

SOCIAL LEARNING AND NETWORKS IN *NESTOR* PARROTS

BY

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A thesis

submitted to the Victoria University of Wellington

in fulfilment of the requirements for the degree of

Doctor of Philosophy

Victoria University of Wellington

2020

Acknowledgements

First and foremost, I would like to thank Rachael for being an incredibly knowledgeable and patient supervisor. Thank you to Danielle Shanahan, Jo Leddington, Ellen Irwin, and all the staff at Zealandia for accommodating my work. I would also like to thank Matu Booth and the staff at Nga Manu. Thanks to Martina and Amalia for their assistance as field assistants. And finally, thanks to the friends and colleagues who have supported me over the last few years.

Contents

Thesis Summary.....	8
Chapter 1: General Introduction.....	10
1.1 Behavioural research in conservation.....	11
1.2 Social learning.....	13
1.3 Social network analysis.....	16
1.4 <i>Nestor</i> parrots.....	19
1.5 Thesis aims and overview.....	21
Chapter 2: Social learning and play facilitate tool use in kea.....	23
2.1 Introduction.....	24
2.2 Methods.....	26
2.2.1 Site & Subjects.....	26
2.2.2 Procedure.....	26
2.2.2.1 Testing apparatus.....	26
2.2.2.2 Initial apparatus exposure and baseline play measure.....	27
2.2.2.3 Demonstrator training.....	28
2.2.2.4 Testing procedure.....	28
2.2.2.5 Persistence scores.....	29
2.2.2.6 Scrounging scores.....	29
2.2.2.7 Dominance scores.....	29
2.2.3 Statistical analysis.....	30
2.3 Results.....	31
2.3.1 Does play propensity positively correlate with persistence in a novel tool-use task?.....	31

2.3.2 Does play propensity rank positively correlate with learning speed rank?.....	31
2.3.3 Play propensity and scrounging rate.....	32
2.3.4 How do play propensity, dominance rank, social and asocial learning opportunities affect task-solving likelihood?.....	33
2.4 Discussion.....	35
2.5 Supplementary material.....	36
Chapter 3: video playback in kākā.....	40
3.1 Introduction.....	41
3.2 Methods.....	45
3.2.1 Site & Subjects.....	45
3.2.2 Procedure.....	46
3.2.2.1 Testing apparatus.....	46
3.2.2.2 Pre-testing procedure.....	46
3.2.2.3 Testing procedure.....	46
3.2.2.3.1 Social learning of food aversion.....	46
3.2.2.3.2 Social learning of a foraging task.....	48
3.2.2.3.3 Predator recognition.....	48
3.2.3 Statistical analysis.....	49
3.2.3.1 Social learning of food aversion analysis.....	49
3.2.3.2 Social learning of a foraging task analysis.....	49
3.2.3.3 Predator recognition.....	50
3.3 Results.....	50
3.3.1 Social learning of food aversion.....	50
3.3.2 Video demonstrator and asocial learning effects on	

problem-solving likelihood.....	51
3.3.2 Video playback and predator recognition.....	51
3.4 Discussion.....	53
3.4.1 Social learning from live demonstrators.....	55
Chapter 4: Social networks and distribution in kākā.....	57
4.1 Introduction.....	58
4.2 Methods.....	61
4.2.1 Study sites.....	61
4.2.2 Data collection.....	62
4.2.3 Bray's-Curtis dissimilarity analysis between feeding sites.....	63
4.2.4 Social network analysis.....	64
4.2.5 Spatial scale analysis.....	67
4.2.6 Individual social metric analysis.....	67
4.3 Results.....	65
4.3.1 Bray's-Curtis dissimilarity indices between feeding sites.....	66
4.3.2 Wellington's kākā social network.....	66
4.3.3 Spatial scales and social metrics.....	68
4.3.4 Individual attributes and social metrics.....	68
4.4 Discussion.....	68
Chapter 5: General Discussion.....	73
5.1 Summary of the main findings.....	73
5.2 Social learning and video playback in <i>Nestor</i> parrots.....	75
5.3 Social networks and distribution in kākā.....	80
5.4 Does behaviour have a role in conservation?.....	82

5.6 Concluding remarks.....	84
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Thesis summary

Social learning and network analyses are theorised to be of great utility in the context of behavioural conservation. For example, harnessing a species' capacity for social learning may allow researchers to seed useful information into populations, while network analyses could provide a useful tool to monitor community stability, and predict pathways of pathogen transfer. Thus, an understanding of how individuals learn and the nature of the social networks within a population could enable the development of new behavioural based conservation interventions for species facing rapid environmental change, such as human-induced habitat modification. Parrots, the most threatened avian order worldwide, are notably underrepresented in the social learning and social network literature. This thesis addresses this knowledge gap by exploring social learning and networks using two endangered species of parrot; kākā (*Nestor meridionalis*) and kea (*Nestor notabilis*). The first study explores social learning of tool use in captive kea, using a trained kea demonstrator. The results from this experiment indicate that both social learning and play behaviour facilitated the uptake of tool use, and suggests that kea are highly sensitive to social information even when presented with complex tasks. The second study assesses whether wild kākā can socially learn novel string-pulling and food aversion behaviours from video playbacks of conspecific demonstrators. Although there was no evidence to indicate that kākā learn socially, these individuals also show no notable reaction to video playback of a familiar predator. Therefore, these results are likely due to difficulties in interpreting information on the screens, and not necessarily a reflection of their ability to perceive social information. In the final study, social network analysis (SNA) was performed to map social connectivity within wellington's urban kākā population. SNA indicates that kākā form non-random social bonds, selectively associating with some individuals more than others, and also show high levels of dissimilarity in community composition at different feeding sites. Taken together, these results provide rare empirical evidence of social learning in a parrot species and suggest that even complicated seeded behaviours can quickly spread to other individuals. These findings may also be indicative of the difficulties in conducting video playback experiments in wild conditions, which is an area in need of future research. Overall, these findings contribute to the very limited body of research on social learning and networks in parrots, and provide information of potential value in the management of these species.

Chapter 1

Introduction

Behavioural flexibility allows animals to rapidly adjust their behaviour without the need for genetic change over multiple generations (Brown, 2013). Such behavioural plasticity can facilitate adaptation and promote individual fitness (Sih, 2013), allowing animals to cope with environmental stochasticity (Ducatez, Sol, Sayol, & Lefebvre, 2020), and creating a cognitive buffer to extinction (Sol, 2009). One key cognitive process underpinning adaptation is learning (Greggor, Thornton, & Clayton, 2017), which allows individuals to flexibly alter their behaviour based on prior experience. As human-driven habitat modification continues to rapidly alter the environment globally (Angel, Parent, Civco, & Blei, 2011; Griffin, Netto, & Peneaux, 2017), presenting non-human animals with countless challenges and novel threats (Greggor, Clayton, Fulford, & Thornton, 2016; Griffin et al., 2017), understanding how behavioural processes can be harnessed in the context of conservation is of growing interest in both theoretical and practical contexts (Brakes et al., 2019; Caro, 2016; Donnell, Webb, & Shine, 2010; Gabriel & Golightly, 2017; Greggor et al., 2017). Two areas of social behaviour are of particular promise; social learning and social networks (Brakes et al., 2019; Greggor et al., 2017; Webber & Vander Wal, 2019).

Social learning allows animals to gain information by interacting with, or observing, others and their artefacts (Heyes, 2012). Use of social information can accelerate the rate at which individuals acquire novel information (Aplin et al., 2015; Auersperg, von Bayern, et al., 2014; Gunhold, Whiten, Bugnyar, & Gunhold, 2014), and facilitate the spread of this information throughout populations (Aplin et al., 2015; Kawai, 1965) and across expansive geographic ranges (Fisher & Hinde, 1951). As social diffusion also occurs with experimentally-seeded behaviours (Aplin et al., 2015; Reader, 2010), seeding fitness-enhancing information into at-risk populations could result in positive conservation outcomes (Greggor et al., 2017). Social network analysis (SNA), which maps the connectivity between individuals (Scott, 2000), can also be used to increase the rate of social diffusion by identifying the most socially connected individuals, who will therefore make the most effective demonstrators (Greggor et al., 2017; Lusseau & Newman, 2004; Snijders, Blumstein, Stanley, & Franks, 2017). Additionally, SNA

can provide a valuable tool for monitoring the stability of at-risk population (Rosenbaum, Maldonado-Chaparro, & Stoinski, 2016) and predicting pathways of pathogen transmission (VanderWaal, Atwill, Isbell, & McCowan, 2014), allowing conservationists to make more informed and effective interventions in instances such as disease outbreak and wild-harvesting (Rushmore et al., 2014; Williams & Lusseau, 2006). Although approaches that utilise behavioural interventions remain largely hypothetical, urban habitats provide a promising avenue to explore such possibilities (Ducatez et al., 2020).

To survive and reproduce in such highly modified landscapes (Van Heezik & Seddon, 2018), animals must learn to exploit novel food sources (Møller et al., 2012; Sol, Lapiedra, & González-lagos, 2013), cope with novel predators (Bílá, Beránková, Veselý, Bugnyar, & Schwab, 2017; Woolley & Hartley, 2019), and adjust communication strategies to cope with elevated noise levels (Kight & Swaddle, 2015). However, species that can navigate the perils of urban living, may thrive under such conditions (Lombardi, Comer, Scognamillo, & Conway, 2017; Møller et al., 2012) by exploiting the high abundance of resources contained within anthropogenic landscapes. Behavioural flexibility allows exploitation of resources such as artificial nesting sites (Jerolmack, 2008; Reynolds, Ibáñez-Álamo, J. D., Sumasgutner, & Mainwaring, 2019) and abundant food and water supplies (Coccon & Fano, 2020; Galbraith, Beggs, Jones, & Stanley, 2015; Galbraith, Jones, Beggs, Parry, & Stanley, 2017; Orros & Fellowes, 2015; Plummer, Siriwardena, Conway, Risely, & Toms, 2015; Van Heezik, Freeman, Davidson, & Lewis, 2020). As greater relative brain size is correlated with innovation and behavioural flexibility (Lefebvre, Nicolakakis, & Boire, 2002; Reader & Laland, 2002; Sol, 2009; Sol, Lefebvre, & Rodríguez-Teijeiro, 2005), it is perhaps not surprising that large-brained species, despite a declining trend globally (Gonzalez-Voyer, González-Suárez, Vilà, & Revilla, 2016; Vergara-Tabares, Cordier, Landi, Olah, & Nori, 2020), have the most success in colonizing urban habitats (Ducatez et al., 2020).

1.1 Behavioural research in conservation

The concept of utilising behavioural research in conservation gained significant traction in the mid-1990s when several speculative and theoretical papers made the case that knowledge derived from animal behaviour studies should supplement traditional conservation methods (Caro, 1999; Curio, 1996; Martin, 1998; Sutherland, 1998). At this time, however, it appeared that the field of animal behaviour was yet to make any significant contribution to

conservation. While the contribution made to conservation by behavioural research remains limited (Berger-Tal et al., 2016; Webber & Vander Wal, 2019), improved research methods and a greater general understanding of cognition and behaviour, gives a more optimistic outlook for the utility of behaviour in this context. Social behaviour research, particularly social learning and social networks, appear to be promising avenues to achieve this (Brakes et al., 2019; Greggor et al., 2017; Webber & Vander Wal, 2019).

Learning is a key cognitive process underpinning adaptation (Greggor et al., 2017), as it allows individuals to quickly alter their behaviour in response to changes in the environment (Brown, 2013). With anthropogenic habitat modification occurring at a global scale (Palumbi, 2001), species are required to modify their behaviour to persist in these altered landscapes. This may involve the creation of new behaviours, such as foraging techniques for exploiting novel food sources (Sol, Timmermans, & Lefebvre, 2002), or altering existing behaviours to better cope with human-driven environmental pressures (Ducatez et al., 2020). The ability to adapt via learning has been demonstrably crucial for numerous species in facilitating survival in a variety of modified landscapes (Brown, 2013; Donato & Potts, 2004; Donnell et al., 2010; Ducatez et al., 2020; Sol, 2009).

Behavioural flexibility has been indispensable for facilitating adaptation to introduced toxic cane toads (*Bufo marinus*) in Australia (Doody et al., 2006; Llewelyn, Webb, Schwarzkopf, Alford, & Shine, 2010). A number of species have modified their behaviour by avoiding consuming cane toads all together (Donnell et al., 2010), while others have learned to feed on the toads while avoiding the toxic body parts (Donato & Potts, 2004). In urban environments, several finch species are able to reduce the presence of nest parasites, by intentionally incorporating smoked-cigarette butts in their nest builds, resulting in greater survival of offspring (Reviewed in Reynolds et al., 2019). Animals can also become perceptive of human behavioural patterns, and adjust their responses to reduce risk and conflict (Stankowich & Blumstein, 2005). Given these naturally occurring events, experimentally introducing adaptive information may prove to be an effective means of achieving conservation goals (Brakes et al., 2019; Caro, 2016; Donnell et al., 2010; Gabriel & Golightly, 2017; Greggor et al., 2017).

A popular approach used to apply behaviour in a manner relevant to conservation is aversive conditioning. This method has been successful in deterring common planigales (*Planigale*

maculate) from consuming introduced toxic cane toads (Llewelyn et al., 2010), to teach kākā (*Nestor meridionalis*) not to consume poisons used in pest control operations (Hickling, 1997), and to decrease predation rates of Steller's jays (*Yanocitta stelleri*) on endangered marbled murrelet (*Brachyramphus marmoratus*) nests (Gabriel & Golightly, 2017). Aversive conditioning can also be effective in enhancing antipredator behaviour, allowing scientists to educate naïve animals on unfamiliar predators (Griffin, Evans, & Blumstein, 2001; Maloney & McLean, 1995) and increase survival odds in captive breed-and-release operations (Lopes et al., 2017; Maloney, van Heezik & Seddon, 1999). Although exposing each individual to such training can create strong conditioned responses, allowing for rapid learning and behavioural change (Gabriel & Golightly, 2017; Llewelyn et al., 2010), the practical applicability of this approach has various limitations.

A notable concern is that training each individual is labour intensive and difficult to do at the scale required to meet conservation goals. Though the examples above give accounts of aversive conditioning effectively reducing consumption of toxic substances (Donnell et al., 2010; Hickling, 1997), these were conducted in captivity and could not effectively be applied to whole populations of wild animals. In a rare example in which a behavioural intervention was empirically shown to increase fitness outcomes, antipredator training did initially improve post-release survival of captive-bred houbara bustards (*Chlamydotis undulata*) (Maloney et al., 1999). However, no long-term survival data was collected, and unfortunately, other research has shown that knowledge acquired through antipredator training can be lost within a single month (Griffin, Blumstein, & Evans, 2000; Miller et al., 1990). Although resource requirements and short-lived retention pose substantial barriers to utilising behavioural interventions at the level of the individual, if knowledge can spread socially to other individuals, then it may persist across multiple generations (Cornell, Marzluff, & Pecoraro, 2012), and become embedded within the culture of an animal population (Whiten & Mesoudi, 2008; Whiten, Ayala, Feldman, & Laland, 2017; Whiten, Hinde, Laland, & Stringer, 2011)

1.2 Social learning

The phenomenon of social learning was brought to the forefront of animal behaviour following Fisher and Hinde's (1952) pioneering study on milk-bottle opening in British titmice. This research documented the spread of a novel foraging innovation, in which titmice would

pierce the foil caps of milk bottles to feed on the upper layer of cream, across geographically separated subpopulations throughout the United Kingdom. The subject of social learning gained further traction following the documentation of sweet-potato washing in Japanese macaques, a behaviour that was spontaneously performed by a single female and subsequently spread to other members of the troop (Kawai, 1965). While these studies illustrate the potent effects of social learning, such naturally occurring innovations are rare, and alternative methods to a purely observational approach were therefore required. As such, subsequent social learning research adopted a more experimental focus (Franz & Nunn, 2009; Kendal, Kendal, Hoppitt, & Laland, 2009; Whiten & Mesoudi, 2008).

Diffusion experiments, in which a specific behaviour is manipulated or introduced, and its spread across individuals tracked, are a prominent technique for experimentally detecting social learning (Whiten & Mesoudi, 2008). This is most commonly achieved by training demonstrators to perform a particular behaviour, which they may then introduce to the wider group or population (Aplin et al., 2015; Whiten, 2013). In the first study to utilise this approach, Marler & Tamura (1964) experimentally introduced different song dialects to captive groups of white-crowned sparrows (*Zonotrichia leucophrys*). Diffusion studies since have largely focussed on foraging behaviours, and predominantly utilised two different methodologies.

One approach is the option-bias method, in which demonstrators are trained to perform a task using one-of-two distinct but equivalent actions (Kendal et al., 2009). As only half of the naïve observers should be expected to choose the seeded option by chance alone, a bias for the demonstrated option can be taken as strong evidence of social learning (Aplin et al., 2015; Whiten & Mesoudi, 2008; Whiten, 2005). In a recent study on great tits (*Parus major*), demonstrators were trained to access a feeding station by either sliding a door to the left or the right (Aplin et al., 2015). Although both methods of extracting food were discovered in all populations, the majority of birds preferred the method of their demonstrator. Further illustrating the advantages of the option-bias method, it was observed that when individuals emigrated from one sub-population to another, they would adopt the technique favoured by their new community, revealing a sensitivity to conformity-bias in this species (Aplin et al., 2015). The option-bias method has also been applied using 2-dimensional representations of social demonstrators (Gunhold et al., 2014; Thorogood, Kokko, & Mappes, 2017). Laboratory

experiments have shown that great tits can distinguish between two artificial prey types (distinctly marked food packets), and interpret the responses of foraging conspecifics shown in video playback (Thorogood et al., 2017). Naïve individuals were able to successfully avoid the packets that demonstrators had shown disgust responses to, further illustrating the sensitivity that some animals have to social information.

In a relatively rare field-based social learning experiment (Van de Waal et al., 2013; Whiten & Mesoudi, 2008), four groups of wild vervet monkeys (*Chlorocebus aethiops*) were presented with maize dyed two distinctive colours; pink and blue (Van de Waal et al., 2013). In each group, one of the two colours were treated to make it unpalatable, therefore conditioning the group to only eat one of the two options. When naïve offspring were born into these sub-populations, they also showed a strong preference for the colour consumed by the rest of the group, despite both colours being palatable at this stage. While the option-bias method is now very well established (Aplin et al., 2015; Aplin, Sheldon, & McElreath, 2017; Hämäläinen, Mappes, Rowland, & Thorogood, 2019; Kendal et al., 2009; Van de Waal et al., 2013), two potential issues may arise when using this approach.

Firstly, test subjects may be predisposed to choosing one option over the other. In a recent study, blue tits (*Cyanistes caeruleus*) were shown demonstrators feeding from locations marked with either a cross or a circle, and their subsequent choices were examined (Hämäläinen, Rowland, Mappes, & Thorogood, 2019). Although it was predicted that observers would copy the option used by their demonstrator, the food marked with a circle was most often selected, irrespective of the social information received. A second issue can be encountered should individuals choose to abandon socially acquired information in favour of overt exploration. Kea (*Nestor notabilis*), a notoriously playful and explorative species (Diamond, J. & Bond, 1999; Goodman, Hayward, & Hunt, 2018; Nelson & Wein, 2017), can use social information to facilitate the solving of novel problems (Huber, Rechberger, & Taborsky, 2001). However, when given multiple solving options, kea will quickly abandon social information in favour of their own exploratory behaviour (Gajdon, Amann, & Huber, 2011). In these cases, the latency to solve a novel problem may be a more suitable variable for assessing social learning.

Social information has been demonstrated to accelerate the rate at which individuals will learn a novel foraging technique (Aplin et al., 2015; Auersperg, von Bayern, et al., 2014;

Gunhold et al., 2014). It is, therefore, possible to test for social learning by presenting individuals with a novel foraging task, and examining the effect of social information on the latency to learn the required action (Auersperg, von Bayern, et al., 2014; Gajdon, Fijn, & Huber, 2004; Huber et al., 2001). After a single captive Goffin cockatoo (*Cacatua goffini*; named Figaro) innovated a tool-use behaviour, in which he would use long sticks to retrieve food and play items from behind a mesh screen, social transmission of this behaviour was explored (Auersperg, von Bayern, et al., 2014). Six naïve individuals were split into control (n=3) and demonstration (n=3) conditions. The control group viewed 'ghost' demonstrations in which a tool and food item were moved by magnets, while the demo group observed Figaro performing the tool-use behaviour to acquire the food reward. After five demonstrations, all three cockatoos in the demonstration group successfully learned the task, while no members of the control group did. If it is not possible to separate and control individuals in separate groups, as is often the case under field conditions, quantifying individual exposure to social information may be necessary. This approach was used to assess whether social learning would facilitate uptake of a novel behaviour in wild kea. A single demonstrator was trained to push a tube up and off of a pole to access the food contained within, and the number of times naïve subjects observed this behaviour was recorded (Gajdon et al., 2004). However, although the intention was to analyse the effect of observing a solving demonstrator on solve-likelihoods, exclusion caused by a dominant individual resulted in too few kea solving the task for meaningful analyses to be performed.

