Sensory Preferences and Personality Traits of Captive Red Crowned Kakariki (*Cyanoramphus novaezelandiae*) and Antipodes Island Parakeets (*C. unicolor*).

A thesis presented in partial fulfilment of the requirements for the degree
of

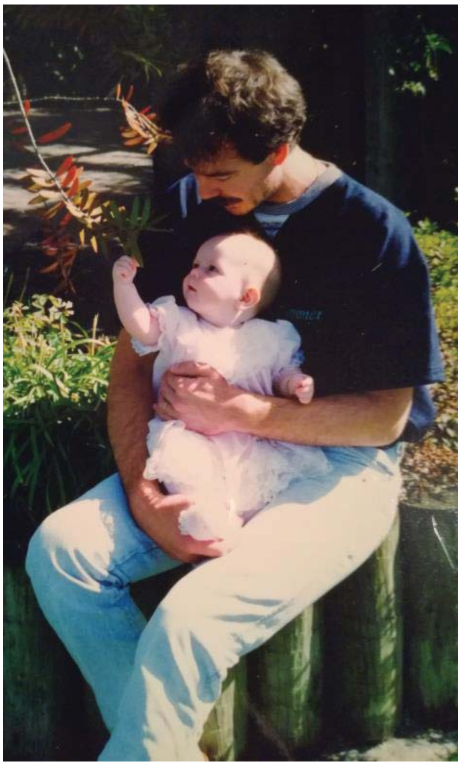
Masters of Science in Zoology

At Massey University, Palmerston North, New Zealand.

Rebekah Mary Ingram
2017

“Life isn’t measured by the years that you spent but by the things that you did and the love that you gave.”

Scott Ingram 15.11.1963 – 03.02.1999



Abstract

The way in which most animals sense and interpret the environment around them differs from species to species. Even two closely related species such as the red-crowned parakeet (*Cyanoramphus novaezelandiae*) and the Antipodes Island parakeet (*C. unicolor*) may respond to the same stimulus in very different ways. Individual birds can also show different personality traits or temperament phenotypes when presented with a novel environment.

Despite being closely related, the two species used in this study have evolved in different natural habitats and use different foraging strategies. The Antipodes Island parakeets are naturally found on a group of sub-Antarctic islands known as the Antipodes Islands where they live in the tussock and sledge fields that cover the large islands and feed on the grasses and other vegetation. The red-crowned parakeets can be found on the small remnants of podocarp forests around New Zealand where they can be seen living in the canopy and on the forest floor, where they feed on mostly fruits, flowers and berries with a small proportion of invertebrates. I postulated that the evolutionary selection pressures on these two species will have resulted in differing behaviour and sensory physiology that could be measured in an experimental setting.

Five individuals from each species was presented with four options in four different sensory experiments (sound, taste, colour and smell). The four different options were presented on top of a metal pole that was placed in each corner within a 1m^3 perspex box. The behaviours shown by the birds over each 20-minute testing period was recorded and analysed in terms of both sensory preferences and personality traits. Each sensory experiment was repeated four times with each of the 10 birds. This mean that each bird was tested a total of 16 times (four repeats for each of the four sensory tests).

The Antipodes Island parakeets showed interest in all four sensory experiments and spent time investigating all of the options presented to them, but showed the clearest preference for the olfactory stimulus of carrion. They were overall more active and showed a lower level of neophobia towards the novel environment of the testing apparatus. The red-crowned parakeets showed the opposite reaction to the novel environment of the testing apparatus by being less active and preferring to stay in one place rather than investigating more of the testing box. The red-crowned parakeets also only showed interest in the colour sensory test spending more time investigating the four colour options more than any other sensory option.

Both the Antipodes Island parakeet and the red-crowned parakeets were captive bred and raised in the same captive facility. This meant that all the birds were exposed to the same captive environment and may have a low level of genetic diversity. The results of this study showed that

even though all the birds were raised in the same conditions there were still measurable differences between the two species in behaviour and sensory choices. This suggests that in each species, some innate behaviours driven by evolutionary selection on their ancestor's life history have persisted despite their common early learning environment in captivity.

Acknowledgements

First, I would like to thank my supervisors Dr. Ngaio Beausoleil, Associate Professor Phil Battley and Professor Brett Gartrell for helping navigate my way through everything that my thesis has thrown at me, without you I don't know what I would have done when everything started to crumble. Thank you for all your help and kind words that have made this process tolerable.

A huge thanks to Carolyn Gates for helping me sort through the numerous data points and being so tolerant with my lack of R and statistics ability. Your help and patience was greatly appreciated as I would have never been able to get this finished without your R wizardry skills.

I also like to say the biggest thank you to Brett as you gave me the chance to fulfil my dream of working with some of New Zealand's rarest and endangered birds through Wildbase wildlife hospital, the timing of this couldn't be more perfect when my thesis was starting to fall to pieces. The skills I have learnt through Wildbase has allowed me to move into a career working with New Zealand wildlife and I can't thank you enough for giving a little zoology student like me the chance to pretend to be a wildlife technician, hope I didn't screw too many things up.

To the team at Wildbase a massive thank you for taking me under your wing and making me realise that I can do a whole lot more than just study birds from a far. I have learnt so many new things and I hope I wasn't too much of a burden with my lack of technician training. Pauline, you were right you did make a technician out of me in the end all it took was for things to go wrong in my thesis for me to realise I can do so much more.

Thank you to Peter Russell without out you my thesis experiments would have never gotten started. I'm thankful for your willingness to let your birds be used in my experiments, I promise I treated them well.

A huge thank you to Cleland Wallace for being able to work your magic and take my half-constructed drawing of a testing box and turn it into a useable reality. I'm sorry it was so big and the door way was so small.

To the people in Ecology, especially those who had to deal with me when everything started to fall apart, thank you for your endless support, your shoulders to cry on, the drinks that were poured and the kind words about the brighter side to research. We all have been through the same up's and down's but at least we are all on the sinking ship together. So let's pour a glass of something strong and drink to the bright light that eventually comes at the end of this dark and scary tunnel we call postgrad.

Thank you to Melanya for the coffee and lunch breaks that gave both of us a reason to stop working for a little bit and the encouraging “pep talks” that gave me the kick in the butt that was needed at times. Thank you to Gg for the numerous trips to Taupo, Wellington and Mt Bruce when we both needed to get out of this place. Thanks to Tazi for putting up with me when I was freaking out and stressed. The numerous cups of tea and trashy reality shows were a good distraction. To the flat mates I lived with over the course of the last couple of years, I’m sorry if my baking made you fat or gave you diabetes but at least it hopefully tasted good.

Thank you to my family, even though you might not have understood everything I was doing you still encouraged me to get things done and finally finish.

Finally, to my amazing mum, I got there in the end which I guess you always knew I would. Thank you for everything that you have done for me over the past 25 years, I hope I didn’t waste too many of them. Your endless support and encouragement allowed me to become the person I am today. Thank you for taking me to all the zoos and nature reserves growing up and trying to help with my assignments even though it didn’t make any sense to you at all. I am forever thankful for all the things that you have done for me and now it’s your time to do the things that you have always wanted to do.

Table of Contents

List of Figures

List of Tables

Chapter One: Introduction

"Back off, man. I'm a scientist"- Ghostbusters (1984).

The way in which an organism interacts with its environment is greatly influenced by its ability to perceive the environment. Sensory perception varies between species and is one factor which is thought to shape the cognitive experience, or umwelt of different species (Jordan & Ryan, 2015).

