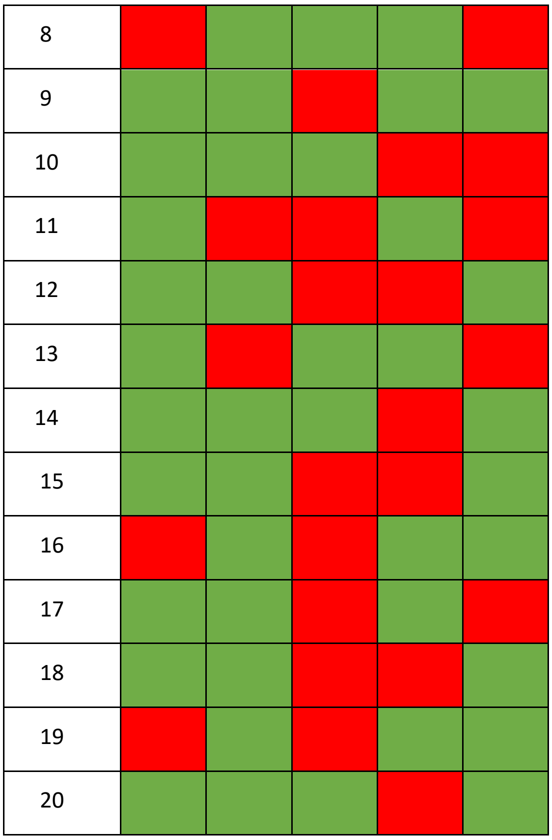
Experiment 5: solo / duo apparatus choice test (working alone or together preference)

Table A.8: Performance of each bird in Experiment 5

Subject	Number of duo choices out of 20
Neo	16 & 16
Zak	7
Taz	11
Kati	11

Table A.9: Trial by trial performance in Experiment 5 (Red = solo, Green=duo)

Subject	Neo 1	Neo 2	Zak	Kati	Taz
1	🟩	🟩	🟩	🟩	🟥
2	🟩	🟩	🟥	🟥	🟩
3	🟥	🟩	🟩	🟩	🟩
4	🟩	🟥	🟥	🟩	🟥
5	🟩	🟩	🟥	🟥	🟥
6	🟩	🟩	🟥	🟩	🟥
7	🟩	🟥	🟥	🟥	🟩



8	🟥	🟩	🟩	🟩	🟥
9	🟩	🟩	🟥	🟩	🟩
10	🟩	🟩	🟩	🟥	🟥
11	🟩	🟥	🟥	🟩	🟥
12	🟩	🟩	🟥	🟥	🟩
13	🟩	🟥	🟩	🟩	🟥
14	🟩	🟩	🟩	🟥	🟩
15	🟩	🟩	🟥	🟥	🟩
16	🟥	🟩	🟥	🟩	🟩
17	🟩	🟩	🟥	🟩	🟥
18	🟩	🟩	🟥	🟥	🟩
19	🟥	🟩	🟥	🟩	🟩
20	🟩	🟩	🟩	🟥	🟩

Appendix 3 - Supplementary Figures for Chapter 3

Prosociality in kea

Table A.10: Number of times each bird chose the prosocial token in each condition for round 1.

Condition				
Neo Subject 7	Spontaneous 28 (out of 60 trials)	Alternating 26 (out of 30 trials)	31 Yoked (out of 30 trials)	Partner absent (out of 60 trials)
Zak	26	16	15	40
Kati	47	28	28	53
Taz	47	30	29	59

Table A.11: Number of times each bird chose the prosocial token in each condition for round 2.

Condition				
Subject	Spontaneous (out of 60 trials)	Alternating (out of 30 trials)	Yoked (out of 30 trials)	Partner absent (out of 60 trials)
	51	30	30	60
Zak	24	15	24	44
Kati	25	13	15	15
Taz	43	23	15	25

Appendix 4 – Supplementary Figures for Chapter 4

Kea fail to show evidence of inequity aversion in a classic token exchange paradigm

Table A.12: Number of successful exchanges for each bird in each condition (out of 50 possible trials)

Subject	EC	IC	FC	FG	NRIC	NRPA
Neo	50	50	50	50	24	16
Zak	50	35	50	50	16	16
Kati	50	50	50	50	17	27
Taz	50	50	50	41	13	18

Table A.13: Number of abandoned trials for each bird in each condition

Subject	EC	IC	FC	FG	NRIC	NRPA
Neo	0	0	0	0	24	22
Zak	0	15	0	0	34	33
Kati	0	0	0	0	25	16
Taz	0	0	0	9	34	25

Table A.14: Number of refusals for each bird in each condition

Subject	EC	IC	FC	FG	NRIC	NRPA
Neo	0	0	0	0	1 push back 1 ignore	4 refusals 8 ignore
Zak	0	1	0	0	1 ignore	1 refusal
Kati	0	0	0	0	6 refusals 2 ignore	6 pushback 1 refusal
Taz	0	0	0	1	3 ignore	5 pushback 1 ignore 1 refusal

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