The inherent difficulties associated with testing cognition in the wild has meant that the vast majority of social learning studies have been conducted in captivity (Whiten & Mesoudi, 2008). A relatively new method being employed by behavioural researchers, social network analysis, is proving to be a useful tool for the study of social learning in the free-ranging populations (Aplin et al., 2015). Other uses for social network analysis include the study of pathogen transmission (Webber et al., 2016) and social stability (Rosenbaum et al., 2016; Williams & Lusseau, 2006).

1.3 Social network analysis

Social network analysis (SNA), by which groups and populations are mapped by the strength of the interactions between individual members (Scott, 2000), was first applied in the social sciences in the early 1900s (reviewed in Scott, 2000). However, over the past two decades,

SNA has become a key analytical technique in behavioural ecology (Webber & Vander Wal, 2019). This methodology has now been used on a variety of taxa, including various mammals (Rosenbaum et al., 2016; Williams & Lusseau, 2006), birds (Aplin et al., 2015; Aplin, Major, Davis, & Martin, 2020), reptiles and invertebrates (reviewed in Webber & Vander Wal, 2019). The dramatic increase in the usage of social network analysis in behavioural ecology is largely due to factors such as improved methodologies, more accessible and affordable technology (Aplin et al., 2020; Wilmers et al., 2015), and novel statistical tools (Farine, 2013; Hoppitt & Laland, 2011; Krause, Lusseau, & James, 2009).

The connections between individuals, upon which social networks are constructed, can be measured using various types of interactions. Two individuals may be considered to be associated if they engage in behaviours such as fighting, grooming, mating (Farine & Whitehead, 2015), or simply by being within a defined spatial or temporal distance of each other (Aplin et al., 2015; Boogert, Reader, Hoppitt, & Laland, 2008). Early studies were largely focussed on cetaceans, which could be studied relatively easily as individuals are highly recognizable for visual identification (Lusseau & Newman, 2004; Williams & Lusseau, 2006). The approach of real-time observation was also used to assess social connectivity in captive starlings (*Sturnus vulgaris*), by recording the social interactions of focal individuals (Boogert et al., 2008). However, focal observation approaches were limited, as individuals could only be viewed in one specific location, and researchers were likely to miss crucial data points. In recent years, this limitation has been largely alleviated due to advancements in technology.

Technological advances, largely driven by developments in consumer electronics (Wilmers et al., 2015), now allow researchers to simultaneously record the social interactions of multiple individuals, across numerous locations (Aplin, Farine, Morand-Ferron, & Sheldon, 2012; Ferreira et al., 2020; Webber & Vander Wal, 2019). Data has been effectively collected using GPS proximity collars (Cross et al., 2013; Prange, Jordan, Hunter, & Gehrt, 2006; Prange, Gehrt, & Hauver, 2011), passive integrated transponders (Aplin et al., 2015, 2017), and mobile applications that utilise citizen scientists (Aplin et al., 2020). Beyond the initial limitations of data collection, a lack of accessible computer software for analyses added significant difficulty to implementing SNA in behavioural ecology (Webber & Vander Wal, 2019). Emphasis on methods papers (Blonder, Wey, Dornhaus, James, & Sih, 2012; Farine & Whitehead, 2015; Franz & Nunn, 2009; Krause et al., 2009) and the creation of open-source statistical software

(Farine, 2013, 2017; Hoppitt & Laland, 2011) has likely played a crucial role in the increase of behavioural ecology studies exploring social networks in the past decade (Webber & Vander Wal, 2019). This development has been critical for expanding our knowledge of sociality in wild animal populations.

A growing body of research has revealed that pathways detected by SNA can predict the transmission information such as problem-solving techniques (Aplin et al., 2015) and the locations of foraging sites (Aplin et al., 2012). SNA can also be used to predict the pathways of pathogen diffusion (Webber et al., 2016), and to identify the influence of individuals in maintaining group stability (Rosenbaum et al., 2016; Williams & Lusseau, 2006), indicating that SNA may be a valuable technique for application in the context of conservation. Although SNA is yet to contribute to conservation in practice, this is likely due, at least in part, to the lack of taxonomic diversity in the social network literature, in which at-risk species are particularly underrepresented (reviewed in Webber & Vander Wal, 2019). Despite a reputation for their sociality (Aplin et al., 2020), parrots, the most at-risk order (Heinsohn, Buchanan, & Joseph, 2018), are almost entirely absent from the social network literature (Aplin et al., 2020).

Parrots are well renowned for their curious natures (Diamond & Bond, 1999; Overington, Cauchard, Côté, & Lefebvre, 2011), playfulness (Bond & Diamond, 2004; Burghardt, 2005; Lewis & Burghardt, 2010; Nelson & Wein, 2017), and intelligence (Huber & Gajdon, 2006; Lefebvre et al., 2002; Loepelt, Shaw, & Burns, 2016; Rössler et al., 2020; Werdenich et al., 2014). However, although their intelligence and innovativeness could be predicted to facilitate adaptation in a rapidly changing world (Sol, 2009), Psittaciformes are the most at-risk order today (Heinsohn et al., 2018), with nearly one-third of all extant species (112/398) threatened by extinction (Vergara-Tabares et al., 2020). Parrots have experienced such decline due to pressures from exploitation for the pet trade (Forshaw & Knight, 2017; Pires, 2012), predation by introduced species (Heinsohn et al., 2015; Murphy et al., 2017; Wilson, Karl, Toft, Beggs, & Taylor, 1998), and habitat destruction (Vergara-Tabares et al., 2020). Widespread forest clearance (Brooks et al., 2002; Hansen et al., 2013) has resulted in particularly poor conservation outcomes for forest-dwelling parrots (Vergara-Tabares et al., 2020). As over 70% of parrots are forest-dependent (Newton, 1994; Vergara-Tabares et al., 2020), forest destruction has had a magnified effect on this order. Despite their sensitivity to

habitat change, and forest-dependence, numerous species of parrot have had great success colonizing urban environments (Aplin et al., 2020; Davis, Major, & Taylor, 2014; Davis, Taylor, & Major, 2011; Hobson, Avery, & Wright, 2014; Recio, Payne, & Seddon, 2017; Sol et al., 2013). Urban landscapes are therefore an important consideration in parrot conservation. Additionally, as large brains, behavioural flexibility and innovativeness are correlated with successful urban adaptation (Barrett, Stanton, & Benson-Amram, 2019; Ducatez et al., 2020; Fristoe, Iwaniuk, & Botero, 2017), the parrot-urban intersection makes a unique case for integrating behaviour and conservation.

1.4 Nestor parrots

Kākā (*Nestor meridionalis*) and kea (*Nestor notabilis*) are both endangered species of parrot endemic to New Zealand (Garcia-R & Di Marco, 2020; Wilson et al., 1998), with as few as 1000 individuals of each species remaining in the wild (Dussex & Robertson, 2013). Like all of New Zealand's endemic avifauna, *Nestor* parrots have evolved in the absence of mammalian predators, and therefore lack innate defences against introduced predators such as rats, mustelids, and cats (Garcia-R & Di Marco, 2020; Robertson et al., 2013; Wilson et al., 1998). As such, the survival of these species is heavily reliant on intensive conservation management. Although significant effort is now being put into kea and kākā conservation (Berry, 1998; Maxwell, 2011; Miskelly & Powlesland, 2013), human-wildlife conflict has also been a major cause of decline in these species (Miskelly, 2014; Temple, 1996).

Kākā were registered as a game species from 1887 to 1914, while kea were excluded from nearly all protective legislation until 1986 (reviewed in Miskelly, 2014). Due to attacks on livestock (Reid et al., 2020), persecution against kea was actually incentivised (Temple, 1996). From the early 1800s to the mid-1900s over 150,000 kea were killed according to the government bounty scheme (Temple, 1996). Although both kākā and kea now receive full legal protection from human persecution (Miskelly, 2014), interactions with humans and their artefacts continue to pose significant risks to these species as they colonize areas of human settlement. *Nestor* parrots experience death and illness caused by ingesting anthropogenic foods (Gartrell & Reid, 2007; Zealandia, unpublished data), lead poisoning as a result of chewing on roofing materials (Reid, McInnes, Mclelland, & Gartrell, 2012; Sriram, Roe, Booth, & Gartrell, 2018), and human-wildlife conflict (Gajdon, Fijn, & Huber, 2006; Linklater et al.,

2018; Reid et al., 2020). Conventional conservation approaches have thus far failed to mitigate these issues.

Nestor parrots are charismatic, large-brained species, which possess exceptional cognitive abilities (Reader et al., 2011). Kea have been the subject of extensive cognitive testing in captive conditions, and have displayed a range of notable cognitive abilities such as causal reasoning, tool use, and inhibitory control (Fijn et al., 2006; Huber & Gajdon, 2006; Schwing & Huber, 2016). Cognitive testing on kākā remains relatively limited, however, previous research has demonstrated that kākā are capable of innovating solutions to novel foraging tasks (Loepelt et al., 2016). Additionally, kea are a highly neophylic species and, as such, will readily interact with novel objects (Gajdon et al., 2004). Kākā, despite being neophobic, will interact with novel objects given a little time and encouragement (Loepelt et al., 2016). Both species also show little fear of mammals, having evolved in the absence of mammalian predators, so are largely unimpacted by the presence of human researchers (Gajdon et al., 2004; Loepelt et al., 2016). As highly social species (Bond & Diamond, 2004; Diamond & Bond, 1991; Nelson & Wein, 2017), they are also exposed to large quantities of social information, making them ideal test candidates for researching various elements of social behaviour.

Although kea are an extensively studied species for avian cognition (Auersperg, Huber, & Gajdon, 2011; Auersperg, Von Bayern, Gajdon, Huber, & Kacelnik, 2014; Heaney, Gray, & Taylor, 2017; Huber & Gajdon, 2006; Lambert et al., 2017), studies of social learning are relatively limited. A key constraint to additional testing is a lack of naïve test subjects. As the vast majority of kea research has been conducted in a single laboratory, the individuals available have been used in many studies and therefore already highly familiar with numerous problem-solving tasks (Auersperg et al., 2011; Gajdon et al., 2011; O'Hara, Gajdon, & Huber, 2009; Schloegl et al., 2009). One study conducted with captive kea reported that kea were able to use social information to facilitate problem-solving, however, individuals were quick to abandon copied behaviours in favour of overt exploration (Gajdon et al., 2011). This propensity for kea to explore and innovate casts doubt on the utility of assessing socially learning using a two-option task design, as this method benefits from conformity to socially presented information (Aplin et al., 2015; Van de Waal et al., 2013). An alternative approach is to introduce a complex foraging task and assess the effects of social information on learning time (Alem et al., 2016; Auersperg, von Bayern, et al., 2014; Loukola & Chittka, 2017).

However, though this study design has been attempted with wild kea, no evidence of social learning was detected (Gajdon et al., 2004). Although social learning has never been directly tested in kākā, it was reported that observing knowledgeable conspecifics facilitated uptake of a string-pulling behaviour (Loepelt et al., 2016). As kākā and kea readily interact with humans (Fijn & Huber, 2004; Loepelt et al., 2016), training of elaborate tasks, even in the wild, is likely possible.

1.5 Thesis aims and overview

The primary aim of this thesis is to examine sociality in two species of *Nestor* parrots by exploring two areas of social behaviour; social learning and social networks. The experiments in this thesis test whether social learning will facilitate the learning of novel behaviours, both by utilising trained live demonstrators and video playback. Additionally, monitoring of kākā, both within the Zealandia eco-sanctuary and the surrounding suburban landscape, was conducted to construct a social network for Wellington's kākā population. The contents of each chapter are further outlined below. I also comment on the potential utility of social learning and social network research in the conservation and management of these particular species, and in conservation practice globally.

In **chapter 2** a social-diffusion experiment was conducted with captive kea to assess the roles of social learning, and play as a motivational trait, in the uptake of a novel tool-use behaviour. This was achieved by training a single demonstrator to solve a tool-use task, which required a wooden ball to be picked up and placed into a 'vending-machine-like' apparatus, and tracking the diffusion of this solving technique to other individuals.

The experiment in **chapter 3** builds on the previous study, by investigating social learning in free-ranging kākā. Two behaviours were introduced using video playback; food-aversion and problem-solving. The food-aversion video displayed a demonstrator kākā showing a typical avian disgust response to one food source in a two-option task (Kendal et al., 2009; Van de Waal et al., 2013). For the subsequent test, a video demonstrator was shown solving a string-pulling foraging task. The effects of video playback on the food choices and problem-solving latency of naïve individuals were subsequently examined. To further validate whether kākā could interpret video footage without the added confound of social learning, responses to video playback of a familiar predator were also assessed.

Chapter 4 explores social networks and the distribution of Wellington's kākā population. Monitoring of six established feeding sites, both within and outside of the Zealandia perimeter, was conducted using video recording and citizen science data collection. The data collected were used to construct a social network based on the spatio-temporal clustering events of individuals. Additionally, dissimilarity analysis of individual visits between the sites was performed to provide further information on kākā space use in Wellington.

Concluding this thesis, **chapter 5** provides a summary of the work conducted and the presented findings. I also interpret these results and discuss their implications in both local and global contexts. Additionally, I discuss the limitations to be considered in the study designs, and conservation applicability of this research. Finally, I make suggestions for the future direction of social behaviour research and its applicability to conservation practice.

Chapter 2

Birds just want to have fun: Play facilitates tool use in kea (*Nestor notabilis*)

Abstract

Play behaviour is theorised to facilitate the development of mechanically challenging foraging techniques. However, attempts to quantify individual play motivation have been limited, with no experimental exploration of play behaviour in the development of tool use. To assess the role of play in the learning of a novel tool-use behaviour, we conducted a social-diffusion experiment with captive kea (*Nester notabilis*) using a vending machine-like apparatus. The task required subjects to manipulate wooden balls, by picking them up and placing them into the apparatus to receive a food reward. We quantified individual play propensity by recording the rate at which subjects engaged in play during the initial habituation period for the task. Subsequently, ten out of twelve naïve kea learned to solve the tool-use task over eight days, and the likelihood of solving the task was positively influenced by play propensity, individual and social learning. Subjects that displayed a higher propensity for play showed greater persistence when engaging with the task, and also required fewer trials to become proficient in performing the novel behaviour. This is the first experimental evidence that intrinsic motivation for play facilitates the uptake of tool use, providing further evidence of the adaptive value of play, and how variation in play motivation can explain intrapopulation differences in tool use ability.

2.1 Introduction

Despite decades of study, little is known about the cognitive traits that facilitate tool use, or the environmental selection pressures that shape them (Call, 2013; Koops, Furuichi, & Hashimoto, 2015; McCoy et al., 2019; Seed & Byrne, 2010). With tool use documented in far less than 1% of species (Biro, Haslam, & Rutz, 2013), spontaneous tool use is sufficiently rare to hinder more in-depth study into how it arises and spreads through populations (Seed & Byrne, 2010). Though there has been significant exploration into whether specific species primarily rely on asocial or social learning to acquire tool use (Auersperg et al., 2014; Gajdon, Amann, & Huber, 2011; Hunt & Gray, 2004; Tebbich et al., 2001; Vale et al., 2017; Wild et al., 2019), these studies do little to explain how tool use is innovated, or the occurrence of intrapopulation variation in tool use ability (Seed & Byrne, 2010).

Increases in relative brain size, and the resulting increased capacity for physical cognition (Reader & Laland, 2002), have been proposed as explanations for why few species can use tools (Biro et al., 2013; Emery & Clayton, 2009; Lefebvre, Nicolakakis, & Boire, 2002). Yet tool and non-tool-using congeneric species may have comparable brain mass and perform similarly in physical cognition tasks not involving tools (Mulcahy & Call, 2012; Tebbich, Sterelny, & Teschke, 2010). Environmental factors such as food abundance have also been postulated to drive the innovation of tool use (Moura & Lee, 2004; Tebbich et al., 2002). The ‘opportunity hypothesis’ suggests that a high abundance of foods requiring tool use influences whether a population utilises tools or not (Sanz & Morgan, 2013). However, comparative analyses of chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*) reveal little difference in the need to use tools to access the foods in their respective environments (Koops et al., 2015). Instead, comparative observational research suggests that interspecies differences in motivation to play with objects utilised in foraging are pivotal in explaining why chimpanzees are prolific tool users, while bonobos are not (Koops et al., 2015). To date, however, there have been no experimental evaluations of the correlation between individual motivation for play and the development of novel tool use.

The kea (*Nestor notabilis*), a large alpine parrot endemic to New Zealand (Diamond & Bond, 1999), is well renowned for its remarkable cognitive abilities (Lambert et al., 2017; O’Hara et al., 2009, 2016) and playfulness (Bond & Diamond, 2004; Nelson & Wein, 2017). Though captive kea have been observed using sticks and a variety of compact tools (Gajdon et al.,

2011; Huber, 2011; Huber et al., 2014), tool use is not known to exist in their natural foraging ecology. However, since 2010 wild kea have been triggering mustelid traps by inserting sticks through the protective mesh and feeding on the crushed egg bait that leaks from the trap box (Goodman et al., 2018). Interestingly, objects not suited for triggering the traps (batteries, wrappers, plastic tags and stones) were routinely found inserted through the mesh for several years prior to the development of stick usage (Maxwell, 2011). As kea appear intrinsically motivated to insert objects into openings (Auersperg, Gajdon, & Huber, 2010; Gajdon et al., 2011; O'Hara et al., 2009), it is likely that the initial behaviour of pushing objects into the traps was not an attempt to acquire the food. Instead, it is possible that this initial behaviour was driven by the kea's intrinsic motivation for play, and served as a precursor for the tool use that followed (Auersperg et al., 2015; Marie et al., 2015).

The recent documentation of spontaneous tool use in the wild (Goodman et al., 2018), combined with their propensity for play (Bond & Diamond, 2004; Nelson & Wein, 2017), make kea a unique species to study the role of play on the uptake of novel tool-use behaviours. Here we test the hypothesis that play facilitates the development of tool use in kea. Under this hypothesis, we predicted that more playful individuals would show greater persistence when engaging with a novel tool-use task. To further assess whether persistence simply facilitated tool use by increasing opportunities for learning, or if more playful individuals were also more efficient learners, we explored the relationship between learning speed and playfulness. Additionally, we predicted that; 1) playful individuals would be more accurate solvers, and therefore more likely to solve the task in any given trial, and 2) less playful individuals will primarily be motivated to frequent the apparatus to acquire food, and will therefore engage in higher rates of scrounging.

To test the above hypotheses, a social-diffusion experiment was conducted with captive kea (Whiten & Mesoudi, 2008). The introduced behaviour required subjects to manipulate a wooden ball, dropping it into the testing apparatus to receive a food reward. This behaviour meets the most commonly accepted definitions of tool use, as the wooden balls were freely manipulable, their trajectory was controlled by the user, and they were used to produce a mechanical reaction (St Amant & Horton, 2008). In addition to individual play propensity, the influence of dominance rank, social and asocial learning on tool use acquisition were also examined.

2.2 Methods

2.2.1 Site & Subjects

A total of 13 kea (three females and ten males) participated in the experiment. All individuals were born and raised in captivity except Kati, who was brought in as a fledgeling after suffering the loss of his upper mandible. The kea in this study had very little experience in previous experiments and had not been exposed to any tasks or apparatuses similar to that described in this paper. All subjects were housed together in a large outdoor aviary (approximately 40m L x 20m W x 6m H) at Willowbank wildlife reserve, Christchurch, New Zealand. The aviary was equipped with several feeding platforms, a pond, native flora, as well as additional structures for enrichment (a barn, various bridges and railings to climb on). The floor of the aviary was comprised of dirt, boulders, gravel and vegetation. Outside of testing, the subjects routinely received food in the morning between 0800 and 1000 which consisted of a variety of fruits, vegetables, and nature's diet parrot pellets. Water was available *ad libitum* at all times. The group's staple diet was not provided until after the testing period each day. Individuals were identifiable by unique leg bands and could be viewed in close proximity due to their general lack of fear of humans.