Ecological studies have been conducted on the parakeets of the *Cyanoramphus* genus that inhabit New Zealand and many of its offshore islands to investigate the wild diet, behaviour and the favoured habitat distribution of the three main species, the yellow-crowned parakeet, the red-crowned parakeet and the Antipodes Island parakeet (Elliott, Dilks, & O'Donnell, 1996; Greene T. C., 1999; Greene T. C., 2003; Warham & Bell, 1979). These studies have shown marked differences between members of the *Cyanoramphus* genus but there have been no previous attempts to investigate these differences in an experimental setting.

The experiments conducted in this study were designed to determine whether or not the birds show within and between species differences in preferences for a given sensory stimuli (colour, taste, sound or smell) and whether individual and species based personality traits can be determined, for example the degree of neophilia/neophobia using red-crowned parakeets and Antipodes Island parakeets. I hypothesised that sensory perception and personality characteristics would vary between species, and that these differences might be predicted based on the birds' wild ecology. Specifically, Antipodes Island parakeets (*Cyanoramphus unicolor*) evolved in a resource poor and restricted island habitat, therefore I predicted that they would use a wide range of sensory perception to make foraging choices and that the species behaviour would be predominantly neophilic. In contrast, red crowned parakeets (*C. novaezelandiae*) evolved in the beech forests of mainland New Zealand in comparatively resource rich environment. Therefore, I predicted that they would be more specialised in the senses used for foraging choices and would thus exhibit predominantly neophobic behaviour.

The results of this study could also increase the environmental enrichment opportunities available to the captive birds used in this study by providing more specialised information about how each species uses their environment and what enrichment opportunities can created a more natural environment for the birds while they are in captivity.

1.1 Study Species: Red Crowned Parakeet

The red-crowned parakeet is one of three birds known by the Māori of New Zealand as Kākāriki. Red-crowned parakeets are listed as "Near Threatened" by the International Union of the Conservation of Nature (IUCN) and are considered "relicts" by the Department of Conservation (DoC) which means they have undergone a decline within the last 1,000 years and now occupy

<10% of their former range (Robertson, et al., 2013). Their population is in decline due to habitat loss and predation by introduced mammalian predators, primarily stoats (*Mustela erminea*) (Greene T. C., 2003). Red-crowned parakeets along with the other two members of the Kākāriki, the yellow-crowned parakeet *(C. auriceps)* and the orange-fronted parakeet (*C. malherbi*) have been placed into captive breeding programs in order to halt the rapid decline in their respective populations.

1.1.1 Taxonomy

The red-crowned parakeet belongs to the genus *Cyanoramphus* which is made up of 12 parakeet species globally (Triggs & Daugherty, 1996). This genus is found not only in New Zealand but on many of the surrounding islands and as far as New Caledonia and Norfolk Island, a brief summary of this is displayed by figure 1.1. There are many subspecies of red-crowned parakeets that have been described over the years; these include the Chatham Island red-crowned parakeet (*C. n. chathamensis*), the Kermadec Island red-crowned parakeet (*C. n. cyanurus*) and the now extinct Macqurie Island red-crowned parakeet (*C.n.erythrotis*†) (Boon, Kearvell, Daugherty, & Chambers, 2001; Triggs & Daugherty, 1996). Other species include Reischek's parakeet (*C. hochstetteri*), New Caledonian parakeet (*C. saisseti*), Lord Howe parakeet (*C.subflavescens*), Norfolk Island parakeet (*C. cooki*) and Forbes parakeet (*C. forbesi*) which is still under debate over its genetic placement within the *C. novaezelandiae* species.

1.1.2 Ecology

1.1.2.1 Distribution

Red crowned parakeets were once widespread throughout all of the mainland islands of New Zealand but due to habitat loss and predation or competition from introduced mammalian predators their population is now restricted to small patches of forest blocks in Northland, the Coromadel and in the Central North Island (Greene T. C., 2003). Many populations have established on the islands that surround New Zealand including Kapiti Island, Stewart Island, Somes Island, the Auckland Islands and the Antipodes Islands (Higgins P. , Order Psittaciformes, 1999a). Red crowned parakeets can also be found in some predator free nature reserves on the mainland including Karori/Zealandia Wildlife Sanctuary in Wellington.

1.1.2.2 Habitat

Red-crowned parakeets have been observed in a wide variety of habitats from dense temperate rainforests, coastal forests, and scrubland, to forest edges and open areas (Forshaw J. M., 1978). This wide variety of habitats allows the red crowned parakeets to live alongside other *Cyanoramphus* species such as yellow crowned parakeet and Antipodes Island parakeets (Higgins P. , 1999a). Red crowned parakeets forage from the top of the canopy to the forest floor depending on the habitat in which they are found, this flexibility allows them to coincide in close proximity to other closely related species (Higgins, 1999a).

In this study, I hypothesise that the red-crowned parakeets being a forest dwelling species would not show any preference for vertical orientation as they have been seen in all levels of the forest from the canopy to the forest floor.

1.1.2.3 Diet

Many studies have been conducted over the past years investigating the diets of many of the *Cyanoramphus* genus including red crowned parakeets. These studies have found that red crowned parakeets diet consists of mainly fruits, flowers, seeds, leaves and flower buds with only a small number of invertebrates eaten (Greene, 1998; Forshaw J. M., 1978; Warham & Bell, 1979). The proportions of each part of the red crowned parakeets' diet changes according to the season with flowers being eaten in larger amounts during the winter and spring and seeds being eaten more in summer and autumn (Greene T. C., 1998).

.