2.2.2 Procedure

2.2.2.1 Testing apparatus

The testing apparatus (Fig. 1) consisted of an L-shaped wooden box (H 50cm x W 30cm x L 47cm). The lower section of the L-shape served as a platform on which the kea could stand while participating in the task. The top of the box could also be perched on. The front face of the apparatus had two coloured cups, and at the bottom-centre of the front face, equal distance to both cups, was a ball dispenser. A wooden ball (20mm diameter) was always available, when it was removed another ball was automatically released after a 10 s delay. Once a ball was placed into one of the two cups, parrot pellets and sunflower seeds were dispensed automatically from the apparatus from an opening above the ball dispenser.



Fig. 1. Front view of the testing apparatus and three participating kea. The individual on the left is holding a ball while on the apparatus and is therefore engaged in a trial. A solve can be completed by inserting the ball into either the blue or green cups. Also visible is the food dispenser (the orange square), and below that the ball dispenser with a ball available.

2.2.2.2 Initial apparatus exposure and baseline play measure

Prior to demonstrator training, kea were given access to the apparatus for three hours, between 0800 and 1100 to assess their baseline behaviour toward the apparatus and to select a demonstrator. To ensure all subjects had access to the apparatus, the puzzle box was moved between three locations over this initial exposure period. All 13 kea made contact with the apparatus and engaged in at least one trial during this habituation phase (see section 2.2.4 for the definition of a trial). A single individual, Taz, spontaneously solved the puzzle once during this time and was therefore selected as a demonstrator for the main experiment.

During the habituation period, baseline play rates for all kea were recorded. The play behaviours were those categorised by Bond & Diamond (2003, 2004), described in supplementary table 1. Object-play events involving the vending-machine ball were excluded from the play measure. As predicted by the neophylic nature of kea (Diamond & Bond, 1999; Gartrell & Reid, 2007), the subjects quickly focussed on the novel apparatus. All 13 kea made contact with the apparatus, although one subject (Angelina) only contacted the apparatus four times throughout the entire experiment so was omitted from all analyses. The trained demonstrator (Taz) was also excluded from analyses. The remaining 11 kea performed 102

play behaviours during this initial exposure period. Play behaviour rates were weighted by the total amount of time each individual was observed to give a play-events-per-minute score. No food rewards were given during this period.

2.2.2.3 Demonstrator training

Taz was a mid-ranking male within the social group, so although he could monopolize the apparatus from some individuals, he was unable to exclude all other subjects from participating. Despite having spontaneously solved the apparatus on day one, Taz still required training to reliably perform the desired action of inserting the ball into the coloured cups on the apparatus. The training was conducted near a corner of the aviary where viewing by naïve kea was obscured by a shed, flora, and research assistants. Non-demonstrators were also distracted during this time by feeding occurring away from the training area. Taz was trained on a single colour so that it could be examined whether naïve individuals would favour the option used by the demonstrator. However, while Taz was reliably using the blue cup by the end of the training, once other birds were allowed to interact with the apparatus, he began to solve the apparatus using both coloured cups. As such, the effect of demonstrator colour choice on conspecific colour preference could not be accurately measured (methods and results for social learning of colour preference are included in the supplementary material section of this chapter).

2.2.2.4 Testing procedure

The apparatus was placed in the aviary between 0800-1100 for eight consecutive days. Testing was restricted to the mornings as the kea became relatively inactive as the temperature increased. Despite all being housed in the same aviary, social dynamics influenced where in the aviary each individual was likely to go, therefore the test apparatus was moved between four locations at approximately half-hour intervals to maximise the likelihood that all kea would have access to the puzzle. To account for participant fatigue, the location order was pseudorandomized each day. On the last two days of testing, sites were prioritised which would allow inexperienced subjects a greater chance of interacting with the apparatus.

During testing, data were recorded in real-time by one researcher and filmed using GoPro cameras by three research assistants. Behaviours (described below) were narrated while

filming and later coded from videos. A trial was defined as occurring when a bird was holding the ball while in contact with the apparatus. A trial ended either when an individual left the apparatus, completed a solve (defined as an individual placing the token into one of the two cups), or failed the trial (the token was dropped into a position where it could not be recovered, or was picked up by another individual). Subjects were counted as having observed a solve only when in the line of sight of a solving demonstrator. If an individual was engaged in an activity that would hinder viewing, such as preening or drinking, an observation was not counted.

2.2.2.5 Persistence scores

Assessments of individual levels of persistence are commonly based on variables such as apparatus contact time, trial time or attempt rates (Horik & Madden, 2016; Chow, Lea, & Leaver, 2016; Ulrich, Johnson, & Kay, 2018). However, these prior experiments were almost exclusively performed with individuals isolated from one another, where standardisation of conditions such as access time to an apparatus is easier to achieve. As all test subjects in this experiment were housed together, when quantifying persistence, it was necessary to account for differences in trial opportunities resulting from access disparities. Additionally, as the balls used were dispensed one-by-one with a 10s delay in between, at times individuals were in contact with the apparatus but could not participate in a trial due to the absence of a ball. Therefore, persistence was assessed by calculating the amount of time individuals spent engaged in trials (manipulating the ball while on the apparatus), divided by the amount of time when participating in a trial was possible for a subject throughout the experiment (i.e., when an individual was in contact with the apparatus and a ball was available). Thus, a persistence score of 0 would represent the lowest persistence in the task and a score of 1 would indicate the maximum task persistence possible.

2.2.2.6 Scrounging scores

When food was dispensed from the apparatus after a successful solve it was often targeted by other individuals. When an individual took the reward from a solve performed by another subject this was counted as a scrounging event. The number of scrounging events for each individual was divided by the number of times they contacted the apparatus to account for access disparities, giving a final scrounge score.

2.2.2.7 Dominance scores

Before each testing session, each kea was given a small amount of peanut butter as part of a daily headcount and health check. Due to the high value of the food, agonistic interactions occurred as individuals jockeyed for position to get their peanut butter serving. The winners and losers of these agonistic interactions were recorded, along with all other agonistic interactions viewed throughout the experiment. David's scores for individuals (Gammell et al., 2003) were calculated to obtain a dominance hierarchy for the group.

2.2.3 Statistical analysis

To test whether more playful individuals would also show greater persistence when learning a novel tool-use behaviour (manipulating a ball to obtain a food reward), the correlation between individual play-propensity and persistence score was calculated using a Spearman rho test. Additionally, to test whether propensity for play correlated with individual learning speed, individual learning rates were calculated by counting the total number of failed trials each individual required before becoming proficient in the task (5 sequential solves, criteria used in prior kea learning studies (Auersperg, Gajdon, & Huber, 2009)). Initially, the behavioural measures for play and learning speed were used, which yielded a non-significant correlation (Spearman rho: $\rho = -0.49$, $p = 0.177$, $n = 9$). However, this analysis excluded the two individuals with the lowest play-scores (Johnny and Boh), as they never reached the task learning criterion (5 consecutive solves). To enable these individuals to be included in the analysis, the data were reanalysed using individual play-propensity ranks (rank 1= fewest play events, rank 11 = most play events) and learning speed rankings (rank 1 = higher number of failed trials before reaching proficiency, rank 11 = fewer failed trials before reaching proficiency). Neither Johnny nor Boh reached proficiency, therefore as Johnny had not solved the task within 21 trials, but Boh had, he was ranked the least efficient learner (rank 11) and Boh was ranked second to last (rank 10).

To test whether playful individuals were more accurate solvers, logistic generalized linear mixed models (GLMMs) were used to test the effects of play-propensity on solve likelihoods, while accounting for dominance rank, social learning, and asocial learning opportunities. The response variable was whether or not the trial was solved (0/1). Opportunities for individual learning were measured by quantifying the total amount of trial time (seconds) that each

individual had before the current trial. Opportunities for social learning were measured by counting the number of times an individual observed conspecifics successfully solve the task prior to the current trial. These measures of individual and social learning were rescaled to remove convergence errors and included as fixed factors in the model, together with play-propensity and dominance ranks. Individual ID was included as a random factor. All possible models were derived from a global model containing the variables above, and for each model in the resulting set, the Akaike Information Criterion corrected for small samples sizes (AICc) was calculated, as well as the change in AIC relative to the best model in a set (ΔAICc), and the Akaike weight (AICw) which gives the conditional probability of the model (Burnham & Anderson, 2002). As multiple candidate models for best fit were identified (i.e., $\Delta\text{AIC} < 2$), a multi-model averaging approach was employed to calculate estimates for model parameters by averaging coefficients across all possible models in the set (Burnham & Anderson, 2002). Lastly, we used a Spearman rho correlation to assess the relationship between play propensity and scrounging rate for each individual.

2.3 Results

All 11 naïve kea participated in the experiment, with a total of 559 trials and 309 solves occurring over the eight-day period. The 11 subjects engaged in an average of (mean \pm SD) 50.8 ± 26.9 trials each with all but one (Johnny) solving the task at least once. The remaining 10 kea completed an average of (mean \pm SD) 28.1 ± 26.8 solves each.

2.3.1 Does play propensity positively correlate with persistence in a novel tool-use task?

Individual persistence score was strongly positively correlated with play propensity score (Fig 2A: Spearman rho: $\rho = 0.79$, Bonferroni corrected $p = <0.001$, $n = 11$). On average, playful individuals spent a greater proportion of their time engaged in trials when they had the opportunity to do so (i.e., when they had access to a ball and the apparatus).

2.3.2 Does play propensity rank positively correlate with learning speed rank?

Learning speed ranks were strongly correlated with play propensity ranks (Fig 2B: Spearman rho: $\rho = 0.83$, Bonferroni corrected $p = <0.001$, $n = 11$). Compared to less playful conspecifics, individuals that engaged in higher rates of play were ranked as more efficient learners, requiring fewer trials before reaching proficiency.

2.3.3 Play propensity and scrounging rate

There was a strong negative correlation between scrounging rates and play-propensity (Fig 2C: Spearman rho: $\rho = -0.78$, Bonferroni corrected $p = <0.001$, $n = 11$). This indicates that the more prolific scroungers were also less playful individuals.

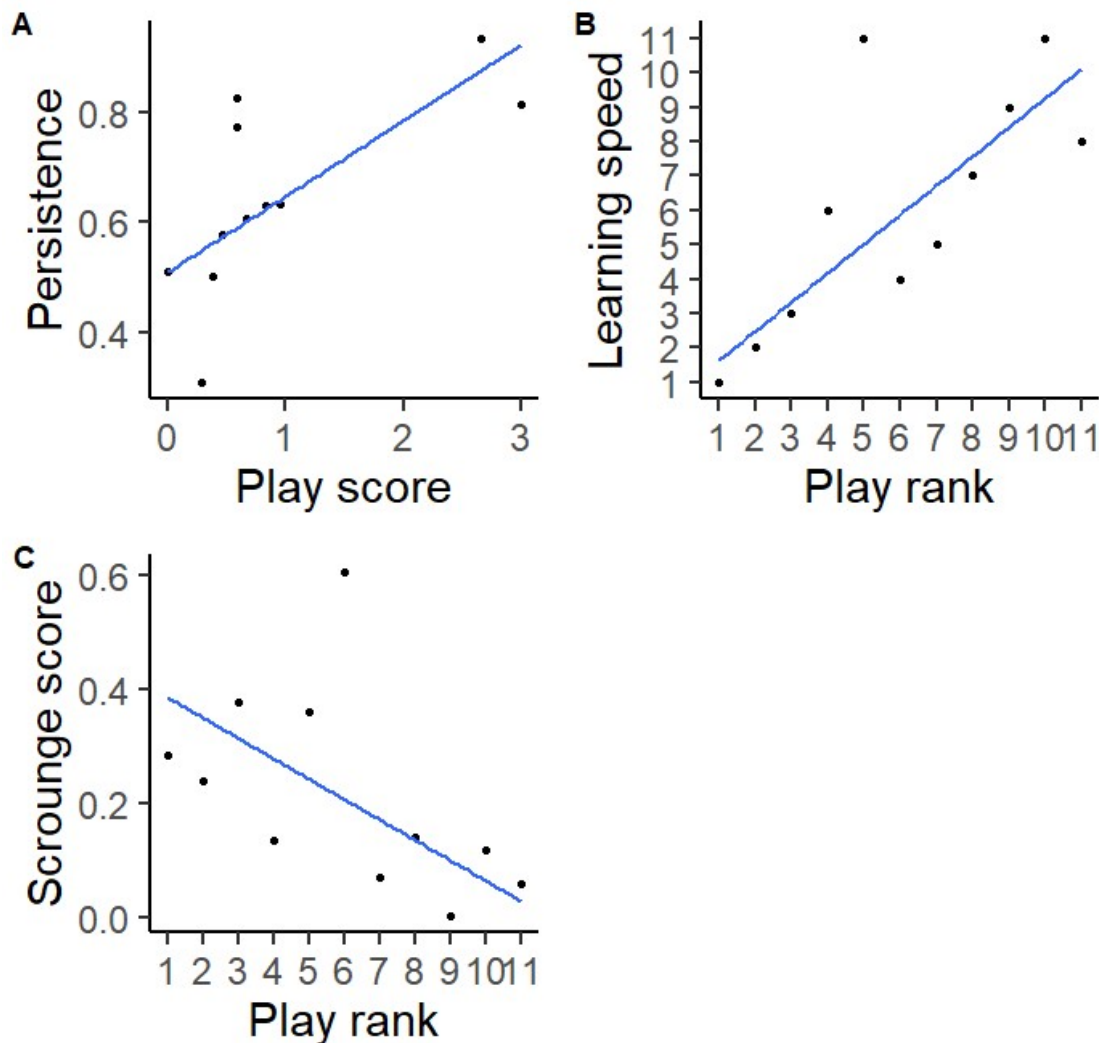


Fig.2 (A) Individuals that engaged in higher rates of play also showed greater levels of persistence. Values on the x-axis represent the number of play events individuals engaged in per minute, values on the y-axis show the proportion of time individuals spent engaged in trials. (B) Individuals that engage in higher rates of social play were more efficient learners and required fewer failed trials before learning the seeded task. Kea represented by higher values on the x-axis engaged in more play events. Higher values on the y-axis represent subjects that were faster learners. (c) Rates of play were negatively correlated with scrounging rates. Individuals with higher play ranks engaged in more play events per minute. Values on the y-axis show the proportion of visits to the apparatus where individuals engaged in scrounging. The lines represent the best fit.

2.3.4 How do play propensity, dominance rank, social and asocial learning opportunities affect task-solving likelihood?

The two candidate models determined as the best fit included play-propensity score, dominance rank, individual learning (time spent in trials) and social learning opportunities (observations of solving conspecifics) with an interaction term (Table 1). Coefficient averaging across all models (table 2) indicates that playful individuals are more likely to solve the task in any given trial, and the likelihood that an individual successfully solves the task significantly improves as both their time engaged in trials and number of observations of solving conspecifics increases (Fig. 3). Dominance rank did not affect solve likelihood.

Table 1. The Null and top three models for play, individual and social learning on solve likelihood.

The variables included are; the number of solves each individual has observed (social information), the amount of time(s) each individual has spent engaged in trials prior to their current attempt (asocial learning), play-propensity scores and dominance ranks. Support for the Null and top three models are shown. AICc is the small sample Akaike Information criteria, $\Delta AICc$ is the change in AICc relative to the top model, AICw (Akaike weight) is the conditional probability of the model.

Models	AICc	$\Delta AICc$	Weight
Null	655.27	176.83	0.00
Number of solves observed * Time in trials + Play-propensity	478.43	0.00	0.60
Number of solves observed * Time in trials + Play-propensity + Dominance rank	480.33	1.89	0.23
Number of solves observed * Time in trials + Dominance rank	482.06	3.63	0.10

Table 2. Multi-model average for the models of play, individual and social learning on solve likelihood. Related to Figure 3. For each predictor we list the regression coefficient, the SE, 95% CI, and the Relative Variable Importance (calculated as the sum of AIC weights for all models containing the predictor). Predictors that influence the response variable (as indicated by CI that do not bound zero) are highlighted in bold.

Variable	Estimate	SE	95% CI	RVI
Number of solves observed	0.708	0.186	0.344 to 1.072	1
Time in trials	1.072	0.169	0.741 to 1.403	1
Number of solves observed * Time in trials	-0.164	0.062	-0.278 to -0.059	0.97
Play-propensity	0.876	0.500	0.264 to 1.771	0.84
Dominance rank	-0.009	0.632	-0.262 to 0.195	0.28

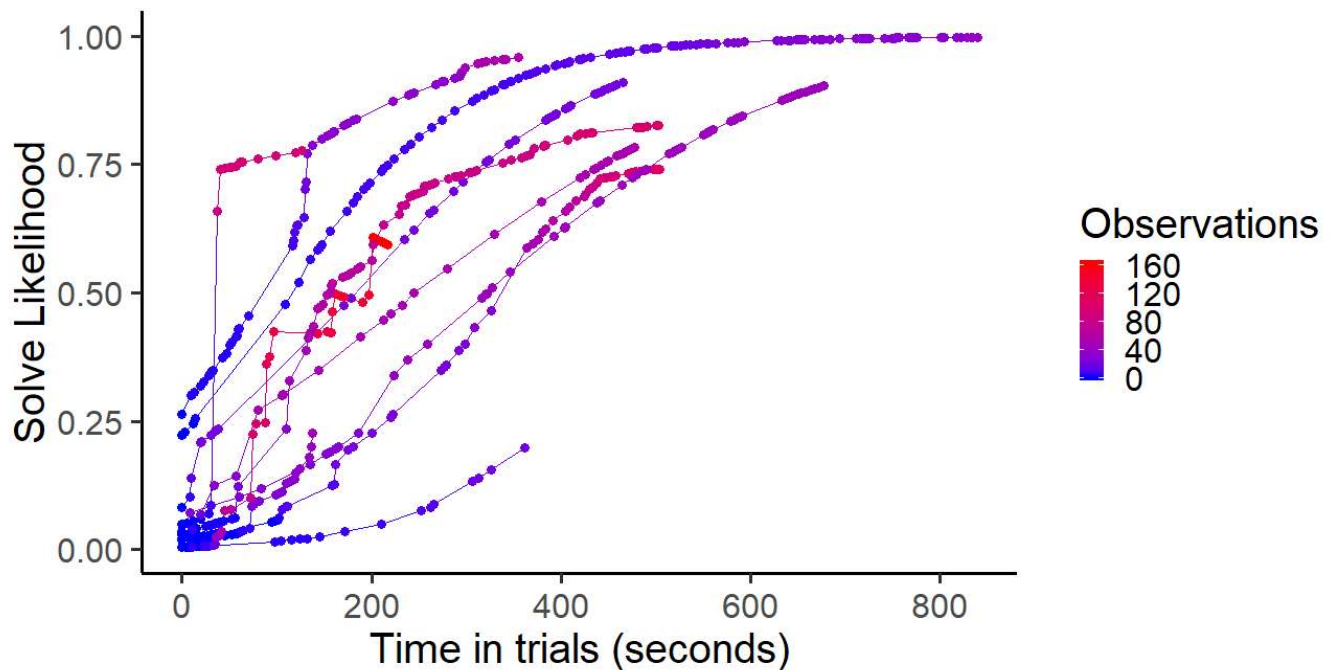


Fig 3. Solve likelihood for each of the 11 kea, as predicted by time engaged in trials and number of observations. As each individual's time in trials (movement along the x axis) and social information (colour change from blue to red) increases, the likelihood of them solving any given trial increases.

2.4 Discussion

Investigations of the role of play in the development of tool use have previously been limited to observational, comparative studies (Bond & Diamond, 2004; Kenward et al., 2011; Koops et al., 2015). This experimental approach provides the first intraspecific evidence in support of the hypothesis that play facilitates the development of tool use. Analyses show a positive correlation between an individual's play propensity and persistence in a novel tool-use task. More playful kea were also faster learners, requiring fewer trials to reach tool use proficiency. Finally, playful individuals were also more accurate learners, as they were more likely to solve the task in any given trial. In addition to play, the uptake of the novel tool-use behaviour was facilitated by social learning, with the likelihood that an individual would solve the task in any given trial increasing with more observations of solving conspecifics. This suggests that differences in play motivation may not only explain interspecific differences in tool use ability (Koops et al., 2015) but may also influence intraspecific variation in tool use behaviour.

Wild kea have been documented spending extensive periods (>1hr) in play, often involving objects (Bond & Diamond, 2004; Goodman et al., 2018). Thus play could be expected to facilitate the development of tool use behaviours in this species (Gajdon, Lichtnegger, & Huber, 2014), as more time spent interacting with objects leads to greater learning opportunities (Horik & Madden, 2016; Chow et al., 2016). The data in the chapter supports this suggestion, as more playful individuals did invest a larger proportion of their time engaging in trials. However, persistence does not typically translate into greater learning efficiency (Griffin & Guez, 2014; Johnson-Ulrich et al., 2018). Perhaps surprisingly, more playful kea also required fewer trials to become proficient tool users and were more likely to solve each trial. This suggests that the learning facilitation of play in our study was not due to increased trial and error learning opportunities alone but likely invoked another cognitive process. We suggest that the superior learning efficiency of playful individuals resulted from how they prioritise their attention.

Differences in attentional biases have been suggested to explain differences in tool use ability between chimpanzees and bonobos, as chimpanzees will pay greater attention to an object that is being manipulated, while bonobos maintain focus on social cues (Koops et al., 2015). Similarly, it is possible that more playful individuals in this study may have invested more effort into tracking the object of play, the ball, when observing others, and this directed

attention potentially accelerated the social learning process (Ahissar & Hochstein, 1993). Meanwhile, as less playful individuals were more prolific scroungers, they likely focussed on the pellet dispenser to better detect scrounging opportunities, and thus received lower-quality social information when a solve was performed by a conspecific (Call, 2013). Such attentional differences have been proposed to explain why scrounging pigeons are less efficient social learners than non-scroungers (Lefebvre & Helder, 1997), as scroungers prioritised their attention towards the ground to better detect scrounging opportunities, and as such received poorer social information from informed members of the flock in foraging tasks. Given the common use of objects in the kea's play repertoire (Bond & Diamond, 2004; Diamond & Bond, 2003), tracking of the ball as an object of play is likely. Interestingly, some individuals also used the food rewards in play rather than consuming them, placing them back into the machine after which they could not be consumed. This further suggests that the higher pay-off for some individuals may be intrinsically derived from play itself, rather than obtaining an extrinsic food reward. This is particularly noteworthy of Kati, the most prolific solver, who received no extrinsic food rewards as he was unable to eat the hard pellets due to a missing upper mandible.

In conclusion, this chapter provides novel experimental evidence that motivation for play can facilitate the acquisition of novel tool use, not only by increasing rates of engagement in the task but also, potentially, by enhancing the effects of social learning. Although further exploration of play and learning is required to tease apart the specific learning mechanisms involved, the experimental approach used here to assess play variation between individuals opens new possibilities for an empirical science of play, and future explorations of how play motivation affects learning rates in social and asocial contexts. Ultimately, an intraspecific experimental approach will provide an avenue for future research examining the heritability and adaptive value of play.

2.5 Supplementary material

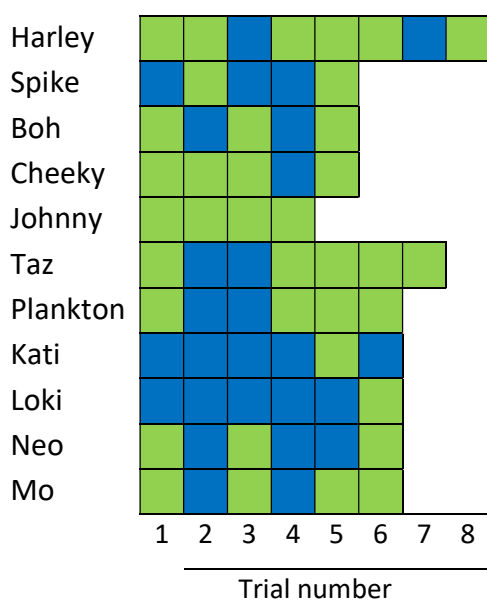
Social learning of colour preference

Baseline colour preference

Prior to exposure to the apparatus, we gave 11 individuals a colour preference test to establish baseline colour preferences. As no food was being offered during this test two

individuals could not be enticed to participate. The experimenter held two coloured blocks (one blue and one green), made of the same plastic material as the test apparatus cups, at an equal distance in front of the subject until the first block was touched/pecked. The left-right orientation of the two colours was pseudorandomized with each new trial. Though some kea appeared to show a colour preference (Fig. 1), the absence of a food reward resulted in too few trials per subject to get meaningful measures of individual colour biases, therefore initial colour preference was not used in subsequent analyses. However, as green was selected more often than blue across the whole group (green = 37, blue = 27), we chose blue as the colour on which a demonstrator would be trained.

Figure 1. *Colour preference test choices*



Demonstrator training

Demonstrator training began with the usage of a smaller training apparatus with a single blue cup. Once Taz was competent in completing the action of putting the ball into the blue cup, he was trained on the two-option testing apparatus, with food rewards only being given when the blue option was used. After Taz was only using the desired option, all individuals were allowed to interact with the apparatus, and to view the demonstrator solving the task.

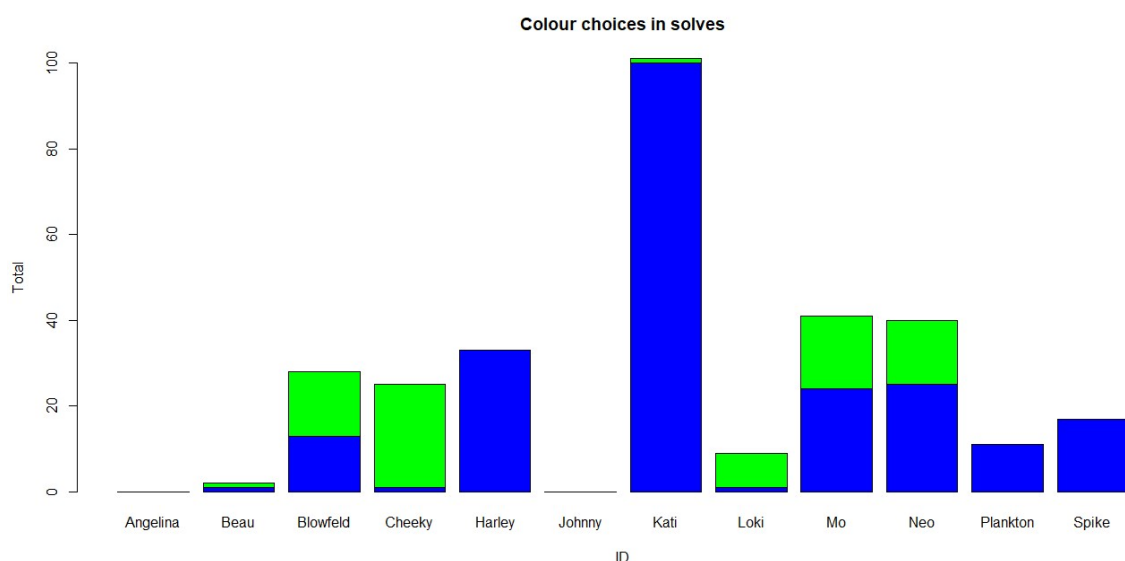
Data analysis

To test for the presence of colour conformity, the task provided had two distinct but equivalent solve options, a blue and a green insert. An initial colour preference test indicated that there was no significant preference for either of the two options based on colour (Green = 37, Blue = 27) or due to side bias (L = 27, R = 37). I analysed whether prior actions of conspecifics would influence the colour option used by individuals. Variables describing the individual's history of observing the colour choices of conspecifics were coded including the last colour choice observed, the total number of each colour viewed, the proportion of blue solves witnessed throughout the experiment, and the proportion of blue solves observed by day. These variables were analysed using a GLMM with colour option chosen as the dependent binary variable. The model of best fit was values obtained using maximum likelihood ratio tests. Taz, the demonstrator, was excluded from the analysis as his colour preference was developed through training. Beau was excluded due to having only solved the task twice. Cheeky, the lowest ranking test subject, was also omitted as he only used the option that was furthest away from the other individuals.

Social effects on colour choice

The eight subjects used in this analysis completed a total of 242 solves (Blue = 192, Green = 50), with each kea completing an average of (mean \pm SD) 35.25 ± 27.46 successful actions. Two individuals solved more using the green rather than blue options. The remaining six participants all used blue for the majority of their solves (Fig. 2).

Figure 2. Individual colour choices in colour preference test



The model that best predicts the colour outcome indicates that the most significant determinants of colour choice are the colour option used in the last solve observed, the total proportion of blue solves previously observed in the experiment, and the proportion of blue solves observed per day (GLMM, $\chi^2 = 4.11$, $df = 1$, $p = <0.042$). Individuals who had witnessed a higher proportion of blue solves, were more likely to solve using the blue option themselves. However, individuals were more likely to use the opposite colour to what they had most recently seen used (-4.11 ± 1.58 , (χ^2) = 2.60, d.f. = 2, $P < 0.009$).

Discussion

Analyses suggest when presented with a two-option task, the option used by kea is influenced by which option they have seen in the majority of previous observations, as well as the option used in the last solve observed. However, due to their highly explorative nature, detection of conformity in kea is difficult, as social information can be outweighed by a tendency for individual exploration (Gyula Koppany Gajdon et al., 2011). Additionally, the sample size in this study is too small for analyses on overall conformity to be meaningful. Although the seeded option was favoured throughout the duration of this study, this was heavily skewed as the most prolific solver, Kati, almost exclusively used the blue option. Kati's possessiveness of the apparatus also made it highly likely that other solvers would see mostly blue solves, skewing the results further. Lastly, dominant individuals would monopolise the apparatus, subordinate individuals were sometimes forced to hold tokens until an opportunity to solve the task presented itself. This led to multiple instances of subordinates solving in the opposite colour cup to what had just been used, as dominant individuals were still engaged on the opposite side of the machine. This likely lead to a positive result, that indicates individuals prefer the opposite colour to what was viewed most recently. As colour choice often appeared to be opportunistic in order to avoid conflict, colour preference results should be interpretation with caution.

Ethics

The research presented here was approved by the Victoria University of Wellington Animal Ethics Committee (application no. 0000026313).

Chapter 3

Kākā (*Nestor meridionalis*) show no evidence of social learning from video playback

Abstract

Social learning can accelerate the diffusion of information through populations and across generations, thus providing a powerful mechanism to facilitate behavioural adaptation to environmental change. Numerous laboratory experiments have shown that animals can learn via video playback of demonstrators, adding an additional method to the social learning toolkit. Although there are several benefits to utilising video playback over live demonstrators, such as the ability to choose and display consistent and desirable information, field applications of this method are very rare. This chapter tests wild kākā (*Nestor meridionalis*), an endangered species, on three video playback tests; two social learning tests, and one test of predator recognition. The two social learning tasks explored 1) whether naïve kākā would avoid a novel food source after viewing video playback of a conspecific showing a disgust response when consuming it, and 2) if video playback would facilitate learning in a string-pulling task. The last experiment assesses whether kākā would be less willing to feed in the presence of playback of an endemic predator. Twenty-six individually recognisable individuals participated in the experiments. Video playback had no significant effect on observer behaviour in any of the three test conditions, and therefore these experiments provided no evidence that kākā could interpret the images presented. The findings of prior laboratory studies suggest that video playback could be a useful paradigm in social cognition research in the wild. However, this study suggests that more work is needed to understand the limits of this approach in field studies, and provides a cautionary case against what is largely viewed as a promising approach in cognition research.

3.1 Introduction

The study of social learning in non-human animals has been a topic of substantial interest for over half a century (Fisher & Hinde, 1951; Kawai, 1965; Sherry & Galef, 1984), with evidence for the social transmission of information now detected in a wide range of taxa, including mammals, birds, reptiles, fish, and arthropods (Alem et al., 2016; Aplin et al., 2015; Brown & Laland, 2003; Kis, Huber, & Wilkinson, 2015; Schnoell & Fichtel, 2012). Use of social information may allow individuals to acquire knowledge about their environment, without the risks and costs associated with individual learning (Galef Jr, 1993), and has the potential to influence numerous behaviours, such as foraging decisions (Hämäläinen, Mappes, Rowland, Teichmann, & Thorogood, 2019; Hämäläinen, Mappes, Rowland, & Thorogood, 2019; Van de Waal et al., 2013), migration routes (Jesmer et al., 2018), and predator response (Cornell et al., 2012; Curio, 1988). Sensitivity to social information even appears to be sufficient for some animals to learn via two-dimensional demonstration material, in the form of video playback (Gunhold et al., 2014; Smit & Van Oers, 2019; Thorogood et al., 2017).

Social learning studies have conventionally focussed on the transmission of foraging behaviours, often in the context of extractive-foraging tasks (Aplin et al., 2015; Gajdon et al., 2004; Van De Waal, Claidière, & Whiten, 2015). This has largely been mirrored in research utilising video-playback, which typically involves recording a live animal performing a foraging behaviour, and subsequently displaying this to naïve test subjects (Guillette & Healy, 2019; Gunhold et al., 2014; Hämäläinen, Rowland, Mappes, & Thorogood, 2017; Hämäläinen et al., 2019). Video playback of a conspecific feeding has been documented to facilitate feeding, and increase total food consumption, in budgerigars (*Melopsittacus undulates*) when compared to videos of non-feeding conspecifics (Ikkatai & Seki, 2016). Video playback can also allow great tits (*Parus major*) to more efficiently locate food (Smit & Van Oers, 2019). Given the positive results of such prior experiments, and the advantages of being able to capture and edit exact behaviours for social demonstration purposes (Hämäläinen et al., 2019), video playback has also been considered for its potential application in conservation contexts (Lopes et al., 2017).

Prior research provides strong support that experimental conditioning can be used to alter behaviours relevant to conservation via asocial learning (Griffin et al., 2000; Llewelyn et al., 2010; Steindler, Blumstein, West, Moseby, & Letnic, 2020; Ward-Fear, Pearson, Brown,

Rangers, & Shine, 2016). For example, a small threatened species of mammal, the planigale (*Planigale maculate*), can be taught to avoid eating poisonous cane toads when subjected to aversive conditioning achieved through exposure to sub-lethal quantities of toad (Llewelyn et al., 2010). While this finding suggests that learning-based approaches can be effective in conservation practice, planigales that do survive consuming cane toad may not attack them again after suffering severe aversive effects, and therefore provide no information to naïve conspecifics (Donnell et al., 2010; Greggor et al., 2017). Relying on individual learning is unlikely to be an effective means to address conservation concerns at the landscape scale, however, if social learning can also be utilised then seeded information may spread across vast geographical range (Fisher & Hinde, 1951), and even persist over multiple generations (Cornell et al., 2012). The potency of social learning is well demonstrated by another Australian predator; the torresian crow (*Corvus orru*).

Shortly after the arrival of cane toads, torresian crows developed techniques for consuming cane toads which avoided toxic parts of the body (Donato & Potts, 2004). This feeding behaviour rapidly spread via social diffusion and persists in multiple areas throughout Australia (Donato & Potts, 2004). As Australia's avifauna possess higher toxic resistance to cane toads (Beckmann & Shine, 2009), subsequent attacks after aversive conditioning are more likely to occur. While seeding specific behaviours may be sufficient for widespread social diffusion to occur in particular species, alternative methods will be needed in cases where there are limited opportunities for social learning to occur. Video playback for social demonstration purposes may be of particular use in such instances.

Video playback allows researchers to present subjects with constant social information, without added complications associated with live-action demonstrators, such as aggression and exclusion by dominant individuals (Gajdon et al., 2004). Additionally, by recording responses to aversive stimuli, researchers can provide playback of behaviours that demonstrators may not otherwise repeat (Thorogood et al., 2017). Recent studies have shown that great tits are capable of interpreting disgust responses of conspecifics demonstrated through video playback, and are also able to recognize and subsequently avoid the food eliciting this response ((Hämäläinen et al., 2019; Thorogood et al., 2017). Video playback has also been successfully used to educate naïve individuals about predatory species. Juvenile rhesus monkeys (*Macaca mulatta*) became fearful of snakes after viewing

videos of their mother showing fear responses to them (Mineka & Cook, 1988). Fear responses to videos of snakes have also been observed in black tufted-ear marmosets (*Callithrix penicillate*) (Emile & Barros, 2009). This methodological approach may therefore be applicable to conservation management to dissuade predators from targeting vulnerable prey species (Gabriel & Golightly, 2017; Umbers et al., 2020) and educate naïve animals on predator recognition (Griffin et al., 2000; Maloney & McLean, 1995; Steindler et al., 2020), and to deter individuals from consuming noxious foods (Donnell et al., 2010; Gartrell & Reid, 2007). Such behaviourally focussed interventions may be of particular value in highly modified landscapes, such as urban environments (Fristoe et al., 2017; Sih, Ferrari, & Harris, 2011; Sol et al., 2002).

Although the majority of New Zealand's endemic fauna are at-risk (Garcia-R & Di Marco, 2020; Robertson et al., 2013), with many species only persisting in areas with intensive conservation management (Robertson et al., 2013), a predator-free sanctuary has allowed numerous endemic forest-dwelling birds to become established in suburban areas of New Zealand's capital city; Wellington (Brockie & Duncna, 2012; Linklater et al., 2018; Miskelly, 2018). Zealandia Ecosanctuary includes 225 ha of regenerating forest and is surrounded by a 9 km fence designed to exclude all introduced mammalian predators (Recio et al., 2017). Since its establishment in 1999, numerous threatened native bird species have been introduced to the sanctuary (Miskelly & Powlesland, 2013), most of which were previously extinct in the region (Innes, Kelly, & Gillies, 2010; Wilson et al., 1998). The sanctuary is located around 2 km from the city centre and surrounded by neighbouring reserves and suburban landscapes (Charles & Linklater, 2014; Recio et al., 2017). The location of Zealandia and success of species reintroductions results in a high spill over of birds from the sanctuary into surrounding areas, where they must adapt to numerous threats (Brockie & Duncna, 2012; Miskelly, 2018; Sriram et al., 2018; Woolley & Hartley, 2019). One such species is the kākā (*Nestor meridionalis*) (Linklater et al., 2018; Miskelly, 2018; Recio et al., 2017).

Kākā (*Nestor meridionalis*), are an endangered, forest-dwelling parrot, endemic to New Zealand (Garcia-R & Di Marco, 2020; Greene & Fraser, 1998; Wilson et al., 1998). Although kākā were regionally extinct in Wellington, since the initial reintroduction of six kākā to Zealandia in 2002 the population has now likely increased to over 250 individuals (Linklater et al., 2018; Recio et al., 2017). Approximately 80 kākā are now hatched and banded in

monitored nests within Zealandia in summer (December-January) each year. Upon fledging, juvenile kākā become prevalent at supplementary feeding sites within the sanctuary (unpublished data), providing an opportunity for training to be conducted prior to individuals dispersing from the sanctuary. This supplementary food, and artificial nest boxes, are thought to contribute to the success of Wellington's kākā by encouraging them to forage and nest within the safety of the sanctuary (Recio et al., 2017). However, kākā that travel beyond the Zealandia perimeter are exposed to a number of novel threats. Issues of particular concern are lead poisoning (Sriram et al., 2018), metabolic bone disease, and predation by introduced mammals (Zealandia, unpublished data).

Anthropogenic lead use has had severe negative effects on wildlife globally (Tranel & Kimmel, 2009; Vallverdú-Coll et al., 2015). However, despite the high levels of heavy metals present in cities (Stewart et al., 2016), the impacts of lead on wildlife inhabiting urban habitats are rarely studied (Sriram et al., 2018). Research exploring lead poisoning in Wellington's kākā population has reported that a large proportion of the population (43%) have elevated lead-blood concentrations, likely from ingesting roofing materials. Metabolic bone disease (MBD) has been documented in several avian species and often results in mortality due to complications resulting from malformed skeletons (Adkesson & Langan, 2007; Cousquer, Dankoski, & Patterson-Kane, 2007). While the exact causes and symptoms of MBD in birds varies (Adkesson & Langan, 2007; Cousquer et al., 2007), consumption of nuts provided by members of the public is the most likely cause of MBD in Wellington's kākā. This results in a 'cross-bill' condition, in which the upper and lower mandibles overlap, usually resulting in death by starvation or euthanasia (Zealandia, unpublished data). Conventional conservation approaches alone are unlikely to be sufficient to address these concerns, however, learning-based interventions may provide a suitable means to help mitigate such issues. Although kākā cognition remains largely understudied, kākā have been shown to be capable of innovative problem solving (Loepelt et al., 2016). Limited evidence also suggests that kākā are capable of learning from knowledgeable demonstrators (Loepelt et al., 2016), indicating that they are a suitable species for further explorations of social learning.