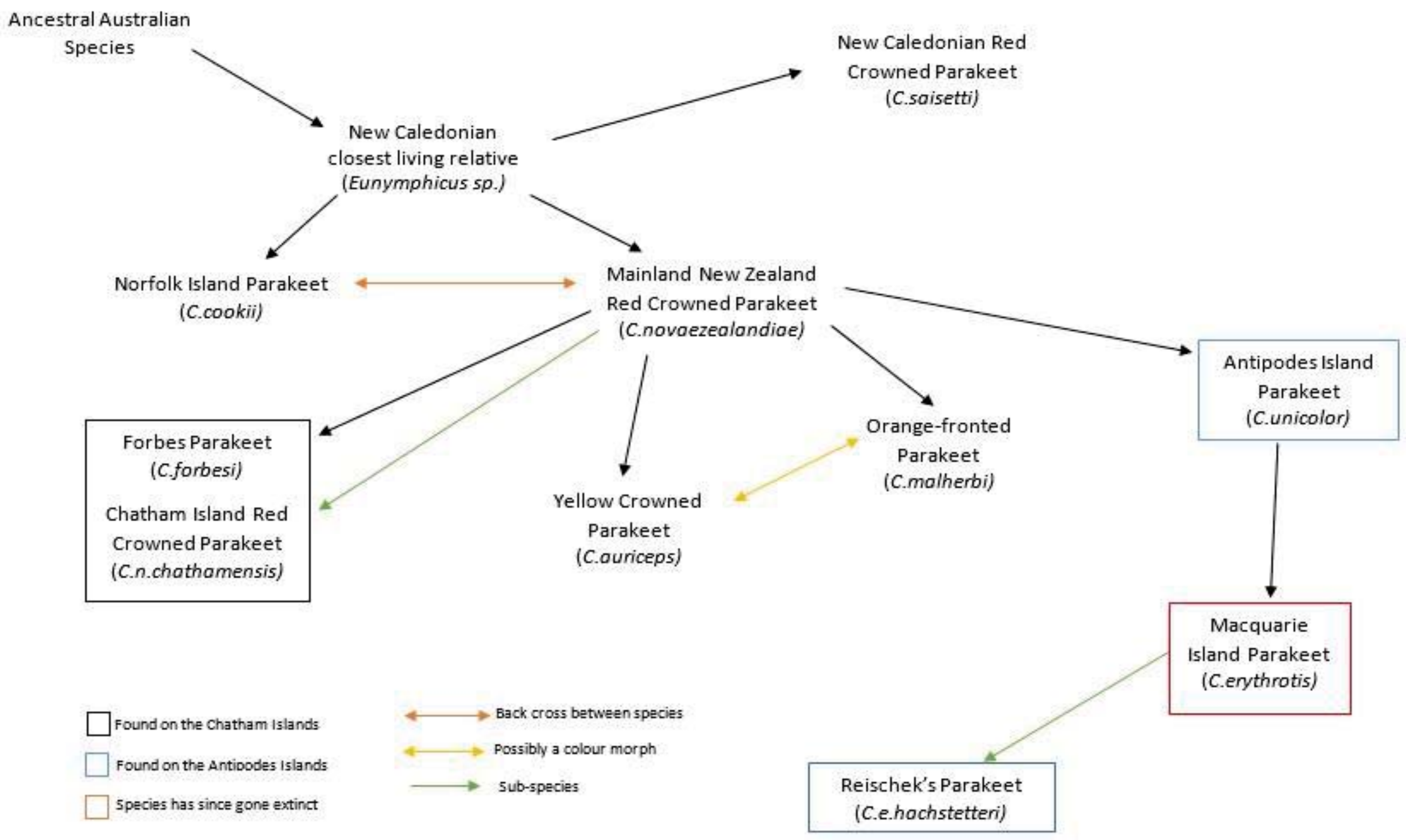


Figure 1.1 Brief evolutionary history showing the spread of the genus Cyanoramphus throughout New Zealand and the surrounding islands in the Pacific Ocean, based off the data collected by Boon et al. (2001)

1.2 Study Species: Antipodes Island Parakeet

Antipodes island parakeets are the largest of the *Cyanoramphus* species and are listed as vulnerable by the IUCN and "naturally uncommon" by DOC which means their distribution is limited to a specific geographical area where this is not the result of human disturbance (Robertson, et al., 2013). The Antipodes Island parakeets kept in captive institutes around New Zealand are intended as a "back-up" population if anything was to happen to the wild population on the Antipodes Islands. The first documented translocation of wild Antipodes Island parakeets to captive institutes in New Zealand took place in the 1970's and 1980's when approximately 11 birds were taken from the Antipodes Island's to form a captive population in New Zealand (West, Tisdall, & Aviss, 1995).

1.2.1 Ecology

1.2.1.1 Distribution

The Antipodes islands are a group of islands which can be found 860km southeast of Stewart Island (Warham & Bell, 1979). This group of Sub-Antarctic Islands are made up of one main island known as Antipodes Island, Bollons Island to the north and various numbers of small islets and stacks. Antipodes Island parakeets are commonly found on the Antipodes and Bollons islands with smaller numbers found on Archway, Windward and Leeward islands. The population of Antipodes Island parakeets has been estimated at between 2,000 and 3,000.

1.2.1.2 Habitat

Antipodes Island parakeets can be found in the areas of tall dense tussocks and sedges that cover most of the sub-Antarctic Antipodes islands. They can also be found alongside streams and on slope around the island group (Greene T. C., 1999). Antipodes island parakeets are known as one of the few ground dwelling parrots found throughout the world along with the Kakapo (*Strigops habroptilus*).

In this study, I hypothesise that the Antipodes Island parakeets are more likely to spend most of their time on the ground in the testing box as they are a ground dwelling species.

1.2.1.3 Diet

Antipodes Island parakeets have a diet that primarily consists of leaves, seeds and other vegetation. They have been observed to prefer the leaves and seeds of *Poa litorosa* and *Carex appressa*. The components of the Antipodes Island parakeet diet can vary with the seasons as some plants are only available in certain seasons. Antipodes island parakeets supplement their vegetation rich diet with flowers, berries and invertebrates. The parakeets also show carnivorous behaviour and will enter storm petrels' burrow, and kill any adults and young that are on the nest as well as eating any eggs that are in the burrows. They will also scavenge from seabird carcasses found along the coastline, an example of this is shown in figure 1.2.

1.2.1.4 Behaviour

Antipodes island parakeets are usually sedentary and quiet in nature and are observed in pairs, small family groups or by themselves in the wild (Higgins P. J., 1999b). The juveniles however, have been shown to display destructive behaviours like those of the alpine Kea (*Nestor notabilis*). However, there has been very little research conducted on the sensory perception of the *Cyanoramphus* species therefore only assumptions based on anecdotal evidence can be made about their sensory perception. Antipodes Island parakeets are the only parakeet that has been observed actively hunting seabirds and feeding on carcasses that wash up on the shore of the Antipodes Islands. (Greene T. C., 1999). Antipodes island parakeets actively hunt the Grey-backed storm petrel (*Garrodia nereis*) during their breeding season (Greene T. C., 1999).

Figure 1.2 Antipodes Island Parakeet scavenging on blood filled quills of an Albatross chick corpse. Photo by K. Walker. Sourced from milliondollarmouse.org.nz/2015/08/21/island-of-strange-noises-and-predatory-parakeets/

The differences in the ecology of the Red-crowned parakeets and their close relative the Antipodes Island parakeets, are thought to be due to the different habitats in which they live and along with their different diets, it would be assumed that these two species would interact with their environments differently and may prefer certain sensory stimuli. This assumption will be tested in this thesis by putting both species through four different sensory choice selections in order to assess whether or not these closely related species have any preferences for any sensory stimuli. In order to understand why the birds might be showing any preferences towards a certain sensory stimulus, what the birds can or cannot perceive in terms of sensory perception must first be investigated.

1.3 Sensory Perception

Many different animals including birds use their different senses in several ways to interact and interpret their environment. Some species rely heavily on one sense when interacting with their environment, for example the brown kiwi (*Apteryx mantelli)* predominately uses its sense of smell to search for its food as they are a nocturnal species with very small eyes (Bang & Cobb, 1968). Most animals may use a combination of their senses to interact with the environment, forage for food and attract mates. Having information about what the animals can perceive in terms of their different senses allows researchers to conduct tests looking at how the animals find their food and other ecological behaviours using the right sensory options, thus ensuring the animal is able to perceive the options presented to them (Floyd & Woodland, 1981; Heppner, 1965; Montgomerie & Weatherhead, 1997).

For the purposes of this thesis, I will use the definition of a sense as "a system which consists of a group of sensory cell types that will respond to a specific physical phenomenon and can also respond to a particular group of regions within the organism's brain, where the signals are received and then interpreted by the brain" (Domann, Voets, & Nilius, 2008). One category is known as exteropceptive or proprioceptive senses and these are senses that can perceive one's body position, motion and state. This includes the five traditional five senses; which are known as are touch (tactioception), smell (olfacoception), sight (ophthalmoception), hearing (audioception) and taste (gustaoception), along with thermoception (the ability to sense temperature differences) and weak magnetoception (ability to sense a magnetic field) (Breedlove, Watson, & Rosenzweig, 2010). The other type of sense is known as interoceptive senses and these are sense that perceives sensations in the internal organs of the animal's body, these will not be considered further.

Sensory perception is defined as the organisation, interpretation and identification of information from one's sensory organs to understand their surrounding environment (Schacter, Gilbert, Wegner, & Hood, 2011). This involves a signal being sent to the central nervous system of the animal as a result of a physical or chemical stimulus that they have encountered in their environment. These signals are not passed through a passive process but by a cognitive process that can be altered through learning, memory, attention and expectation (Schacter, Gilbert, Wegner, & Hood, 2011). The actual definition of what constitutes a sense is still under debate in the scientific community as different animals have different capacities to sense the world around them. This makes it hard to define precisely what a sense is.