This chapter adds to the limited literature on both the social learning abilities of kākā and the use of video playback in the field. Video playback was used to test individual responses in three different contexts: socially learned food aversion, socially learned foraging innovation,

and predator recognition. To test whether kākā were able to interpret the video playback of a conspecific disgust response, kākā were presented with nectar mix in two distinctly coloured sipper bottles; yellow and red. A video loop displayed behind the bottles either showed a kākā drinking from the red bottle and exhibiting a typical avian disgust-response, or presented images of the bottles with no social information. If social learning occurred, we predicted that subjects exposed to the aversion video would show a preference for the yellow bottle. To test whether video playback of a knowledgeable conspecific facilitated the learning of a novel foraging behaviour, kākā were presented with a novel foraging apparatus that was paired with either a video of a knowledgeable conspecific solving the task, or a video of the apparatus and a conspecific that was not solving the task. If social learning occurred, it was predicted that individuals that received greater exposure to the video of a conspecific solving the puzzle would be faster learners, requiring less time at the apparatus to learn the novel task. Lastly, to test whether kākā could recognise a cue presented in video playback, without also requiring social learning, video playback of an endemic predator was used. If kākā can discriminate and use cues presented in video playback, we predicted that they would be less willing to feed in the presence of a known predator, and would therefore spend less time at the apparatus when a video of a predator was playing.

3.2 Methods

3.2.1 Site & Subjects

Testing was conducted between June-August 2019 at two sites within Zealandia Ecosanctuary, Wellington. This reserve includes 225ha of regenerating forest, surrounded by a fence designed to exclude all introduced mammalian predators (Recio et al., 2017). The sanctuary is home to a population of more than 250 kākā (Linklater et al., 2018), and has two permanent kākā feeding sites where parrot pellets and sugar water are available 24/7. For these experiments, a testing site was established within 10 meters of each of the two established feeding sites to increase the likelihood of kākā discovering them. The testing locations were largely obscured in tree cover, both to avoid interference from the public, and to reduce the exposure of kākā to aerial predators. Twenty-six individually identifiable kākā participated in the experiments. During testing, data was recorded using three GoPro cameras at each apparatus. Individuals had little or no experience in previous experiments (for

previous work with this population see Leopelt et al., 2016) and were identifiable by unique leg band combinations, plumage patterns, and distinctive beak markings.

3.2.2 Procedure

3.2.2.1 Testing apparatus

The testing apparatus (figure 1A) consisted of a wooden box (H 33cm x W 33cm x L 30cm) with one open side. A dowel rod was positioned horizontally at the open face of the box where kākā could perch while participating in the task (figure 1B). An iPad screening demonstration videos was positioned inside the box so that it could be viewed from the perching platform. The videos were displayed using iPads with 9.7-inch LCD screens which are thought to remove the flicker fusion frequency concerns associated with other technology types (Bird & Emery, 2008). All demonstration videos were also recorded and played at 60 frames per second (FPS), which was reported to have more success than other FPS rates in video playback experiments in pigeons (Ware, Saunders, & Troje, 2015). Under field conditions screen glare is likely to occur, the screens were recessed into a box to reduce this effect (Gunhold et al., 2014). Both apparatuses were secured to trees under forest cover at a height of approximately 150 centimetres.

3.2.2.2 Pre-testing procedure

Prior to testing, the apparatuses were positioned at the two testing sites with Wombaroo nectar mix available in transparent green plastic sipper bottles, of a shape different to the red and yellow bottles used in subsequent testing, for three weeks. The bottle was attached to the front and centre of the open side of the box and could be reached when a bird stood on the perch. The wombaroo mixture was available for 6 hours each day and was continuously topped up over this time. This allowed individuals to discover the site and the use of a high-value reward in a dispenser the kākā were familiar with (sipper bottles) encouraged them to return frequently to these locations.

3.2.2.3 Testing procedure

3.2.2.3.1 Social learning of food aversion

This experiment examined whether kākā would adjust their food preferences after viewing a conspecific's disgust response to a novel food. During the initial 10 days of the experiment,

the single green sipper bottle used in the pre-testing stage was positioned in the centre of each apparatus. The bottles contained a high-value nectar food reward which was replenished to always be in constant supply. Positioned behind the bottle was an iPad screening the video stimuli. At the treatment site, a video displayed two alternating scenes of six-second duration. One video showed a kākā feeding from a pink sipper bottle which had the sipper nozzle brushed with anthraquinone solution. Upon feeding from the bottle, the demonstrator showed a typical avian disgust response, puffing out its feathers and vigorously shaking its head (Skelhorn, 2011; Thorogood et al., 2017). The second video displayed a yellow bottle which would be used in the subsequent testing stage, as well as the pink bottle, to account for effects of neophobia. At the control site, two videos of six-second duration were also alternated. The same video of the yellow bottle as was used at the treatment site, and a video of the pink bottle only, with no demonstrator present. The videos were all filmed on the same day and in the same field location. The videos were played with the background forest sounds that were heard during filming. No notable sounds that would cause interference, such as people or alarm calls, were heard in the videos. The initial 10-day period allowed test subjects to view the demonstration videos while feeding from a bottle of a neutral colour. Following this, the single green bottle was replaced with yellow and pink bottles for four days. The videos continued to be shown during this time. The orientation of the bottles (left or right of the iPad) was alternated each day to account for potential side-bias.

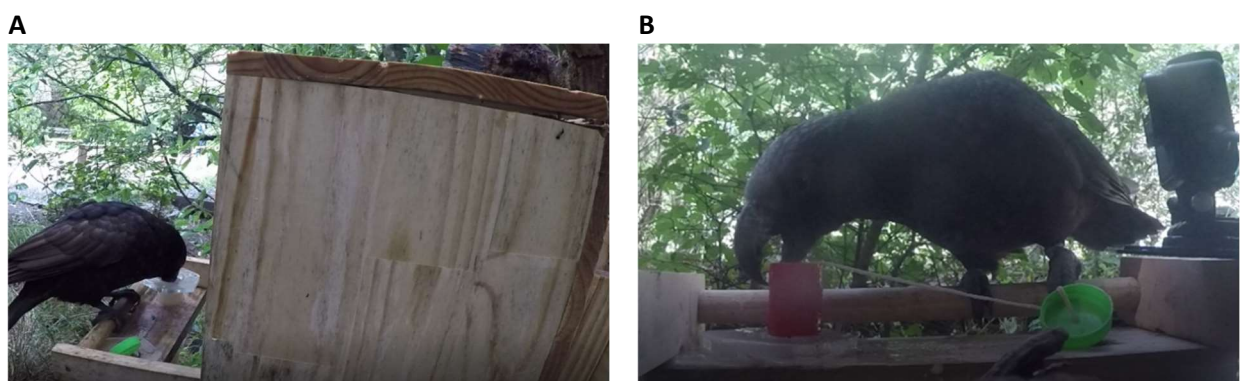


Figure 1 (A) Side view of the testing apparatus **(B)** A kākā is solving the novel foraging task. It has pulled up the string and is holding it in its left foot, suspending the bucket at a height where it can be fed from.

3.2.2.3.2 Social learning of a foraging task

To assess whether social learning via video playback facilitated the uptake of a novel foraging behaviour, wild kākā were presented with a novel string-pulling puzzle. To retrieve the reward, subjects had to pull a bucket up from within a tube using a string-pulling action (Figure 1B). The tube was recessed below a platform and filled with nectar mix. The top of the string was attached to a plastic cap which obscured the view of the food reward below. The bucket was secured so it could be raised approximately 3cm above the lip of the tube, and would drop back down and refill once the string was released. At the treatment site, a 12-second video was played on a loop on an iPad, showing a captive kākā demonstrating the string-pulling action. A still image of the demonstrator at the apparatus was screened at the control site, however, this conveyed no information about the task itself. The two apparatuses were placed in the field for 5-6 hours per day, 5 days per week between 1000-1600 hours over three weeks. The number of trials and solves performed by visiting birds in this time were subsequently coded from videos. Kākā were engaged in a trial when they were in contact with the perching platform in front of the apparatus. A solve was recorded when kākā gained access to the food reward via string-pulling. Individuals achieved this by two means; 1) by pulling the string up and holding it with one food, keeping the food bucket raised above the platform, or 2) by pulling the string with enough force that the nectar would spill out over the platform, which would then be licked up by the kākā.

3.2.2.3.3 Predator recognition

To validate whether kākā could interpret 2D images presented on a video, without including the confounding variable of social learning, test subjects were presented with a soundless video of an endemic aerial predator; the New Zealand falcon (*Falco novaeseelandiae*). Kākā were presented with two videos over a two-day period. One video featured a front view of a falcon resting on a perch. The falcon occupied approximately 30% of the screen. The second video featured the same perch without the falcon present. Both videos were screened for one day each at the two testing sites. At site one, the video without the predator was played on the first day, and the video with the falcon present was played on the second day. This order was reversed for the second site.

3.2.3 Statistical analysis

3.2.3.1 Social learning of food aversion analysis

Of the 15 kākā that participated in this task, no individuals used both apparatuses. This resulted in one group of birds that only had exposure to the aversion video playback ($n = 9$) and a group that only had exposure to the control video ($n = 6$). A chi-square analysis was performed to assess whether the video playback condition would have a significant effect on the first bottle chosen by each individual between the two groups. Generalized linear mixed models (GLMMs), with binomial and Gaussian error structures, were also used to assess whether video playback of a demonstrator showing a disgust response influenced the food choices of observers. Analyses were performed for two response variables; 1) the colour bottle chosen first in each visit to the apparatus (0/1), and 2) the proportion of the total feeding time in which individuals used the aversion demonstrated colour in any given visit. We measured opportunities for social learning by quantifying the total amount of time that each individual had spent on the perch in front of the apparatus while the aversion video was playing prior to their current trial. The amount of time spent at the apparatus (rescaled to remove convergence errors), bottle orientation (to account for side bias), and test condition (demonstrator/no demonstrator) were included as fixed factors. Individual ID was included as a random factor. As individuals at one site showed a notable side bias, an information-theoretic approach was used to facilitate separating the importance of each variable. A global model was derived by including the four variables listed above, and for each model in the resulting set, we calculated the Akaike information criterion corrected for small samples sizes (AICc), as well as the change in AIC relative to the best model in a set (ΔAICc), and the Akaike weight (AICw) which gives the conditional probability of the model (Burnham & Anderson, 2002). As two candidate models for best fit were identified (i.e., $\Delta\text{AIC} < 2$), a multi-model averaging approach was employed to calculate estimates for model parameters by averaging coefficients across all possible models (Burnham & Anderson, 2002).

3.2.3.2 Social learning of a foraging task analysis

For the 19 kākā that participated in this task, no individuals used both apparatuses during this experiment, resulting in a group of birds that only had exposure to the demonstrator video playback ($n = 10$) and a group that only had exposure to the control video ($n = 9$). We used

logistic GLMMs to explore the effects of individual learning opportunity and video playback of a demonstrator (social learning) on solve likelihoods. The response variable was whether or not the task was solved in any given trial (0/1). We measured opportunities for individual learning by quantifying the total amount of time that each individual had spent at the apparatus prior to their current trial. Individual learning time (rescaled to remove convergence errors) and presence/absence of a video demonstrator during the trial were included as fixed factors in the model. Individual ID was included as a random factor.

3.2.3.3 Predator recognition

A GLM with a Gaussian error structure was used to assess whether video playback of a known predator species influenced the duration that a kākā spent using the feeding apparatus in any given trial. As the opaque box that enclosed the iPads obstructed the view of the screen until subjects were directly in front of it, other dependent variables such as latency to approach were not appropriate behavioural measures. The presence/absence of a predator playback was included as a fixed factor (0/1), with individual ID as a random factor.

3. Results

3.3.1 Social learning of food aversion

A total of 15 individually identifiable kākā participated in the experiment. These individuals visited the apparatus 52 times during the initial learning stage, totalling 88.83 minutes at the apparatuses. These same individuals completed 67 trials when presented with the two bottle options, spending a combined total of 194.73 minutes drinking from the two bottles (Pink: 58.57, Yellow: 136.17). Individuals that could not be identified visited the apparatus 13 times (totalling 18.98 minutes) during the initial learning stage (when the Green plastic bottle only was available) and five visits (2.17 minutes) during the two-option testing. This data was excluded from analyses.

Kākā that were shown playback of a conspecific displaying an aversion response to the pink bottle were more likely to choose the yellow bottle as their first choice (8 out of 9 individuals), while kākā that had not seen the aversion video chose both colours equally (Pink = 3, Yellow = 3). However, chi-square analysis indicates that this difference in initial choices is not significant ($df = 15$, $\chi^2 = 2.784$, $p = 0.095$). AIC analysis exploring predictor variables on initial

food choices in each new feeding session indicated two potential models of best fit (Table 1). These included effects of a video demonstrator (time spent observing the aversion response video) and bottle orientation (whether the pink bottle was positioned to the left or right of the iPad). Coefficient averaging across all models (table 2) indicates that the aversion response video had no significant effect on the initial food choices of kākā. Additional AIC analyses were performed to explore the effect of these same predictor variables on the relative proportion of time kākā spent feeding from either bottle. AIC analysis exploring predictor variables on the proportion of time kākā fed from the pink bottle indicated a single model of best fit (Table 3), which only included bottle orientation. Kākā showed a significant side bias (Table 4) and, therefore, spent a larger proportion of feeding time using the bottle on the right, irrespective of the colour.

3.3.2 Video demonstrator and asocial learning effects on problem-solving likelihood

Nineteen identifiable kākā participated in the experiment, with a total of 298 trials and 773 solves occurring during this period. A total of 10 kākā viewed playback of a conspecific solving the task, of which six became successful solvers. An additional nine kākā viewed the video which did not provide a demonstration, of these three learned to solve the task. An additional 27 trials and 0 solves were performed by individuals that could not be identified. These trials were omitted from all analyses. The GLMM results indicate that the likelihood of an individual successfully solving the task significantly improves as their time engaged in trials increases (estimate \pm s.e. = 0.08 ± 0.014 , $z = 5.776$, $p = <0.001$). The effect of a video demonstrator was not significant (estimate \pm s.e. = -1.276 ± 0.969 , $z = -1.318$, $p = 0.18$).

3.3.2 Video playback and predator recognition

Eight individually identifiable kākā participated in this stage of the experiment, visiting the apparatus 47 times, totalling 6676 seconds. There were no kākā that could not be individually identified during this time. The video playback of a predator video had no significant effect on the duration of time individuals would stay at the apparatus in any given visit (estimate \pm s.e. = 81.86 ± 55.6 , $z = 1.411$, $p = 0.15$).

Table 1. The top models ($\Delta AIC < 2$) for the effects of video playback and bottle orientation on the initial food choices of each feeding session. Support for the top four models is shown. AICc is the small sample Akaike Information criteria, $\Delta AICc$ is the change in AICc relative to the top model, AICw (Akaike weight) is the conditional probability of the model.

Models	AICc	$\Delta AICc$	Weight
Effect of video demonstrator + Bottle orientation	75.50	0.00	0.572
Bottle orientation	76.1	0.58	0.428
Effect of video demonstrator	94.6	19.04	0.00
Null	97.10	21.60	0.00

Table 2. Multi-model average for the models of video playback and bottle orientation on the initial food choices of each feeding session. For each predictor we list the regression coefficient, the SE, Z value, 95% CI, and the Relative Variable Importance (calculated as the sum of AIC weights for all models containing the predictor). Predictors that influence the response variable (as indicated by CI that do not bound zero) are highlighted in bold.

Variable	Estimate	SE	Z value	95% CI	RVI
Bottle orientation	3.865	1.104	4.147	1.661 to 6.070	1
Effect of video demonstrator	0.079	0.044	0.960	-0.009 to 0.167	0.57

Table 3. The top models ($\Delta AIC < 2$) for the effects of video playback and bottle orientation on the proportion of time feeding from the pink bottle. Support for the top four models is shown. AICc is the small sample Akaike Information criteria, $\Delta AICc$ is the change in AICc relative to the top model, AICw (Akaike weight) is the conditional probability of the model.

Models	AICc	$\Delta AICc$	Weight
Bottle orientation	83.07	0.00	0.98
Null	97.10	8.64	0.01
Effect of video demonstrator + Bottle orientation	93.46	10.40	0.01
Effect of video demonstrator	100.45	17.38	0.00

Table 4. Multi-model average for the models of video playback and bottle orientation on the proportion of time feeding from the pink bottle. For each predictor we list the regression coefficient, the SE, Z value, 95% CI, and the Relative Variable Importance (calculated as the sum of AIC weights for all models containing the predictor). Predictors that influence the response variable (as indicated by CI that do not bound zero) are highlighted in bold.

Variable	Estimate	SE	Z value	95% CI	RVI
Bottle orientation	3.865	1.104	4.698	0.224 to 0.678	0.99
Effect of video demonstrator	0.079	0.044	0.633	-0.009 to 0. 016	0.01

3.4 Discussion

Contrary to the prediction that kākā would learn socially from video playback of a demonstrator in the contexts of food aversion and problem-solving, video playback appeared to have minimal effect on kākā behaviour in either of these scenarios. When presented with two distinctly coloured food options, the presence of a video demonstrator showing a strong disgust response to one option had no significant impact on the foraging choices of conspecifics. However, this result was skewed as kākā showed a strong side bias, and were most likely to consume food from whichever bottle was positioned on the right side of the apparatus. Kākā were subsequently given a novel string-pulling puzzle at two sites, with one site featuring video playback of a trained demonstrator completing the task. There was no significant effect of video demonstrator on the time taken to solve the puzzle, however individual learning time was significant. This result suggests that asocial learning was primarily responsible for the uptake of the string-pulling behaviour. Lastly, kākā were presented with a freely available food supply both with and without playback of a familiar predator. Kākā consumed the available food in every visit made to the apparatus regardless of the video playback, and the presence of a video predator had no significant effect on the amount of time subjects would stay at the apparatus. Collectively, these results suggest that kākā were not able to interpret the information being conveyed in the videos. These experiments are, to my knowledge, only the second attempt to test social learning using video playback in a wild setting. In contrast to the first study (Gunhold et al., 2014), these results indicate that no significant social learning or comprehension of the videos is occurring.

Prior behavioural research provides strong support that individuals can socially learn food aversion and predator recognition from video playback of demonstrators (Hämäläinen, Mappes, Rowland, & Thorogood, 2019; Mineka & Cook, 1988; Thorogood et al., 2017), and that teaching of these behaviours can increase the survival rates of wild animals (Gabriel & Golightly, 2017; Maloney et al., 1999; Ward-Fear et al., 2016), potentially providing a viable means of behavioural intervention in the context of conservation. As kākā are highly impacted by introduced predators (Garcia-R & Di Marco, 2020; Wilson et al., 1998) and are known to consume toxic substances (Hickling, 1997; Sriram et al., 2018), seeding information about these behaviours may be of great value in the conservation and management of Wellington's kākā population. However, despite the positive results yielded by previous video playback experiments (Guillette & Healy, 2019; Hämäläinen et al., 2019; Ikkatai & Seki, 2016), and supporting evidence that kākā are capable of learning socially (Loepelt et al., 2016), the results described in this chapter provide little evidence that kākā were able to interpret the images presented in demonstration videos. These negative findings may be the result of numerous contributing factors.

A key concern for behavioural research assessing responses to video playback is that there is no way to be certain that the objects being presented appear natural to non-human viewers (Ware et al., 2015). This consideration is of particular importance when animals have visual systems that are drastically different to our own, such as birds (Fleishman & Endler, 2000). Parrots may have particular difficulty viewing technology-based for mammalian vision, given their sensitivity towards the ultraviolet end of the light spectrum (Cuthill et al., 2000). Additionally, with prior exposure even affecting the ability of humans to interpret 2D images (Deregowski, Muldrow, & Muldrow, 1972; Miller, 1973), there's no guarantee that animals will be able to interpret such information even if their visual systems are suited to do so. Such issues may also be exacerbated when video playback is used under field conditions, as light conditions cannot be controlled. Wild animals are also unlikely to have experience with video screens which may facilitate comprehension of the images over time (Deregowski et al., 1972; Miller, 1973). To best account for these issues, all videos were recorded at 60-FPS, which has been more used more successfully in avian video playback experiment than lower motion quality rates (Ware et al., 2015). The screens used were also recessed into box enclosures to reduce surface glare (Gunhold et al., 2014).

Despite its apparent promise, the negative results reported in this chapter, and a notable absence of field testing within the broader animal behaviour literature, suggest that much work is needed before the applicability of video playback is well understood. As such, future research should look to fill specific knowledge gaps and establish a much-needed foundation for this methodology. To date, only one published study has sought to directly understand whether the social information received from live and video demonstrators is comparable in its efficacy (Hämäläinen et al., 2019). In this study, blue tits (*Cyanistes caeruleus*) were shown demonstrators choosing food from locations marked with two distinct symbols, both by live and video demonstrators. However, as subjects showed a preference for one option regardless of the demonstrators' choices, and there was therefore insufficient evidence to support social learning, the effects of live and video demonstrators could not be compared (Hämäläinen et al., 2019). Ascertaining the extent to which videos can provide a true substitute for live demonstrators is crucial for future social learning research. The relative applicability of video playback in captive and wild settings should also be explored. While it is likely that different species will be unique in how they respond to video playback (Ikkatai & Seki, 2016), and generalisations across taxa will therefore be difficult, filling the current knowledge gaps would be most readily achieved using model species. *Parus major*, for example, are highly perceptive of social information in a range of contexts (Aplin et al., 2015; Fisher & Hinde, 1951; Louis Lefebvre, 1995), including video playback experiments ((Hämäläinen et al., 2019; Thorogood et al., 2017). This species is also highly suited to social learning experiments under field conditions (Aplin et al., 2015, 2017; Farine, Aplin, Sheldon, & Hoppitt, 2015). Comparative studies exploring live and video demonstrators, and captive and field-based video playback experiments, would be highly informative and achievable in such a species.

3.4.1 Social learning from live demonstrators

In addition to video playback, testing of social learning from live demonstrators was also conducted. Three free-roaming kākā (2F, 1M) of various ages and dominance rank were trained to operate a novel extractive foraging apparatus. The apparatus required individuals to push small wooded balls (as used in chapter 2) along an upward slanted tube and into a cup. The apparatus would subsequently present a nozzle with a Wombaroo nectar reward. Over a four-week period, the demonstrators solved the puzzle regularly, however

observations of solves by naïve kākā were rare. Observations of solves were primarily limited by conflict at the testing site. The demonstrators became highly possessive of the apparatus, and would chase away subordinate observers. More dominant observers were also likely to displace knowledgeable demonstrators without witnessing successful use of the apparatus. No uptake of the seeded behaviour by naïve individuals was recorded.

The task was designed to be of sufficient difficulty that asocial learning alone would be insufficient to learn it, however, a complete absence of behaviour acquisition rendered the resulting data unsuitable for meaningful social-learning analysis. Despite the shortcomings in statistical results, the outcome of this experiment highlights the need for establishing a baseline presence of social learning in kākā, as well as many other species.

Conclusion

While there are several advantages to using video playback over live demonstrators (Hämäläinen et al., 2019), the foundational work for this approach is currently limited. Most notably, comparisons of live and video demonstrators, and field-based applications, remain very uncommon (Hämäläinen et al., 2019). Additionally, a bias towards publishing positive findings (Dawson & Dawson, 2018; Mlinarić, A., Horvat, M., & Šupak Smolčić, 2017) may be giving a deceptive impression of video playbacks ease of utility, with few studies reporting negative results (Brecht, Ostojić, Legg, & Clayton, 2018; Hämäläinen et al., 2019). This chapter adds to this literature by conducting three video playback tests in which wild kākā were exposed to three different types of information; Problem-solving/foraging, and two information types relevant to kākā conservation; aversion (Sriram et al., 2018) and predator recognition (Wilson et al., 1998). None of these tests yielded results to suggest that kākā could interpret the information presented during video playback. The negative results provided from these experiments further illustrate the chasm between our current understanding of social learning via video playback and its practical applicability, and provide a cautionary case in what is largely viewed as a promising approach in cognition research.

Ethics

The research presented here was approved by the Victoria University of Wellington Animal Ethics Committee (application no. 0000023295 & 0000026122).

Chapter 4

Kākā (*Nestor meridionalis*) social networks and distribution

Abstract

Social dynamics can significantly impact fitness, group stability, predation risk, and information and disease transfer. Recently, our understanding of how social behaviour impacts animals' lives has been transformed by the development of tools for studying animal social networks. Moreover, simulations suggest that social network analysis could be used to inform threatened-species management. Problematically, as endangered species are often found in remote locations and in low numbers, the vast majority of social network studies are conducted on common model species. Yet, as social networks differ between taxa, the study of social networks in specific endangered species is crucial to implementing social network analysis in conservation practice. In the past decade, several at-risk endemic species have become a common sight throughout the suburbs of Wellington city, as a result of reintroductions to a predator-free sanctuary, Zealandia. One of these species is the kākā (*Nestor meridionalis*), a charismatic, forest-dwelling parrot. By recording kākā visitation events at six supplementary feeding sites, we assessed social networks within the wider population and examined the feeding site fidelity of individuals for 15 days over a three-week period. Associations between individuals based on visiting times and locations were found to be non-random, suggesting that kākā will preferentially form stronger bonds with some individuals than others. Additionally, there was surprisingly little overlap in the individuals that were present at the six feeding sites, as the majority of individuals only used one site, despite sites being separated by as little as 250m. These findings provide a rare examination of social networks and space use in an endangered species, and only the second application of social network analyses to parrots. Furthermore, the spatial separation occurring between supplementary-feeding sites has significant implications for population monitoring, information, and pathogen transfer, in this endangered species.

4.1 Introduction

Social network analysis (SNA), maps groups and populations by the strength of interactions between individual members (Scott, 2000), has seen a surge in popularity in the field of behavioural ecology over the past two decades (for review, see Webber & Vander Wal, 2019). This growing body of research has demonstrated that social dynamics and structure can have significant implications at both the individual and population level, including fitness (Vander Wal, Festa-Bianchet, Réale, Coltman, & Pelletier, 2015), group stability (Rosenbaum et al., 2016; Williams & Lusseau, 2006), dominance (Bierbach et al., 2014), diffusion of information (Aplin et al., 2015; Farine et al., 2015), disease transmission (Webber et al., 2016), and access to food sources (Aplin et al., 2012). Given the wide ranging impact of social networks, SNA is now of growing interest to the field of conservation behaviour (Angeloni, Schlaepfer, Lawler, & Crooks, 2008; David W Macdonald, 2016; Snijders et al., 2017; Webber & Vander Wal, 2019).

SNA can be used to both monitor existing populations (Williams & Lusseau, 2006), and to inform direct conservation-focused interventions (Hamede, Bashford, McCallum, & Jones, 2009; Rushmore et al., 2014). Instability in social structure can have detrimental effects, such as reducing individual fitness (Linklater, Cameron, Minot, & Stafford, 1999) and increasing occurrences of aggression (Macdonald, Harmsen, Johnson, & Newman, 2004). SNA can be used to identify key individuals that disproportionately maintain or destabilise social cohesion (Baigger, Perony, Reuter, & Leinert, 2013; Williams & Lusseau, 2006), allowing researchers to better predict the outcomes of changes to community structure (Lusseau & Newman, 2004; Snijders et al., 2017; Williams & Lusseau, 2006), and to better house captive animals in breeding programs (Dunston et al., 2017). The ability to track and predict the pathways of pathogen transmission (VanderWaal et al., 2014) may also allow conservationists to more efficiently address disease outbreaks. Simulations indicate that, by identifying likely transmission points in a chimpanzee (*Pan troglodytes*) population, the spread of a pathogen could be halted with a 35% reduction in vaccinations (Rushmore et al., 2014). Additionally, as social structure can be heavily impacted by habitat change (Webber & Vander Wal, 2019), SNA can provide a valuable tool to monitor how populations are coping with human-induced habitat modification, such as urbanisation (Snijders et al., 2017). However, complications may arise from attempts to generalise between species. For example, while targeted

immunization of individual chimpanzees appears to be effective in chimpanzees (Rushmore et al., 2014), targeted removals of infected individuals were ineffective in reducing the spread of facial tumour disease in Tasmanian devils (*Sarcophilus harrisii*) (Hamede et al., 2009). Similarly, while removal of individuals significantly reduces group stability in species such as killer whales (*Orcinus orca*) (Williams & Lusseau, 2006), other species, such as pigtailed macaques (*Macaca nemestrina*), appear to be robust to such disturbances (Flack, Girvan, De Waal, & Krakauer, 2006). As data are currently insufficient to make generalisations across taxa (Snijders et al., 2017; Webber & Vander Wal, 2019), vulnerable species of specific interest will need to be studied if SNA is to be used effectively in the context of conservation (Webber & Vander Wal, 2019).

Although the social network literature includes over 338 empirical studies, the number of species studied remains limited (reviewed in Webber & Vander Wal, 2019). The majority (55%) of the species studied to date are mammals (predominantly primates), while aves are the second most represented group (23%). There are also overly represented species within these groups. For example, 5% of all existing social network studies have been conducted on great tits (*Parus major*). Compounding the lack of species diversity, the majority of prior studies have also explored social networks in species of least concern, with only 18.5% of species studied categorised as at risk, endangered and critically endangered. While research on common species has been helpful for methodological development (Aplin et al., 2012, 2020; Boogert et al., 2008), social network analyses will likely need to be specifically targeted towards vulnerable taxa to effectively apply social network analysis in a conservation context (Webber & Vander Wal, 2019). While parrots are of high interest in studies of sociality (Aplin et al., 2020; Nelson & Wein, 2017), the body of work exploring sociality in free-ranging parrots remains limited, and has predominantly relied on indirect evidence such as bio-acoustics (Wright & Dahlin, 2017). However, instances where parrots have successfully colonized urban habitats, provide opportunities to explore sociality in these species using more direct methods (Aplin et al., 2020). New Zealand is home to a plethora of endangered endemic species (Garcia-R & Di Marco, 2020; Holdaway, 1989), most of which remain unstudied in the context of social networks (Franks et al., 2020).

Having evolved in the absence of mammals (Holdaway, 1989), New Zealand's avifauna lack innate defences against introduced predators such as rats, mustelids, and cats (Garcia-R & Di

Marco, 2020; Robertson et al., 2013; Wilson et al., 1998). As a result, many species can only persist in areas with intensive conservation management, such as offshore island sanctuaries (Miskelly, 2018; Miskelly & Powlesland, 2013; Robertson et al., 2013). However, in the past decade, several threatened forest-dwelling species have become a common sight in several suburbs of New Zealand's capital city, Wellington (Brockie & Duncna, 2012; Linklater et al., 2018; Miskelly, 2018), creating a unique urban study system. The increasing abundance of these species is largely due to reintroductions to a predator-free sanctuary, Zealandia (Brockie & Duncna, 2012; Linklater et al., 2018; Miskelly, 2018).

Zealandia ecosanctuary includes 225 ha of regenerating forest and is surrounded by a 9 km fence designed to exclude all introduced mammalian predators (Recio et al., 2017). Since establishment in 1999, numerous threatened native bird species have been introduced (Miskelly & Powlesland, 2013), most of which were previously extinct in the region (Innes et al., 2010; Wilson et al., 1998). The sanctuary is located around 2 km from the city centre and surrounded by neighbouring reserves and suburban landscapes (Charles & Linklater, 2014; Recio et al., 2017). The location of Zealandia and success of species reintroductions results in a high spill over of birds beyond the sanctuary perimeter, with several species increasing in prevalence in residential areas (Brockie & Duncna, 2012; Miskelly, 2018). This creates a unique study system, in which urban adaptation can be studied in numerous threatened species in a central and accessible location (Linklater et al., 2018; Miskelly, 2018; Recio et al., 2017). Given the global context of climatic change, species range shifts, and increasing human-induced habitat modification, understanding the effects of urbanisation on species social behaviour and distribution is of growing importance (Davis et al., 2014; Galbraith, Stanley, Jones, & Beggs, 2017; Griffin et al., 2017; Sriram et al., 2018; Van Heezik & Seddon, 2018). Furthermore, community engagement with wildlife can create opportunities to utilise residential properties as research sites (Linklater et al., 2018; Plummer et al., 2015; Van Heezik et al., 2020), and citizen-scientists may also provide large quantities of data on conspicuous species (Aplin et al., 2020; Greig, Wood, & Bonter, 2017; Thabethe & Downs, 2018). One of the most notable and emblematic species to recently establish in Wellington is the kākā (*Nestor meridionalis*) (Linklater et al., 2018; Recio et al., 2017).

Kākā are a medium-sized parrot endemic to New Zealand (Bond & Diamond, 2004). After being regionally extinct in Wellington, six kākā were first reintroduced to Zealandia in 2002

(Recio et al., 2017). Since then, the population has had several successful breeding seasons, with over 1000 kākā chicks banded from nests occurring within the sanctuary. In 2013 the kākā population was estimated to number ~180-250 individuals (Karori Sanctuary Trust, 2013, unpublished data) and although no subsequent attempts have been made to update this figure, the population size is likely increasing (Linklater et al., 2018; Recio et al., 2017). The growth of Wellington's kākā population is attributed to Zealandia, which provides supplementary food and nest boxes to encourage kākā to forage and nest within the safety of the sanctuary (Recio et al., 2017). However, kākā are now commonly seen beyond Zealandia's fence where they are exposed to a number of novel threats, such as lead poisoning (Sriram et al., 2018), illness from consuming anthropogenic foods, and predation by mammals (Zealandia, unpublished data). The accessibility of kākā in Wellington, and the presence of established feeding sites both within Zealandia and its neighbouring suburbs, provides a rare opportunity to study social networks and distribution in an understudied and endangered species of parrot as they establish themselves in an urban environment. In this study, social networks in kākā were examined by monitoring six established supplementary feeding sites; two within the Zealandia Ecosanctuary perimeter, and four at residential properties in neighbouring suburbs. By recording kākā visitation at these sites using cameras and in-person record keeping, a social network was constructed for Wellington's kākā population. Visitation events were further analysed using Bray's-Curtis dissimilarity analysis to examine how distinct kākā community composition was between all locations.

4.2 Methods

4.2.1 Study sites

Data were collected in July 2018 at six established kākā feeding sites; two sites were within the Zealandia Ecosanctuary perimeter, an additional four sites were located on residential properties in suburbs surrounding Zealandia (Fig. 1). The occupiers of the residential properties used were contacted via a bulk mail out to suburbs within two kilometres of Zealandia. Properties were selected if respondents were both regular feeders of kākā and willing to permit monitoring at their residences.

4.2.2 Data collection

Data were collected simultaneously over three weeks at the residential properties and inside Zealandia. Nectar feeders were positioned at three of the residential sites. These were filled daily with sugar-water, a common supplementary food for kākā (Recio et al., 2017). Fledging kākā in nests within Zealandia are banded using one large steel cohort band and two smaller steel bands to provide a unique colour-coded identification. GoPro cameras were positioned at each feeder to record leg band IDs of kākā (Fig. 2) between approximately 1100 and 2100 hours, five days a week, for three consecutive weeks. However, footage after approximately 1800 hours was unusable due to poor light conditions. At the fourth residential property, food was supplied by the occupier, who also continued their daily routine of opportunistically recording kākā visits and submitted this data for use in this study. Because this data was not collected using the same video-capture method as the other sites, as setting up additional cameras in this location was not feasible, data collection was not continuous and some visitation data is likely missing. The two feeding sites within Zealandia each consist of four pellet dispenser units and one nectar feeder. GoPro cameras were positioned at each of the pellet dispensers to record the leg bands of visiting kākā between approximately 1000 and 1700 hours, five days per week, for three weeks.

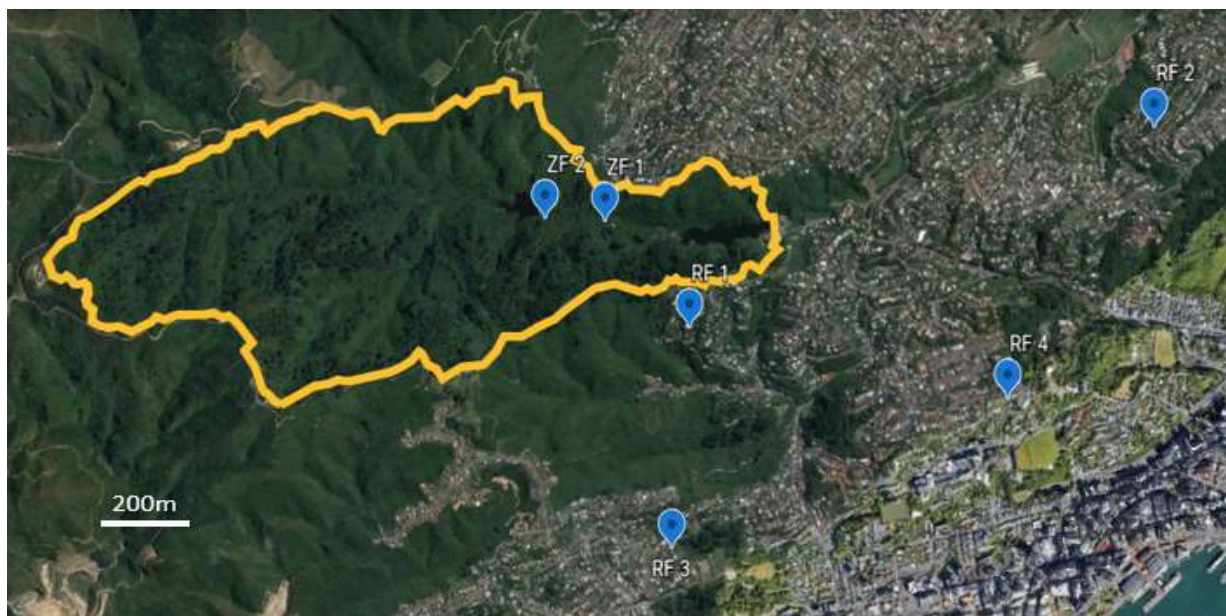


Fig. 1. Aerial view of the Wellington region (source: Google Maps). Zealandia Ecosanctuary is outlined in yellow. The blue markers show approximate locations of feeding sites where data was collected. Two feeding sites are within the Zealandia perimeter (ZF1, ZF2) and four are in residential properties within the surrounding suburbs (RF1-RF4).

4.2.3 Bray's-Curtis dissimilarity analysis between feeding sites

To assess the level of feeding site fidelity shown by individuals we ran Brays-Curtis analyses (Bray & Curtis, 1957) using visitation data for each individual, at each feeding site. This analysis considers both the presence and absence of specific individuals at each site, as well as the frequency of visits to each location. The resulting output gives a dissimilarity index ranging from 0 to 1 which represents the overlap in community composition between each site. A value of 0 indicates that sites are identical, while a value of 1 indicates that there is no overlap of individuals between the sites. This analysis was performed using the *Vegan* package (Oksanen et al., 2016) in R (R Core Team, 2014).



Fig. 2: GoPro image recording the legs of kākā for identification via each individual's unique leg band colour combinations. The combination shown here is G-BY (a green cohort band on the left and blue over yellow on right).

4.2.4 Social network analysis

Data from all feeding sites were pooled for social network analyses, including the time, location and ID of visiting kākā. Individuals that were seen on fewer than five occasions were omitted as they had insufficient data to assess social connectivity (Aplin et al., 2012). Unbanded individuals, accounting for 377 visits across all sites, were also excluded from analyses. The remaining spatio-temporal data, consisting of 98 individuals and 1982 visitation events, were combined into a single stream of time-stamped observations. The resulting data was analysed to identify instances of co-occurrence between individuals within a movable time window. The duration of the time window was determined by applying a Gaussian mixture model to the data, which detects clustering events between periods of inactivity, removing the need for researchers to set a defined time window (Psorakis et al., 2015). To account for missing datapoints and unbanded individuals that could not be identified, a half-weight association index was also applied (Whitehead, 2008). This results in an association matrix, where edges values (the connections between individuals) can range from 0 (never observed within the same time window) and 1 (only observed within the same time window). Use of association matrices is recommended for use over raw edge values which simply measure the number of co-occurrences without weighting for the number of times individuals are detected (Webber & Vander Wal, 2019). The resulting association matrix was used to create a social network for all individuals. This network was then compared to networks randomly generated using a bootstrap method, to test whether the relationships are more structured than would be expected from random.

Permutations of the data are achieved by sequentially swapping observations between individuals (Bejder, Fletcher, & Bräger, 1998), producing new networks with the same nodes, but with randomized edges (Farine & Whitehead, 2015). This process was repeated 1000 times, resulting in a distribution of coefficient of variation values (CV) that were used to examine whether the clustering patterns detected differed from what would be expected if associations were random.

To test if relationships were more organised than would be expected at random, the CV of the actual network was compared to the CV of 1000 randomized versions of the network. The P value was then calculated by taking the number of times the CV value of the observed network is smaller than a randomized network, divided by the number of randomizations

(Farine & Whitehead, 2015). All social network analyses were performed using the *asnipe* package in R (Farine, 2013, 2017).

4.2.5 Spatial scale analysis

The four residential feeding sites used for data collection consisted of either a single feeder, while each of the two Zealandia sites had a cluster of four individual feeders. Analyses were therefore performed to assess whether the number of feeders at each site had a significant effect on the number of social interactions or the strength of the relationships detected. Data were divided into coarse (multiple feeders per site) and fine (one feeder per site) spatial categories. Mann Whitney U tests were performed to examine the differences in the mean number of social connections per individual (centrality) and the strength of the interactions (connectedness) that were occurring, between the two categories.