The ability or "strength" of each of the five traditional senses can differ between different species. For example, humans have a relatively weak sense of smell when compared to most other mammals. Some animals may also lack one or more of the five traditional senses i.e. a kiwi's eyesight is relatively poor compared to that of a parrot but their sense of smell is stronger (Cunningham, et al., 2013).

Closely related species can differ in how they use their senses to interact with their environment. This has been shown for olfaction of Kaka (*Nestor meridionalis*) and their close relative the Kea (*Nestor notabilis)* by Gsell, Hagelin & Brunton (2012). The two species were tested for their behavioural reactions to three different scents (fruit, feather and mint) and the results showed that there was a species difference for different odours and scents. Gsell, Hagelin & Brunton (2012) suggested that this species difference was due to the ecological differences between the alpine kea and the forest dwelling kaka. The kea is typically diurnal and live in lower temperatures and humidity, which might result in release of less volatile components from their environment. Therefore, the kea might be sensitive to a different spectrum of scents than the kaka. The kaka in comparison are sometimes nocturnal and live in the forest canopy, olfaction has been shown to be a good signal for forest dwelling birds (Healy & Guilford, 1990; Gsell, Hagelin, & Brunton, 2012; Hagelin, 2004). These different responses in closely related species shows that habitat and foraging behaviour can change the sensory perception of closely related species.

1.3.1 Smell (Olfaction)

Olfaction occurs when an odorant molecule passes through the nasal cavity dissolves into the mucus lining and binds to specific sites on their olfactory receptor. These olfactory receptors form a structure known as a glomerulus. These glomeruli are found on the ends of the olfactory neurons that process information and relay it to the brain via the olfactory bulb (Colville & Basseri, 2001). It is understood that the bigger an animal's olfactory bulb is the better the animal can perceive a wider range of odorants. This is turn can be related to the life history of the birds in relation to their foraging abilities and how important smell is to that particular species. Kiwi's (*Apteryx spp.)* and tubenoses (Procellariiformes) rely on a sense of smell for finding their food (Corfield, Wild, Hauber, Parsons, & Kubke, 2007; Martin, et al., 2007). The olfactory ability of all animals is mostly based on the surface area of the epithelium of the olfactory cavities found in the nasal canals and the size of the olfactory bulb that is found within the forebrain of all vertebrates. The location of the olfactory bulb is the same in birds but the size and shape of the bulb can be different depending on the species of bird as shown in figure 1.3 (Bang & Cobb, 1968).

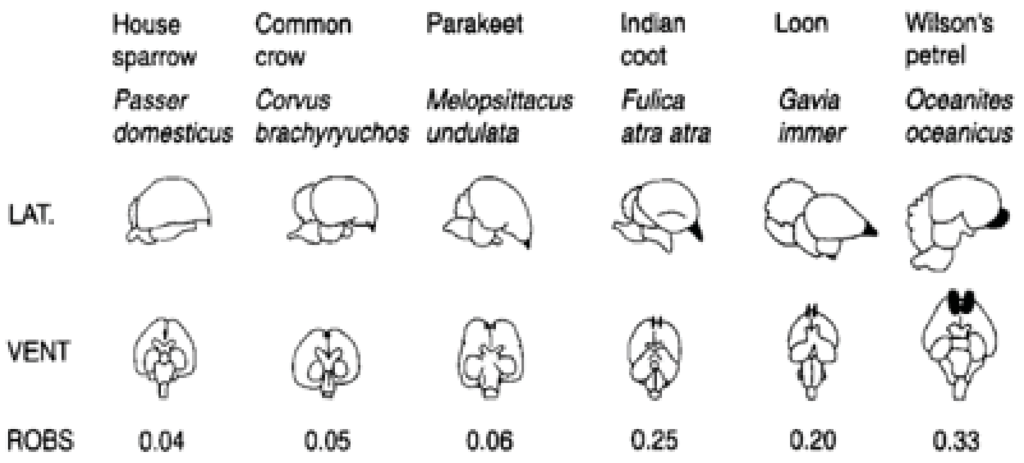


Figure 1.3 Average Size and location of the Olfactory Bulb (black) in Six Species of birds increasing from left to right. An increase in olfactory bulb correlated with the species reliance on olfactory cues when foraging and other behaviours. (Bang & Cobb, 1968)

Table 1.1 shows the relative sizes of a species olfactory bulb is to the rest of its cerebral hemisphere. No information currently exists on the relative size of the olfactory bulb in the *Cyanoramphus* genus. This table shows that the Brown Kiwi (*Apteryx australis)* has a relatively large olfactory bulb of 12mm and is 34% of the birds overall cerebral hemisphere (Bang & Cobb, 1968; Corfield, Wild, Hauber, Parsons, & Kubke, 2007; Martin, et al., 2007). When compared to the olfactory bulb of the Budgerigars (*Melopsittacus undulata),* which is only 0.8mm and is only 6% of their overall cerebral hemisphere, it is therefore assumed that the Brown Kiwi has a better sense of smell as their olfactory bulbs are larger than that of a Budgerigar.

Olfaction can be categorised as chemoreception along with taste as it requires the presence of a chemical stimulant in order for the odorant to be perceived by the receptor cells and transmitted to the olfactory bulb in the animal's cerebral hemisphere (Colville & Basseri, 2001). Most animals have two separate olfactory systems; the main olfactory system which responds to volatile molecules or chemicals and the accessory olfaction system which is designed to perceive pheromones (Colville & Basseri, 2001).

Humans have fewer activated odour receptors than most other primates and in most mammals, each of the olfactory receptor neuron only express one odour receptor. These receptor nerve cells are a lock and key system, which means that the receptor cell will only respond to the correct molecule or odorant and will ignore any other odorants that are not the right size or shape (Colville & Basseri, 2001). Each species has a different level of olfactory sensitivity which is measured through the proportion of an animal's olfactory epithelium compared to their respiratory epithelium within the nasal cavity.

There have been many studies conducted on different species of birds to understand their ability to smell and to also investigate whether their diet or habitat influences their olfactory ability. Bang and Cobb (1968) studied the ratio of the olfactory bulb and cerebral hemispheres of 108 different species of birds. They then summarised their findings and table 1.1 was adapted from these results. This showed that the Brown Kiwi and the Procellariiformes seabirds have the largest olfactory bulbs and therefore the best sense of smell of the 108 species investigated (Bang & Cobb, 1968, Corfield, et al., 2016). Parrots and Passerines generally have very small olfactory bulb ratios and are thought to therefore have a poor sense of smell. For example, experiments on the Kakapo (*Strigops habroptilus)* (Hagelin, 2004) and the Yellow-backed Chattering Loris (*Lorius grarrulus flavopalliatus)* (Roper, 2003) suggest that parrots do have a sense of smell but it is relatively weak when compared to other bird species.

In this study both species were presented with four scent options; flax flowers, parrot seeds, kereru pectoral muscle (carrion) and invertebrate (scale insects). I hypothesise that based on the wild diet of the two species used in this study the Antipodes Island parakeets will show a preference towards the carrion scent as they have been known to feed on shorebird carrion and hunt storm petrels. Whereas the red-crowned parakeets would show a preference towards the flax flowers and seed options as they have a diet consisting of mostly fruit, berries, flowers and seeds.

Table 1.1 Species Comparison of the diameter of both Olfactory Bulb and Cerebral Hemispheres and the ratio between the two adapted from Bang & Cobb (1968).