4.2.6 Individual social metric analysis

The effects of individual attributes, sex and age, on the centrality and connectedness of individuals was also explored. Mann Whitney U tests were performed to detect potential differences in centrality and connectedness between males and females, and between adults and subadults (Moorhouse & Greene, 1991). Simple linear regressions were also performed to assess correlations of exact age (in years) with centrality and connectedness.

4.3 Results

A total of 98 individually identifiable kākā were recorded using feeders five times or more during this study and were therefore included in the social network analyses and subsequent results. Though monitoring was conducted at six feeding sites, 71 (72.4%) individuals only utilised one feeding station, 23 (23.5%) individuals used two feeders, and 4 (4.1%) kākā frequented three feeding sites. Despite the two Zealandia feeding sites only being separated by 250 metres, of 57 individuals that used either of these feeders, only 21 (36.8%) utilised both. Analyses of the individuals in which the sex is known ($n = 72$) reveal a significant, male-skewed, sex bias at feeders within the sanctuary ($M = 29$, $F = 14$; binomial $p=0.016$), however, no sex bias was detected at feeders in residential areas ($M = 14$, $F = 15$; binomial $p=0.144$). The estimated sexes for kākā nestlings banded within Zealandia do not suggest that there is a population-wide sex-bias in offspring (Zealandia, unpublished data).

4.3.1 Bray's-Curtis dissimilarity indices between feeding sites

Bray's-Curtis analysis of individual presence and absent data at each of the six supplementary feeding sites shows very high levels of dissimilarity between all feeding sites (Table 1). The lowest level of dissimilarity occurred between the two feeding sites within the Zealandia perimeter with a dissimilarity score of 0.847.

4.3.2 Wellington's kākā social network

Analysis of the spatio-temporal data stream, limited to individuals recorded five times or more, yielded a social network consisting of 98 nodes (representing 98 individuals) and 406 edges (connections between nodes) (Fig. 3). Comparison to 1000 randomly generated networks indicates that the relationships detected are significant and therefore non-random ($p = 0.039$).

Table 1. Bray's-Curtis dissimilarity matrix displaying dissimilarity indices for all sites. A value of 0 indicates that sites are identical, while a value of 1 indicates that there is no overlap of individuals between the sites.

Site	Zealandia 1	Zealandia 2	Residential 1	Residential 2	Residential 3
Zealandia 2	0.847				
Residential 1	0.993	0.988			
Residential 2	0.973	1.000	1.000		
Residential 3	0.973	0.964	1.000	1.000	
Residential 4	1.000	1.000	1.000	0.867	1.000

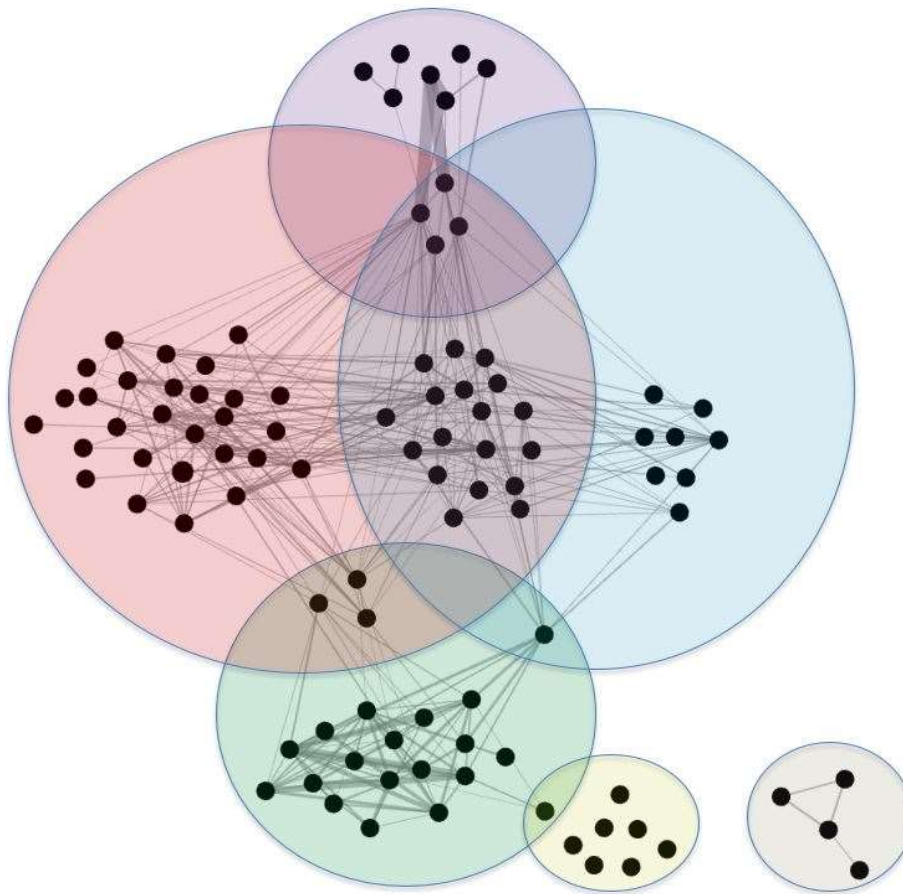


Figure 3. Social network diagram displaying individuals (nodes represented by the black circles) and the edges between all individuals (the grey lines connecting the nodes). The strength of the association between nodes is indicated by the thickness of the lines. The large coloured circles of the Venn diagram represent the six feeding sites that individuals used during this study. The two largest circles represent the sites within the Zealandia sanctuary perimeter; Z1 (red) and Z2 (blue). The smaller circles represent the four residential sites; RF1 (purple), RF2 (grey), RF3 (green), and RF4 (yellow). Individuals that visited more than one site are represented by nodes placed between overlapping circles.

4.3.3 Spatial scales and social metrics

Analysis of the spatial scales at each site indicate that there is no significant difference in the strength of relationships individuals possess at fine and coarse spatial scales (connectedness: $w = 944.5$, $p = 0.4488$). Similarly, no significant difference was detected in the number of relationships individuals have between the spatial scales (centrality: $w = 978.5$, $p = 0.3149$).

4.3.4 Individual attributes and social metrics

There were no significant differences in the strength (connectedness: $w = 944.5$, $p = 0.4488$) or total number of relationships (centrality: $w = 976$, $p = 0.1037$) formed by male or female kākā. Age also had no significant effect on social relationships when examined at the level of exact age (connectedness: $r = -0.06$, $p = 0.5471$; centrality: $r = -0.04$, $p = 0.6677$) or maturity status (connectedness: $w = 1759$, $p = 0.97$; centrality: $w = 1783$, $p = 0.93$).

4. Discussion

By monitoring kākā visitation at several established feeders, both inside and outside of Zealandia Ecosanctuary, this chapter provides new insights into kākā sociality and distribution in Wellington city and builds on the limited body of literature on both parrot and urban social networks (Aplin et al., 2020; Webber & Vander Wal, 2019). Although it is commonly thought that kākā viewed in Wellington's suburbs are still primarily based within Zealandia (Recio et al., 2017), few individuals were sighted at feeders both within and outside of the sanctuary. This potentially indicates that many kākā have now established ranges in urban areas beyond the Zealandia perimeter, and may not make regular visits to the sanctuary. Furthermore, surprisingly few kākā were observed frequenting more than one feeding site. Despite kākā being very strong flyers (Berry, 1998), and the two sites inside Zealandia only being 250m apart, just 21 of the 57 individually recognisable individuals that used supplementary feeders within the sanctuary used both feeding sites. Use of social network analysis also shows that groupings of kākā that appear together at feeders are non-random, suggesting that kākā form stronger associations with some individuals than others.

Previous research has documented that kākā may utilise a surprisingly small area given their strong flying ability (Berry, 1998; Recio et al., 2017). Our research supports this, as individuals monitored in our study seldom used more than one feeding site, despite their proximity. These findings indicate that the supplementary feeding conducted by Zealandia is having its desired effect of keeping individuals within the sanctuary. However, the results of this study suggest that recreational supplementary feeding is also having a substantial impact on kākā distribution and space use in Wellington. Although the short time-span of this study must be considered, the data collected suggests that some kākā may have established home ranges outside the safety of the Zealandia perimeter, or at the very least no longer utilise the supplementary food provided by the sanctuary. Additionally, this data indicates that kākā will also form distinct communities at these feeding sites. Interestingly, individuals using one

location (RF 4) showed no social connectivity at all, indicating that simply using the same feeding site does not imply social cohesion.

This evidence that kākā form non-random social bonds has significant implications for the management and conservation of Wellington's kākā population. As kākā are a suitable species for reintroductions (reviewed in Miskelly & Powlesland, 2013), they are therefore a species of primary interest for future translocations (Robert B. Schadewinkel, pers. coms). Establishing new kākā populations is often achieved by harvesting individuals from wild populations and translocating them to a new location (Miskelly & Powlesland, 2013). Research exploring social networks in gorillas (*Gorilla berengei berengei*) and an at-risk population of killer whales (*Orcinus orca*) revealed that certain individuals play a disproportionately weighted role in maintaining group cohesion (Rosenbaum et al., 2016; Williams & Lusseau, 2006), and that removal of such individuals can significantly impact group stability (Williams & Lusseau, 2006). Given the potential impacts of removing key individuals from within social groups (Rosenbaum et al., 2016; Williams & Lusseau, 2006), careful consideration should be given to how individuals are selected for removal. One documented concern with kākā translocations is homing behaviour, whereby kākā will return to their previous home range (Berry, 1998). Translocating groups of individuals with established social bonds may potentially reduce the likelihood of this behaviour. A better understanding of how resource availability influences kākā distribution may also have significant implications for monitoring and managing Wellington's kākā population.

Although annual banding of kākā chicks and the feeding sites within Zealandia afford useful monitoring opportunities for kākā, given the dissimilarity of individual composition between feeding sites found in our study, it is likely that data collected within the sanctuary alone is insufficient for population-wide assessments. For example, the consumption of nuts provided by members of the public has been implicated in a large number of mortalities in kākā chicks, due to metabolic bone disease (MBD) (Zealandia, unpublished data). Although monitoring of nests within Zealandia indicates that incidents of MBD have significantly decreased (Jo Leddington, pers. comms), further monitoring of nests outside of Zealandia may be required to detect cases occurring beyond the sanctuary perimeter. Reports of kākā with MBD from the public indicate that this condition is still a concern in this population (figure 4; Alison Valentine, pers. Comms). If the distribution of kākā shown in feeding site usage is also

reflected in nesting sites, then it is likely that the individuals with the greatest access to nuts will also be nesting outside of the Zealandia sanctuary. Data collected outside of the sanctuary should also be considered in other matters of kākā management and monitoring, such as population estimates and assessments of sex-biases.

Male-biased sex ratios are common in kākā populations (Greene & Fraser, 1998; Leech, Gormley, & Seddon, 2008), and thought to arise due to high mortality of nesting females from introduced mammalian predators (Wilson et al., 1998). In the current study, feeder use within the sanctuary perimeter also showed a significant male bias, despite the absence of mammalian predators inside the sanctuary. Although the limited kākā dispersal literature (Recio et al., 2017) means that one can only speculate on why this male bias at the feeders occurred, one possibility is that female-biased dispersal after fledging may occur in this species. As suitable cavity nesting sites are a limited resource for kākā (Greene & Jones, 2003), the need to locate nest sites could make female dispersal a necessity. By contrast, equal numbers of male and female kākā were recorded beyond the safety of the sanctuary fence, where the increased risk of mammalian predation on nesting females would be expected to result in a male-biased sex ratio. Inferences from this data are also limited as it is currently not possible to determine what proportion of the kākā population have been accounted for. Opportunistic recording of kākā leg band IDs at non-feeding sites within Zealandia during this study also suggests that a number of kākā present in the sanctuary do not use either feeding station, and are therefore absent from the dataset. As population viability depends on both population size and sex ratio (Leech et al., 2008), inconsistencies in sex ratio between monitoring sites require consideration, particularly for monitoring newly founded kākā populations. Establishing extra feeding sites would likely serve to detect some additional individuals. However, this would add further labour to an already demanding method. The time and labour demands of SNA already pose a significant barrier to having access to real-time social network information, which would be required for conservation focussed interventions. However, recent technological developments may provide alternative means to collect large amounts of data comparatively quickly, in both urban and non-urban settings.

Figure 4: A kākā with MBD photographed at a residential property on 08/08/2020. Photo credit Alison Valentine.



By utilising citizen scientists, and a purpose-built mobile phone application, Aplin et al, (2020) were able to collect GPS and timestamp locations of individual sulphur crested cockatoos across the city of Melbourne and publish the first SNA on parrots (Aplin et al., 2020). Cockatoo wings were fitted with distinctly numbered cattle-tags, allowing members of the public to reliably identify individuals, reducing the need for researchers to individually assess reports. However, given the positive attitudes towards native fauna expressed in New Zealand culture (Russell, 2014), attachment of large and conspicuous tags may not be deemed socially acceptable. Although kākā in conservation projects are often fitted with colour coded leg band combinations, however, the difficulty of reading these would likely result in observer error from citizen scientists. A comparable approach has been employed to gather kākā sighting data by another sanctuary; Orokonui. However, the majority of sightings reported to not include leg-band identification (<https://kākādatabase.orokonui.nz>), further illustrating the potential limitations of a citizen science approach with kākā. Alternatively, recent developments in deep-learning technology may provide a novel and effective means for kākā monitoring and SNA.

Ferreira et al., (2020) have successfully utilised deep learning to identify individual great tits in both captive and wild contexts, vastly reducing the time required for data collection (Ferreira et al., 2020). As many kākā have distinctive markings, such as plumage patterns and

beak scarring (unpublished data). Automated picture-recognition could provide a suitable means to further examine kākā social networks both within and beyond Wellington. Such comparative datasets could provide further insight into how urbanization effects kākā sociality, and provide a useful monitoring tool for at-risk populations.

For behavioural ecologists to conduct research that can be applied in conservation practice, furthering our knowledge of threatened species should be prioritised (Webber & Vander Wal, 2019). This research provides social network data on a previously unexamined species, adding to the currently limited taxa reported in the social network literature. More importantly, it reports on an endangered species, which have been largely neglected in the social network literature to date (Webber & Vander Wal, 2019). However, using conventional approaches to SNA, such as real-time observation (Williams & Lusseau, 2006) and camera traps, is highly labour and intensive, and unlikely to provide the up-to-date and extensive sampling required for practical application in the conservation of kākā or other species (Snijders et al., 2017). Alternative approaches, such as deep learning, may provide more suitable means for conducting social network research on kākā and other species in the Wellington region and beyond. Overall, the findings of this study indicate that kākā form non-random social networks, and highlight the importance of considering dispersal behaviour and space use when planning translocations and reintroductions in this species. These results also suggest that supplementary feeding has significant implications for monitoring population numbers, sex ratios, and disease dynamics in kākā, and potentially, in other urban animal populations globally.

Ethics

The research presented here was approved by the Victoria University of Wellington Animal Ethics Committee (application no. 0000023295), and the Victoria University of Wellington Human Ethics Committee (application no. 0000024877).

Chapter 5

General Discussion

The primary aim of this thesis was to explore social learning and social networks in *Nestor* parrots, and to consider how the knowledge generated may be of value in the conservation and management of these species. To achieve this, social learning studies were conducted with two species; kākā (*Nestor meridionalis*) and kea (*Nestor notabilis*), using live and video demonstrators. A social network for Wellington's kākā population was also constructed by recording visitation events at established feeding sites in suburban Wellington and within a mainland sanctuary; Zealandia.

In this thesis, I report the results of three experiments, which assess the role of social learning in the uptake of; tool use, string-pulling, and food aversion behaviours. I also report the findings from social network analysis conducted using Wellington's kākā population. In this final chapter, I will discuss the key findings, results, and the limitations of these studies, as well as their significance and implications in both local and global contexts. I will also comment on how these findings may be of utility in the conservation of these endangered species, and make suggestions for the direction of future research.

5.1 Summary of the main findings

In **Chapter 2** of this thesis, I examined the roles of social learning and play in the uptake of a novel tool-use behaviour in kea. To achieve this, I conducted a social-diffusion experiment with a flock of captive kea, in which a single demonstrator was trained to operate a vending-machine like apparatus. This task required individuals to manipulate a compact tool; a wooden ball (Auersperg et al., 2010), and place it into the apparatus to receive a food reward. Ten out of twelve naïve kea were successful in learning this action over eight days, and uptake of this behaviour was facilitated by both social and asocial learning. Additionally, individuals that engaged in higher rates of play behaviour were more efficient learners, indicating that play facilitated uptake of the task. While it is commonly theorised that play may promote the learning of novel behaviours (Heintz, Murray, Markham, Pusey, & Lonsdorf, 2017; Huffman & Quiatt, 1986; K. P. Lewis, 2000), this had not previously been experimentally examined.

Chapter 2 addresses this knowledge gap, providing novel evidence that play can facilitate the learning of a novel tool-use behaviour.

The experiments described in **chapter 3** explored the use of video playback in kākā cognition experiments under field conditions. This was achieved by testing wild kākā on three video playback tasks; two social learning experiments, and one predator-recognition experiment. The first experiment tested social learning of food aversion using a two-option task (Kendal et al., 2009), in which subjects were exposed to one-of-two video playback conditions; 1) a conspecific showing an aversive response to one of two distinctly coloured food sources, or 2) the two food sources without the presence of a demonstrator. Following this, the subsequent food choices of naïve kākā were examined. Overall, test subjects showed no significant difference in their food choices regardless of the video condition, indicating that no social learning had occurred.

The second experiment in chapter 3 tested whether video playback of a demonstrator would facilitate the uptake of a novel string-pulling behaviour by presenting naïve kākā with one-of-two video playback conditions. One video showed a demonstrator solving the string-pulling task, the other video displayed a still image of the same kākā perched at the apparatus, but provided no additional information about the string-pulling solution. Observing either video had no significant effect on the time subjects took to solve the task and, therefore, no evidence of social learning was detected in this experiment.

The final experiment of chapter 3 aimed to validate whether kākā could interpret images shown on a screen, without the confounding variable of social learning. Subjects were given access to a freely available food supply under two video conditions; with, and without, playback of a familiar endemic predator. Kākā viewing the playback of a predator showed no noticeable fear responses and spent no less time feeding from the available food source. This would suggest that kākā were either unable to recognize the predator, or did not perceive it as a significant threat.

The final data chapter of this thesis, **chapter 4**, focusses on social networks and community composition in Wellington's free-ranging kākā population. To construct a social network for kākā visitation events were recorded for a three week period at four established feeding sites in suburban Wellington, and two within Zealandia, a fenced sanctuary in the city. The resulting

social network analyses indicate that kākā form non-random relationships, and therefore preferentially associate with some individuals more than others. Additionally, dissimilarity indices were calculated to examine the crossover of individuals between feeding sites. While it is commonly assumed that Wellington's kākā are primarily based within Zealandia, and leave the sanctuary on excursions to the surrounding suburbs (Recio et al., 2017), the majority of kākā recorded in suburban Wellington were never detected at the feeding sites within the sanctuary. Additionally, all sites, including two that are located only 250 metres apart within Zealandia, appeared to be very distinct in their kākā-community composition. Dissimilarity indices indicate that there is little crossover of kākā visitation between sites, which suggests that kākā are highly selective about which feeders they use. This is the first empirical data to support the hypothesis that kākā may have successfully established beyond the sanctuary perimeter. The dissimilarity between locations also suggests that kākā are highly selective of their feeding sites, which has significant implications for population monitoring, disease transmission (Galbraith et al., 2014; Galbraith, Stanley, et al., 2017), and management of this species.

5.2 Social learning in *Nestor* parrots

Despite parrot's remarkable cognitive abilities (Auersperg, von Bayern, et al., 2014; Goodman et al., 2018; Lambert et al., 2017; Rössler et al., 2020) and sociality (Bond & Diamond, 2004; Coulton, Waran, & Young, 1997; Gallup, Swartwood, Militello, & Sackett, 2015; Nelson & Wein, 2017), social learning remains a largely understudied area of parrot behaviour. Prior evidence to indicate that parrots can learn socially has primarily come from highly controlled experiments, in which a single captive observer is able to learn from a visible, but physically separated, demonstrator (Gajdon et al., 2011; Huber et al., 2001). Instances where diffusion experiments have been conducted so that parrots can interact, have failed to provide sufficient evidence of social learning (Gajdon et al., 2004). The experiment described in chapter 2 provides some of the first evidence of social learning in a parrot species under conditions that allow a full array of social interactions to occur.