Species	**Olfactory Bulb Diameter (mm)**	**Cerebral Hemisphere Diameter (mm)**	**Ratio Olfactory Bulb:Cerebral Hemisphere (Percentage)**
Brown Kiwi (*Apteryx australis)*	12.0	35.0	34.0
Diving Petrel (*Pelecanoides georgicus)*	2.0	11.3	18.0
Weka (*Gallirallus australis)*	4.6	19.0	24.0
Pukeko (*Porphyrio poliocephalus)*	4.6	19.7	23.0
Mallard (*Anas platyrhynchos)*	4.0	21.0	19.0
Great Horned Owl (*Bubo virginianus)*	4.5	25.0	18.0
Domestic Fowl (*Gallus gallus)*	2	13.0	15.0
Starling (*Sturnus vulgaris)*	1.4	14.5	9.7
Budgerigar (*Melopsittacus undulata)*	0.8	13.0	6.0

1.3.2 Taste (Gustation)

Taste or gustation is the sensation produced when a substance or food object is placed in the mouth. This causes a chemical reaction with the taste receptor cells that are found in the taste buds, which line the surface of the tongue or around different parts of the mouth cavity. The surface of the tongue is covered with thousands of small bumps called papillae and it is these small papillae that contain the taste buds responsible for the sensation of taste (Zhao, et al., 2003). The taste receptor cells found within the taste buds are specialised known as neuroepithelial cells, which are located within the lingual epithelium of many animals' oral cavities (Medler & Kinnamon, 2004). These taste receptor cells have the ability to act as epithelial cells or sensory neurons and are responsible for the conversion of chemical stimuli into electrical signals, which are then sent to the parietal lobe of the brain.

Not all animals have the same amount of taste buds and birds are thought to have comparatively few taste buds. The full extent of birds' ability to perceive taste is still under debate within the scientific community. The human tongue contains anywhere between 2,000 and 5,000 taste buds that are spread between the front and back on the tongues surface (Medler & Kinnamon, 2004). Taste buds can also be found on the roof, sides and back of the mouth cavity along with some parts of the throat. The more taste buds an animal has, the more likely that they are able to distinguish different tastes of food items and at different levels.

The taste receptor cells can detect a number of chemically different taste qualities; sweet, salty, sour, bitter, and umami (savoury). These tastes can be split into two board categories depending on their overall chemical structure (Medler & Kinnamon, 2004). These categories are ionic and complex stimuli with salty and sour tastes being ionic and sweet, bitter and umami being more complex stimuli.

There have been many studies investigating the structure and function of bird's tongues. The complex structure and diversity of taste buds found on the tongue of many birds can show some evidence of the evolution of species differences in foraging choices and strategies but the oral and lingual anatomy of the tongue can also be used. Charles McCann (1963) investigated the external features of the tongues of four members of the order Psittaciformes*;* the kea, kakapo, Antipodes Island parakeet *and* the yellow-fronted parakeet. McCann also compared the structure and function of different tongue structures of six unique New Zealand birds including the Tui (*Prosthemadera noveaseelandiae)* and Kokako (*Callaeas spp.)* (McCann, 1964). McCann found that the type of food and the manner of which the bird obtains their food had a major influence on the overall structure of the tongue. For example, the brushy apex of the Tui's tongue helps to collect the nectar from flowers which is correlated with its nectar based diet.

The tongue of the Kokako has a row of tooth like structures that line the margin of the glottis. These teeth get progressively larger towards the apex of the tongue. This toothed structure helps the Kokako to feed on young leaves and shoots which make up most its diet (McCann, 1964). They also supplement their diets with fruits and a wide variety of insects.

McCann also found that members of the same genus or family can have either the same or a different tongue structure. Figure 1.4 shows the differences in tongue structure of two members of the *Cyanoramphus* genus. The tongue of the Antipodes Island parakeet (Figure 4A & B) has five large taste pits on either side which may lead to a better sense of taste than that of the yellow-crowned parakeet (Figure 4C), which only has two large taste pits on either side of their tongue (McCann, 1963). The diet of the Antipodes Island parakeet and the yellow-crowned parakeet differ in their major components which may be the reason behind the subtle changes in their tongue structures (McCann, 1963).

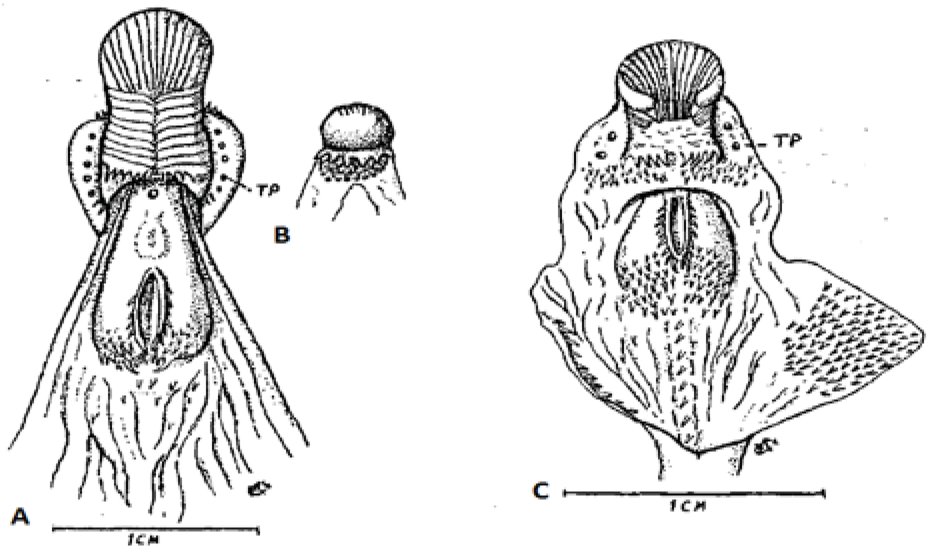


Figure 1.4 Tongue Structure of Two Cyanoramphus spp. C.unicolor (A&B) and C.auriceps (C) from McCann (1963). This shows the position of the taste pits (shown as TP) on both sides of the apex of the tongue along with other structural components and overall tongue shape.

In this study, both species were presented with three taste options based on the percentage of sugar present in the honeydew produced by scale insects over the course of the year in beech forests in New Zealand along with plain tap water (Gaze & Cloud, 1983); low sugar (25g sugar per 100g water), Honeydew concentration (50g sugar per 100g water) and high sugar (75g sugar per 100g water). I hypothesise that based on the wild diet of the two species used in this study, the Antipodes Island parakeets will show a preference towards the low sugar concentration as they have a diet that consist of predominantly vegetation such as tussock grasses, which do not have a high sugar content. Whereas the red-crowned parakeets will show a preference towards the honeydew or high sugar concentrations as their diet is made up of berries and fruits, which have a higher level of sugar than grasses and other vegetation.

1.3.3 Sight (Vision)

The sense of sight or ophthalmoception can be interpreted as the ability of an animal's eyes to focus and detect images of visible light on special sensory cells or photoreceptors that are located on the retina in both eyes (Colville & Basseri, 2001). This in turn generates electrical nerve impulses for varying colours, hues or brightness. The act of seeing an object begins when the cornea and lens of the eye perceives an image of their surroundings through different patterns of light and focuses this image onto a light sensitive membrane known as the retina, which lies on the back of the eyes (Colville & Basseri, 2001). The retina is a part of the brain that isolated from all other parts and acts as an energy converter for the transformation of light patterns into neural signals that can then be processed and understood by the brain. These signals are processed in a hierarchical order by different parts of the brain beginning in the retina (Colville & Basseri, 2001). These neural signals are sent through the optic nerve through the lateral geniculate nucleus (LGN) and then finally ending at the superior colliculus (humans) or the optic tectum (fish, reptiles and birds). This acts as the main visual processor of the brain and transforms the neural signals into an image that the brain can use to help perceive one's surroundings.

The ability to perceive colours is due to the presence of different types of photoreceptors called cones. This cones are found on the retina of the eye along with another photoreceptor known as rods. These rods do not perceive colour but are sensitive to different wavelengths of light (Deeb, 2004; Vorobyev, Osorio, Bennett, Marshal, & Cuthill, 1998; Goldsmith & Butler, 2005). There are three types of cones that are found in the eyes of different animals including birds; each of the different types of cones can perceive a different colour depending on the wavelength of the light that hits the retina of the animal's eye (Olsson, Lind, & Kelber, 2015; Deeb, 2004; Vorobyev, Osorio, Bennett, Marshal, & Cuthill, 1998). Short-wave-sensitive (S) or beta (β) cones are sensitive to light that ranges between 420-440 nanometres (nm) and is associated with the ability to perceive the colour blue. Medium-wave-sensitive (M) or gamma (γ) cones are sensitive to light that ranges between 534-555nm and is mostly associated with the ability to perceive the colour green. Long-wave-sensitive (L) or rho (ρ) cones are sensitive to light that ranges between 564-580nm and is associated with the colour red.

Humans are trichromatic; this means that they possess all three cones in their retina's which allows them to be able to perceive red, green and blue wavelengths. This is called a visual spectrum and different species can have a larger or smaller visual spectrum depending on what cones are present on the retinas. Birds are thought to be tetrachromatic, which means that some species, for example pigeons and budgerigars, have the ability to perceive light from Ultraviolet or UV (370nm) all the way through to the red end of the spectrum (565nm) (Wilkie, et al., 1998; Vorobyev, Osorio, Bennett, Marshal, & Cuthill, 1998; Goldsmith & Butler, 2005).

Figure 1.5 shows the different colours perceived by dichromatic mammals, trichromatic honeybees and a tetrachromatic pigeons. This ability to perceive UV light is thought to be linked to feeding behaviours and mate selection of some birds (Wilkie, et al., 1998). Most animals are either monochromatic or dichromatic and are only able to perceive one or two colours if any at all as they only have one (monochromatic) or two (dichromatic) types of cones cells. The only animals that are able to perceive coloured light are primates (including humans), some insects (e.g. honeybees) and birds. This is thought to be caused by an evolutionary process that increased the number of cones cells present in these animal's retina's and has allowed them to use colour in their foraging strategies whether it is to find a certain kind of flower to pollinate or to distinguish what fruit is ripe and good to eat for primates and birds. Some bird species have feather patterns or plumage that humans cannot perceive as they are only seen in UV light. This may be a mating display or signalling behaviours that only birds can perceive (Vaquero-Alba, McGowan, Pincheira-Donoso, Evans, & Dall, 2016; Wilkie E. S., et al., 1998).

Birds have very good visual acuity and the shape of their eyes along with the size of the optic lobes can vary between species but are both important factors of sight. The optic lobes take up most of the avian midbrain and the eyes themselves take up a large proportion of the skull with the avian skull being modified to house and protect the bird's eyes (Colville & Basseri, 2001). In most birds, the eyes fill much of the orbit, which unlike mammals, leaves very little room for the muscles that control the movement of the eyes. The position of a bird's eyes also varies depending on species and the feeding habits. Seed and grain eaters (including the *Cyanoramphus* spp.) have their eyes placed laterally giving them a wide range of vision without turning their heads, but limiting their stereoscopic vision (Colville & Basseri, 2001).

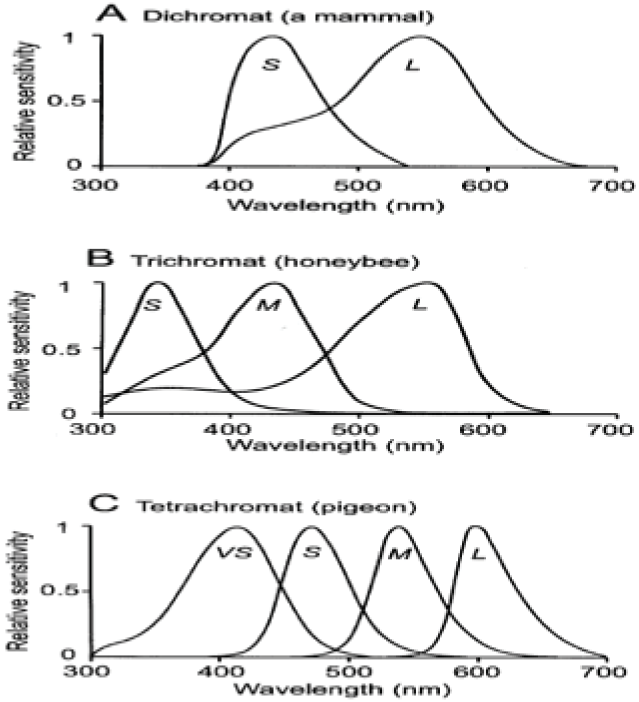


Figure 1.5 Relative sensitivities of the photoreceptors in a dichromatic (mammal), trichromatic (Honeybee) and tetrachromatic (pigeon) animal. Very short wavelength sensitive receptors are shown by VS. Short wavelength sensitive receptors are shown by S. Medium wavelength sensitive receptors are shown by M. Long wavelength sensitive receptors are shown by L. (Kelber, Vorobyev, & Osorio, 2003).

There has been little research looking into the visual capabilities of the members of the *Cyanoramphus* genus. It is known that all birds are at least trichromatic and can perceive red, green and blue wavelengths of light but it is unknown if the members of the *Cyanoramphus* genus are able to perceive ultra-violet light. There have been many studies into the use of ultra-violet in the plumage colouration of many bird species including Hummingbirds (*Trochilidae spp.*) (Goldsmith, 1980), Pigeons (*Columba livia)*, Humboldt penguins (*Spheniscus humboldti)* (Bowmaker & Martin, 1985) and Starlings (*Sturnus vulgaris*) (Parrish, Ptacek, & Will, 1984) (Bennett & Cuthill, 1994). With this information, it can be assumed that the *Cyanoramphus* genus can perceive ultra-violet light in some way, but this was not specifically assessed in this study.

In this study both species were presented with four different coloured seed mixtures based on parts of both species wild diet; green to represent vegetation, yellow and red to represent flowers and berries and blue to represent a small variety of fruits and flowers that aren't presented in large quantities in New Zealand so it acts as a control colour. It is predicted that based on the wild diet of the two species used in this study the Antipodes Island parakeets will show a preference towards the green coloured seed mixture as they have a diet that consist of predominantly vegetation such as tussock grasses. Whereas the Red-crowned parakeets would show a preference towards the yellow or red coloured seed mixtures as their diet is made up of berries and fruits.

1.3.4 Hearing (Auditory)

In order to perceive a sound an animal must first detect the mechanical waves or vibrations that are travelling through the air surrounding them. These vibrations are perceived by the ears, which are the sensory organs responsible for the transformation of the vibrations into nerve impulses that can be perceived by the brain in a region called the temporal lobe (Colville & Basseri, 2001). This sense is known as audition or hearing and along with the sense of touch it can be classified as mechanoreception as they require a movement of a membrane for the sensation to be perceived by the brain.