Although an open-diffusion experiment (Whiten & Mesoudi, 2008) has been conducted with wild kea previously, a dominant individual excluded other birds from the apparatus, resulting in too few kea solving the task for social learning to occur (Gajdon et al., 2004). By contrast, the experiment described in chapter 2 of this thesis illustrates that even cognitively

demanding behaviours, such as tool use, can be socially learned while other social dynamics are in effect. However, the findings of chapter 2 could be subject to captivity bias (Benson-Amram & Holekamp, 2012; Gajdon et al., 2004; Rössler et al., 2020), and may not be replicable under naturalistic field settings¹. For example, comparisons of laboratory-raised and wild-caught Goffin cockatoos indicates that long-term captive animals show greater persistence when presented with novel foraging problems (Rössler et al., 2020). Given the significance of motivation in problem-solving (Koops et al., 2015; van Horik & Madden, 2016), and the difficulty of the vending-machine task, uptake of this behaviour may be inhibited if wild kea are less persistent than their captive counterparts. Testing of free-ranging kea was not possible for this thesis, however conducting experiments under field conditions is vital to understanding the ecological relevance of social learning, and should be prioritised in future research. An observational report provides anecdotal evidence of social transmission of tool-use occurring in wild kea (Goodman et al., 2018; Maxwell, 2011), and also suggests that intrinsic motivation for play may be a key element in the diffusion and persistence of novel behaviours in this species (Goodman et al., 2018). The experiment conducted in chapter 2 of this thesis illustrates how potent a motivator play is in this species.

Kea are known to be an exceptionally playful species (Bond & Diamond, 2004; Diamond & Bond, 1991; Nelson & Wein, 2017), and, although it has been previously suggested that motivation in previous experiments was intrinsically derived, it was also stated that this alone was insufficient, and a food reward was still required to encourage participation from test subjects (Gajdon et al., 2011). Interestingly, the most prolific solver in the experiment described in chapter 2 was unable to eat the food pellets due to a missing upper mandible, and was therefore never rewarded for the solves it performed. Several other kea also exhibited contrafreeloading behaviour (Osborne, 1977), in which they would solve the

¹A single captive kākā was successfully trained to operate the same 'vending-machine' apparatus used in the kea experiment. This captive individual was a competent solver after three training sessions, which is comparable to the amount of training required by the kea. However, attempts to train wild kākā to perform the same task were unsuccessful. Three wild kākā were subsequently trained to perform a modified behaviour, which required individuals to push a wooden ball up a track to receive a food reward. Although wild kākā could be taught this task with relative ease, this social diffusion experiment was unsuccessful, seemingly for the same reasons as a previous study on social learning in wild kea (Gajdon et al., 2004). One trained individual became very dominant of the apparatus, excluding the other demonstrators and naïve birds from interacting with it. More dominant naïve individuals would displace this demonstrator from the apparatus, however they were unlikely to witness the solving behaviour prior to doing so.

vending machine task even when pellets from previous solves were already available. There were also numerous instances whereby kea would insert their food pellets back into the apparatus, in place of tokens, after which they could not be retrieved and consumed. Additionally, as the balls appeared to have value of their own, and were used in games such as chasing and object-tossing, subordinate individuals were still able to interact with the task as the balls inevitably became dispersed throughout the aviary. Being able to interact with the 'tools', despite being mostly excluded from the apparatus, likely reduced the participant fatigue that would come from complete exclusion from the apparatus. The experimental study of play is very rare in animal behaviour (Lewis & Burghardt, 2010; Marks, Vizconde, Gibson, Rodriguez, & Nunes, 2017; Palagi, 2018; Zupan et al., 2019), however, this thesis adds novel evidence for the utility of play in learning, and illustrates why furthering the experimental science of play is warranted. Future research should look to build on these findings, and address some of the following limitations of this study.

A limitation of the social learning experiment conducted in chapter 2 is that all data is collected in a single context, which creates further difficulties when interpreting these results and disentangling variables such as the relevant contributions of asocial and social learning, persistence and aptitude. Use of a more elaborate test battery would allow for more in-depth analysis of learning and play in this species, and would be required to further disentangle potential correlations between individual attributes such as social and asocial learning ability, persistence and playfulness (van Horik & Madden, 2016). However, the most valuable contribution would likely come from conducting comparable research under in the wild. Such field-based studies are required to understand the contributing and limiting factors for social learning in naturalistic settings, and to account for cognitive difference that may be present between wild and captive-raised test subjects (Rössler et al., 2020). The social learning studies described in chapter 3 were conducted with free-roaming kākā, with video playback was used as an alternative to live demonstrators.

Video playback is theorised to be advantageous for seeding information in scenarios where access to social information is limited, and allows researchers to select and show reliable footage of the seeded behaviour (Hämäläinen et al., 2019). Given the tendency for kea to abandon a seeded behaviour, as demonstrated in chapter 2 and previous research (Gajdon et al., 2011), video demonstrations would provide a means of showing reliable social

information if kākā shared this explorative tendency. Although this method did ensure that naïve individuals had exposure to reliable social information, without exclusion by dominant individuals, no evidence of social learning was detected. In addition to this, kākā showed no significant reaction to video playback of a familiar predator. As animal visual systems may differ significantly (Bovet & Vauclair, 2000; Cuthill et al., 2000; Fernández-Juricic, Erichsen, & Kacelnik, 2004; Lisney et al., 2011; Oh, Šlipogor, & Fitch, 2019), an inability to interpret 2D images could be the result of both physiological and cognitive factors. Due to the complex structure of avian visual cortices (Cassey, Honza, Grim, & Hauber, 2008; Hart & Hunt, 2007; Shimizu, Patton, & Husband, 2010), interpreting the negative results reported in chapter 3 is particularly difficult.

Movement is theorised to be the most potent source of information when observing conspecifics (Nakayama, 2010), and a sensitivity to movement over other visual cues is particularly evident in birds (Ware et al., 2015). Both rooks (*Corvus frugilegus*) and pigeons (*Columba livia*) are capable of recognising conspecifics represented in moving videos, however, they are not able to do this when presented with still images (Bird & Emery, 2008; Shimizu, 1998). This reliance on assessing movement cues is potentially problematic as temporal resolution, the speed at which temporally varying stimuli are processed, is poorly understood in birds (Lisney et al., 2011). However, it is likely that birds have a much higher flicker fusion frequency than humans, and may therefore see some videos as a series of still images (Bird & Emery, 2008). All videos displayed in the experiments described previously were played using iPads with LCD screens, which reduce the flicker fusion frequency concerns associated with other technology types (Bird & Emery, 2008). All demonstration videos were also recorded and played at 60 frames per second (FPS), which was reported to be more suitable than other FPS rates in video playback experiments in pigeons (Ware et al., 2015). Additionally, psittacines are thought to have a stronger bias towards the ultraviolet end of the visual spectrum compared to many other birds (Ödeen & Håstad, 2003), and may therefore have particular difficulties interpreting information on screens designed for human vision. However, if kākā were able to interpret the video footage, and identify the individuals featured as demonstrators, this may have significantly affected experimental outcomes.

Two opportunistically chosen demonstrators were used in the kākā social learning experiments covered in this thesis. One demonstrator was a mature male from a captive

facility and was therefore unfamiliar to observers. The other was a mature female that was subordinate to most other individuals. Numerous species show biases when choosing which conspecifics to copy (Greggor et al., 2017), and both familiarity (Swaney, Kendal, & Laland, 2001) and dominance rank (Van de Waal et al., 2013) can significantly affect whether or not social information is used. Therefore, the selection of an inappropriate demonstrator could lead observers to ignore social information (Bird & Emery, 2008; Greggor et al., 2017), even if they are capable of interpreting it. If kākā can recognise individuals in video footage, as both rooks and pigeons can (Bird & Emery, 2008; Shimizu, 1998), selection of these two demonstrators may have reduced the effectiveness of the playback material presented. There is currently no literature to suggest that parrots of any species possess such social learning biases, or that they are similarly capable of recognising conspecifics presented in videos, so the impact of demonstrator selection is unknown and warrants further investigation. Kākā also failed to respond to video footage of a familiar predator, which would not have been affected by the choice of demonstrator. However, whether the absence of a response to the predator was due to kākā not recognising the image, or simply ignoring the video as it was not perceived the same as a live predator, remains unclear.

The degree to which video playback can serve as a true substitute for live demonstrators is crucial to understanding how pre-recorded demonstrators are perceived and interpreted. However, experiments directly comparing the efficacy of live and video social demonstrators are rarely conducted. Bengalese finches (*Lonchura striata. var. domestica*) have been used extensively in video playback experiments (Gallup et al., 2015; Mottley & Heyes, 2003; Mui, Haselgrove, Pearce, & Heyes, 2008; Takahasi & Okanoya, 2013; Watanabe, Yamashita, & Wakita, 1993), and are receptive to social facilitation when live demonstrators are used (Birke, 1974). However, when tested on the same feeding-facilitation task using video demonstrators, no significant effect of social facilitation was detected (Ikkatai & Seki, 2016). This suggests that video demonstrators were not a complete substitute for the presence of physically present conspecifics in this scenario. Although a more recent study reported that blue tits (*Cyanistes caeruleus*) responded to live and video demonstrators similarly in a two-option task (Hämäläinen et al., 2019), this result is difficult to interpret as there was no evidence of social learning in either demonstrator condition. Given the relative ease of conducting such comparisons, and the utility of such studies in deciphering how social

information is used and interpreted (Hämäläinen et al., 2019), future research should aim to further assess the extent to which video playback can truly be substituted for live demonstrators. An additional area which is desperately lacking from the video playback literature is research conducted in wild settings.

Research exploring social learning via video playback under field conditions was first published in 2014 (Gunhold et al., 2014). This study presented free-ranging common marmosets (*Callithrix jacchus*) with an ‘artificial fruit’ which could be opened in two distinct ways, and video demonstrators displaying one of the two actions. Naïve subjects were more likely to solve the task using the option presented on the video, demonstrating that video playback can be a potent source of social information, even under field conditions (Gunhold et al., 2014). Surprisingly, a search of the literature reveals that no subsequent field-based social learning experiments using video playback have been published. The experiments described in chapter 3 therefore add valuable data on the use of video playback in a field context. However, due to a lack of foundational literature on social learning in kākā (Loepelt et al., 2016), the negative results of these experiments are difficult to interpret. While there are a substantial number of animal behaviour studies that report positive results from video playback experiments (Gunhold et al., 2014; Thorogood et al., 2017), some of which leave no reasonable doubt that animals can interpret images on a video screen (Inoue & Matsuzawa, 2007), inconsistencies in the literature (Emile & Barros, 2009; Ikkatai & Seki, 2016; Mineka & Cook, 1988; Mustafar, De Luna, & Rainer, 2015) would indicate that more foundational work is required to fully understand the utility of video playback in animal behaviour research, particularly under field conditions. Future explorations conducted on model species in the wild, with established records in social learning and video playback experiments, would provide a path of least resistance to address these knowledge gaps.

5.3 Social networks and distribution in Wellington kākā

As pathways detected through social network analysis (SNA) can be used to predict the transfer of information (Aplin et al., 2012; Hoppitt, Boogert & Laland, 2010), SNA has become a primary tool in the social learning toolkit (Webber & Vander Wal, 2019). This statistical technique can also be used to predict pathways of pathogen transfer (Hamede et al., 2009; Rushmore et al., 2014; VanderWaal et al., 2014) and monitor group stability in changing environments (Webber & Vander Wal, 2019), and may therefore facilitate informed

management decisions of vulnerable species (Rosenbaum et al., 2016; Rushmore et al., 2014; Williams & Lusseau, 2006). However, the narrow diversity of taxa studied to date, and a lack of research on at-risk species, creates a barrier to applying SNA in conservation practice (Webber & Vander Wal, 2019). The study in chapter 4 of this thesis addresses these knowledge gaps by conducting the first social network analysis on kākā, an endangered species that now occupies an urban habitat. Data gathered by measuring visitation events at established feeding sites in suburban Wellington and within a mainland sanctuary, Zealandia, suggests that kākā form unique, non-random relationships. Additionally, dissimilarity analysis indicates that each feeding site examined has its own distinct community composition. This is the first empirical data to suggest that individuals that utilise suburban feeders may not use supplementary feeders inside the sanctuary, and that kākā, a sensitive indicator species (Leech et al., 2008), have established within the wider Wellington landscape.

Species that successfully colonise human-dominated environments often develop behaviours that lead to human-wildlife conflict (Barrett et al., 2019), and parrots are no exception (Gajdon et al., 2006; Linklater et al., 2018). For example, opening and raiding refuse bins is a persistent behaviour that was spontaneously developed and in both kea and sulphur-crested cockatoos, and is thought to have spread through social learning (Gajdon et al., 2006; Lucy Aplin, pers. comms). Although this behaviour is yet to arise in Wellington's kākā population, SNA could provide an effective means to halt the spread of this behaviour (Greggor et al., 2017; Webber & Vander Wal, 2019), reducing the resulting human-wildlife conflict. 'Bin-raiding' behaviour would likely be particularly problematic in Wellington due to a reliance on rubbish bags², which are already prone to destruction by domestic animals, over the solid bins used in the previous cases. The apparent role of supplementary feeding on kākā distribution also has significant implications for human-wildlife conflict.

Previous research has reported a positive correlation between property damage and recreational supplementary feeding (Linklater et al., 2018). If the community dissimilarity between feeding sites reported in chapter 4 is reflective of kākā space use, feeding kākā may be a more severe driver of localised damage than previously thought, as destructive behaviours are likely concentrated in areas that kākā most frequently. As some property

² <https://wellington.govt.nz/services/environment-and-waste/rubbish-and-recycling/bins-bags-crates-and-skips/council-rubbish-bags>

damage caused by kākā can be extensive, such as tearing into roof cavities to create nesting hollows³, and costly to remedy (Linklater et al., 2018), understanding the extent to which recreational feeders are responsible for such behaviour is likely to be of increasing importance as kākā increase in numbers.

5.4 Does social behaviour research have a role in conservation?

Behavioural researchers have theorised that cognitive studies can make valuable, in some cases essential (Curio, 1996), contributions to animal conservation for nearly three decades (Brakes et al., 2019; Caro, 1999, 2007; Greggor, Clayton, Phalan, & Thornton, 2014; Greggor et al., 2017; Snijders et al., 2017). And although theoretical papers supporting this notion continue to garner interest (Brakes et al., 2019; Caro & Berger, 2019; Greggor et al., 2017), the application of behaviour to conservation practice remains negligible (Berger-Tal et al., 2016). A 2007 review (Caro, 2007) commented on the failure of theory-driven behaviour research to effectively integrate into conservation practice. While research efforts since have largely aligned with the guidelines for effective conservation integration outlined by Caro (2007), such as focussing on specific problems and species of conservation interest, there appears to be a notable lack of consideration for feasibility and scalability in many published studies.

The most compelling evidence that behaviour can be an effective tool in conservation comes from asocial learning experiments. Individuals can be taught to recognise novel predators (Griffin et al., 2001; Maloney & McLean, 1995), avoid eating poisons (Hickling, 1997) and noxious prey (Llewelyn et al., 2010; Ward-Fear et al., 2016), and predators can be deterred from attacking vulnerable species (Gabriel & Golightly, 2017; Umbers et al., 2020). It is therefore not surprising that numerous papers describe how such research is important to conservation (Brakes et al., 2019; Caro & Berger, 2019; Greggor et al., 2017). However, conditioning individual animals is time-consuming and labour intensive, and beneficial behaviours are likely to become extinguished if they do not have a means of reinforcement and self-perpetuation (Griffin et al., 2001). However, if experimentally seeded behaviours can be socially learned then they may spread throughout entire populations, and become permanently entrenched in animal cultures (Brakes et al., 2019; Cornell et al., 2012; Jelbert,

³ <http://wellington.scoop.co.nz/?p=112945>

Hosking, Taylor, & Gray, 2018). Examples of beneficial behaviours socially spreading and persisting across generations have been observed as naturally occurring phenomena (Donato & Potts, 2004) and as a result of experimental interventions (Aplin et al., 2015; Cornell et al., 2012). However, the literature currently lacks examples of behaviours seeded for conservation purposes that have been socially transmitted and persisted within populations.

The highly controlled captive environments in which most social learning research is conducted (Greggor et al., 2017; Whiten & Mesoudi, 2008) is also likely to inhibit the transfer of protocols from fundamental research to an applied conservation setting. Therefore, conducting future social learning experiments in naturalistic settings should be prioritised. Additionally, few studies have reported evidence of social learning in wild populations of endangered species. As each species can differ in how they use social information (Greggor et al., 2017), making interspecies generalisations difficult, foundational work on social learning of at-risk species is needed. Underrepresentation of endangered species also creates a barrier to implementing social network analysis in conservation practice (Webber & Vander Wal, 2019).

Theoretical models indicate that the application of SNA to species management is achievable with relative ease, and could allow conservationists to make informed decisions regarding wild harvesting (Williams & Lusseau, 2006) and mitigating disease transmission (Rushmore et al., 2014). However, current methods, such as RFID tagging (Aplin et al., 2017; Galbraith, Jones, et al., 2017) and real-time observation (Rosenbaum et al., 2016; Williams & Lusseau, 2006) are highly labour and time-intensive, and the resulting delay in retrieving such data is likely to be problematic to deal with conservation issues that spontaneously arise. Methodological advances will therefore be required if SNA is to become a practical approach in conservation. Aplin et al, (2020) were able to streamline data collection of sulphur-crested cockatoos by utilising a purpose-built mobile phone application and citizen scientists across the city of Melbourne. While a citizen-science approach was effective in collecting a large quantity of data over a peopled landscape, it did still require researchers to fit cockatoos with large, distinctly numbered cattle-tags. This alone would be a notable hurdle in many study systems, and attachment of large and conspicuous tags would not be possible in many species. Automated recognition of individuals via deep learning is an approach that may significantly reduce the need for human input in data collection, as well as removing the

requirement to fit each individual with distinct tags (Ferreira et al., 2020). While this approach is only in its infancy, it appears to be a promising avenue for future social network research, and may be the only means by which SNA can be practically applied in conservation contexts for some species.

Although this thesis does not directly attempt to apply behaviour in conservation practice, it does more broadly examine behaviours of interest to the management of two endangered species. As *Nestor* parrots are highly vulnerable to introduced mammalian predators (Garcia-R & Di Marco, 2020; Wilson et al., 1998), suffer mortality due to ingesting anthropogenic foods (Gartrell & Reid, 2007), and subject to poisoning (Hickling, 1997), behavioural interventions that could increase predator awareness and reduce consumption of noxious substances would be of benefit to these species. Limited evidence also suggests that both kākā and kea are capable of social learning (Gajdon et al., 2011; Goodman et al., 2018; Loepelt et al., 2016), and beneficial information that is introduced into populations may therefore be able to spread and persist through social transmission. Although one can certainly make a case for how harnessing social behaviour and learning may be of great value to conservation, the difficulties, and time and labour demands, encountered throughout this thesis illustrate the chasm that lies between theoretical reasoning and real-world application. While I have little doubt that behaviour will intermittently make valuable contributions to conservation going forward, the likelihood of this outcome should be given significant consideration due to the opportunity costs associated with developing such conservation interventions. Until more of the fundamental questions around the limits of social learning are answered, investing in traditional management practices is likely to be the most effective use of resources.

5.5 Concluding remarks

This thesis adds to the limited research on social learning in parrots, and furthermore, alludes to the significance of play and motivation in the uptake of novel behaviours. The study conducted with kea provides novel evidence social information and play can facilitate the uptake of a novel tool-use behaviour. Although no evidence of social learning was found in kākā, this thesis nonetheless contains the first dedicated research on kākā social cognition, and expands on the very limited literature on video playback in the field. Given the paucity of such research, and the compelling findings reported from captive studies, these negative results provide valuable insight into the potential difficulties of conducting video playback

experiments under field conditions. In addition, the final data chapter presents the first social network analysis to be conducted in kākā, and provides novel evidence of the non-random social structure and distribution of this urban parrot population. These findings make a notable contribution to the limited research on social networks in both parrots and endangered species, and have significant implications for future management and social learning research of this species. Overall, this thesis provides novel insights into the social behaviour of *Nestor* parrots, and makes a significant contribution to the limited body of research on social learning in parrots, video playback, and social networks. Taken together, these results suggest that social learning and social networks play significant roles in the behaviour and ecology of *Nestor* parrots, but fundamental research is still required to understand the constraints on social learning, particularly in the wild. This knowledge is crucial if we aim to harness social learning to address the novel conservation challenges that these species may face in a rapidly changing world.

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