The auditory system found in all animals contains similar parts with a few minor changes in the birds as a result of environmental adaptations. The outer ear of most animals begins at the pinna or the visible structure of the ear. The pinna focuses the sound waves down towards the ear canal (Beason, 2001; Colville & Basseri, 2001; Schwartzkopff, 1955). Although birds lack the physical structure of the pinna, they instead have specialised feathers, known as auricular feathers that help protect the ear and may also help to transfer sound waves into the middle ear (Pumphrey, 1948; Pumphrey, 1961; Okanoya & Dooling, 1987). The outer ears of many animals are asymmetric and this causes sound waves to be filtered differently as it travels through the ear canal depending on the vertical location of the sound source (Colville & Basseri, 2001).

The next section of the ear or the middle ear is a small fluid chamber that starts at the tympanic membrane and ends at the cochlea membrane. In the mammalian middle ear there are three small bones that help transfer the sound vibrations from the eardrum to the inner ear (Colville & Basseri, 2001). Unlike mammals, birds only contain one small bone within their middle ear. This small bone is called the columella and this connects the middle ear to the fluid filled inner ear (Colville & Basseri, 2001). Similar to the stapes, incus and malleus bones in the ear of mammals, the columella transfers the sound waves to the inner ear through vibrations through the cochlear window (Saito, 1980). The cochlear window helps to protect the inner ear structures from any damage caused by the different air pressure found in the other parts of the ear.

The inner ear is comprised of a large spiral shaped; fluid filled tube called the cochlea, figure 1.6 shows the internal structure of a Bullfinch's inner ear. This is divided lengthwise by a structure known as the organ of Corti and this is the main site of neural transmission of sound waves (Pumphrey, 1961; Pumphrey, 1948).

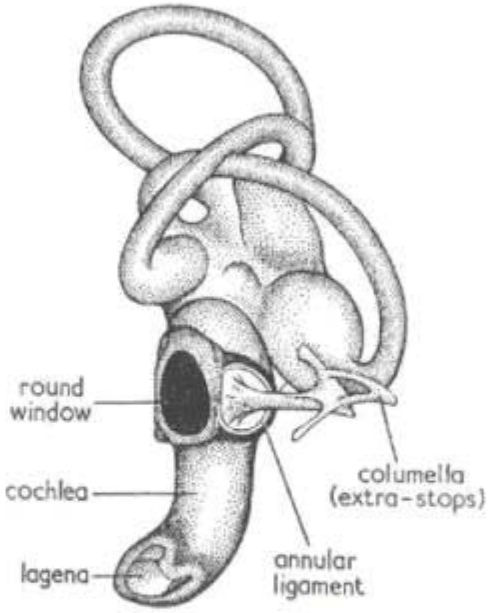


Figure 1.6 Internal structure of a Bullfinch (Pyrrhula spp.) ear depicting the different structures found within a birds' ear (Pumphrey, 1961).

Within the organ of Corti lies a membrane that vibrates when sound waves from the middle ear flows through the cochlear fluid or endolymph (Colville & Basseri, 2001). This is called the basilar membrane and this is a tonotopic membrane, which means that each frequency of sound has a characteristic place along the basilar membrane where it is recognised by the cochlea. At the start of the basilar membrane the high frequency sounds are detected and the further towards the apex of the basilar membrane the lower the frequency of the sound.

The dimensions of the auditory system especially the sensory epithelium known as the basilar papilla have been shown to have some effect on the hearing ranges in vertebrates (Gleich, Dooling, & Manley, 2005). Gleich et al. (2005) compared the frequency of best hearing and a measure of high-frequency hearing that can be derived from behaviourally determined audiograms of 37 different bird species and one species of spectacled caiman (*Caiman crocodilius*) along with two morphological parameters (body mass and basilar papilla length).

Figure 1.7 shows that a species with a long basilar papilla will have the most sensitive or best frequency of hearing in the lower frequency range than species with a short basilar papilla. Songbirds (open triangles) have a relatively short basilar papilla (2-3mm) but are most sensitive to higher frequency sounds (3-3.5 kHz).

Most birds are known to be highly vocal animals and songbirds especially have a wide range of songs and calls that can range some that can be considered "high-frequency" (Okanoya & Dooling, 1987; Gleich, Dooling, & Manley, 2005) (Gleich & Manley, 1988).

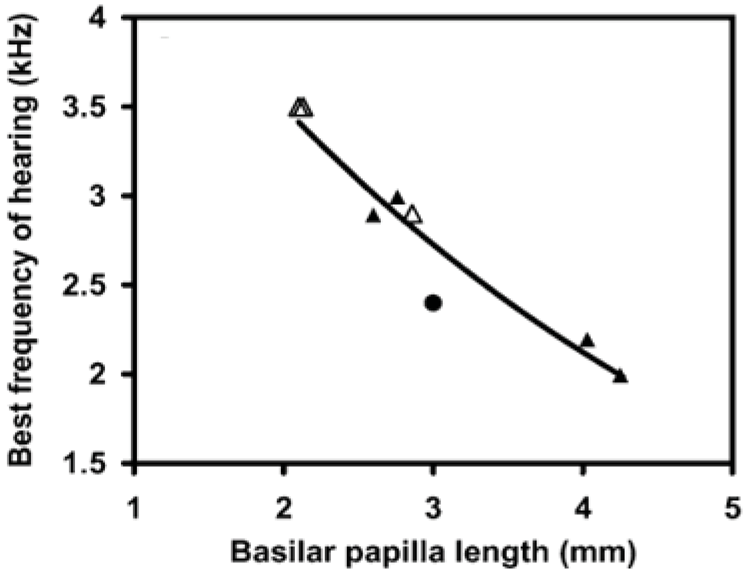


Figure 1.7 The frequency of best hearing as a function of the length of the basilar papilla. The regression line shows a significant relationship between the length of the basilar papilla and the frequency of "best hearing". Waterbirds are represented by the filled circle. Primitive land birds are represented by the filled triangles. Songbirds are represented by the open triangles (Gleich, Dooling, & Manley, 2005).

The size of the bird's skull is thought to have some effect on the length of the auditory system as the larger species such as Emus (*Dromaius novaehollandiae)* will have a larger skull and therefore more room compared to a songbird like a canary (*Serinus canaria domestica)* (Gleich & Manley, 1988; Gleich, Dooling, & Manley, 2005). The overall range of frequencies that an animal can hear is modulated by the size of the skull and the presence of movable or mobile pinna. For example, it has been found that mammals with smaller heads (e.g. mice or hamsters) have the ability to hear high frequency sounds (Heffner & Heffner, 2007). The ability to move the outside or pinna of one's ears allows some animals, mostly mammals, to amplify the sound waves better which results in a larger range of frequencies being heard. Birds lack this movable pinna which may be why they generally have a smaller hearing range when compared to that of humans and other mammals.

There has been a large amount of research conducted into the sensory mechanisms that birds use to locate their live food items. It is not fully understood just how important hearing is to birds in terms of using it to locate food items within leaf litter or wood and even under the soil but it is thought that some birds may be hearing different sound frequencies to humans based on the length of their basilar papilla (Montgomerie & Weatherhead, 1997). Many field and laboratory studies have shown that most birds show a "head cocking" behaviour when they are searching for their food (Heppner, 1965). This head cocking behaviour is when the bird's body is held horizontal to the surface with its head turned at the longitudinal axis to a position that if you were to draw a line between the bird's eyes and extending towards the ground the line would intersect at an angle between 45 degrees and 60 degrees. Figure 1.8 shows the different body positions of the American Robin (*Turdus migratorius*) when searching for food on the ground with figure D showing the body and head position during head cocking behaviour (Floyd & Woodland, 1981). One of the uses of head cocking it thought to be for the birds to focus one eye at a time on the object due to the space between their eyes making them have to rotate their heads in order to clearly focus on object that may be too close for their binocular vision to perceive. This head cocking behaviours may also be used by some birds to focus sound waves better and locate the source of the sound better.

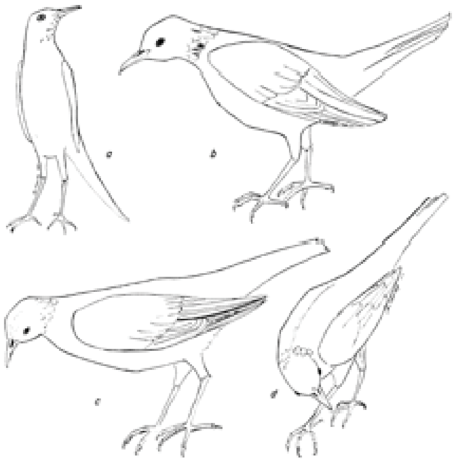


Figure 1.8 Foraging postures of the American Robin (Turdus migratorius) as described by Heppner (1965). Figure A shows the normal standing posture of the Robins. Figures B, C & D shows the foraging movements carried out by the Robin when searching for food. Figure D is the behaviour known as "head cocking".

The hearing ability of parrots has mostly been investigated using the budgerigar (Okanoya & Dooling, 1987; Dooling, 1980; Dooling, 1982; Dooling, 1986). The auditory sensitivity of birds is relatively uniform ranging between 2 – 5 kHz. Okanoya & Dooling (1987) investigated the hearing abilities of seven species of birds including two parrot species, the budgerigar and cockatiel (*Nymphicus hollandicus*). The results of this study showed that the passerine species, the canary (*Serinus canarius*), song sparrow (*Melospiza melodia*) and swamp sparrow (*M. georgiana*), had the best high frequency hearing and the two psittacines (budgerigar and cockatiel) had the best low frequency hearing (Okanoya & Dooling, 1987).

Parrots including the *Cyanoramphus* genus are not known for their vocal ranges unlike songbirds such as the canary. There is very little research on the hearing abilities of the members of the

Cyanoramphus genus, which means that the hearing ability of these species can only be estimated using closely related parrot species including the budgerigar and cockatiel (Okanoya & Dooling, 1987; Dooling, 1980; Dooling, 1982; Dooling, 1986). Using these species as a reference it shows that the *Cyanoramphus* species are able to perceive sounds that range from 2-5 kHz but will have their best range of hearing between 2 and 4 kHz similar to that found in the budgerigars (Okanoya & Dooling, 1987).

In this study both species were presented with two different sound options along with two control options; live mealworms in both leaf litter and bran flakes along with freshly killed mealworms in leaf litter and bran flakes. The dead mealworms were presented to the birds to assess the confounding effect of the smell of the live mealworms without disrupting the sounds produced. Therefore, dead mealworms were used as a control for both substrates. It is predicted that based on the wild diet of the two species used in this study the Antipodes Island parakeets will not show a preference towards either the live and dead mealworms as they do not have a high percentage of invertebrates in their diet and will therefore be interested in all options. Whereas the red-crowned parakeets would show a preference towards the live mealworms in both substrates as they have a small proportion of invertebrates in their diet.

1.4 Methodologies for Evaluating Sensory Preferences in Animals

A non-destructive method of evaluating the relative importance of senses in animals is choice experiments. Sensory preference experiments have been conducted using a number of different species of animals including insects, fish and birds. The testing protocol for each experiment differ in a number of ways but they all offer the animal different options of one or more sense, to figure out if there are any preferences towards one or more sense in that species. This can be done through different coloured food (i.e. coloured flowers or seeds), different olfactory cues (i.e. pollen or flowers) and different levels of nectar or pollen in birds and insects (Stiles, 1976; Floyd & Woodland, 1981; Giurfa, Nunez, Chittka, & Menzel, 1995). All animals use their senses to understand their surroundings but there are clear differences between species in the primary senses used.

Before sensory preferences can be measured, the animal’s ability to perceive the given stimuli (e.g. certain colours or smells) needs to be investigated to ensure that the animals can distinguish between the options given to them before they can show any preference for one or more option. Researchers have looked into the different sensory abilities of a number of different animals including the olfactory capabilities of birds in relation to their olfactory bulb ratio and the structure of their nasal cavity (Bang & Cobb, 1968); taste perception of fish to 21 different free amino acids and a number of classical stimulates and other palatable chemicals

(Kasumyan & DÖving, 2003); and colour vision in birds has been researched in great detail along with colour perception in most other animals (Hart, 2001). These previous experiments provide a baseline against which the sensory perception of different animals can be evaluated.

Single sense testing involves investigating the sensory preference of only one sense at a time. This approach has been used by Gsell, Hagelin, & Brunton (2012) when testing the olfactory sensitivity of Kaka (*Nestor meridionalis*) and Kea (*N. notabilis*) and also by Giurfa et al. (1995), Lunau (1990) and by Lunau, Wacht, & Chittka (1996) when testing the colour preferences of honey bees (*Apis* mellifera) and bumble bees (*Bombus terretris*). Testing one sense allows researchers to determine if the animals showed a preference for one, other stimuli or even no stimuli. This removes the effects of confounding variables. For example, Gsell et al. (2012) found that both the kea and the kaka were both interested in scented tubes and avoided the un-scented tubes used as controls. The birds also showed an aversion towards the smell of their own feathers which may show that they are aware of their own scent and will ignore it when given the option of other bird scents. The kaka and kea were more interested in the fruit scented tubes which may have reflected that their regular diet contained a high percentage of fruit. In contrast, Lunau (1990) found that optical signals were the main sense used by flower-naïve bumblebees when given different coloured flower dummies. Giurfa et al. (1995) found that the flower-naïve bees who had their previous colour experiences kept to a minimum showed a preference towards the colour perceived as UV-blue (410nm) and UV-green (530nm).

An alternate method researchers have used to analyse sensory preference is testing for more than one sense within their experiments, that is, by either using different combinations of two or more sense stimuli or by masking one of two senses to see which the animal favours in certain situations. Stiles (1976) considered the relationship between sugar and colour preference of ten Anna Hummingbirds (*Calypte anna*) by first establishing what type of sugar (glucose, sucrose or fructose) and colour of flowers (red or yellow) the birds preferred in both the wild and under laboratory conditions. Stiles (1976) then tested a combination of their preferred sugar (sucrose) in a feeder that was their non-preferred colour along with their non-preferred sugar (fructose) in a preferred coloured feeder (Stiles, 1976). Once the birds had made three consecutive choices for the same feeder they were then offered two feeders (red and yellow) with their preferred sugar sucrose to investigate what sense is more important to the Anna hummingbirds (Stiles, 1976). Six out of the ten birds initially chose their non-preferred colour, which had been associated with their preferred sugar in the previous test but after repeated trials and without any reinforcements four of the six birds reverted back to their preferred colour choice. This shows that the Anna Hummingbirds had a stronger preference towards colour rather than the type of sugar as most of the birds reverted back to their preferred colour rather than the non-preferred colour that contained sucrose, their preferred sugar.

Floyd & Woodland (1981) also used multiple sensory testing approaches to investigate what sense Black-backed magpies (*Gymnorhina tibicen*) used to locate scarab larvae (*Rhopaea verreauxi,* third instar). The birds were assessed through a series of experiments in which they were presented with three options, one tray with the particular sense that they were investigating present, one tray with the sense masked by something or completely removed and another tray that was had nothing in it to act as a control. This was to investigate whether or not the birds were using that particular sense to locate their food (Floyd & Woodland, Localization of soil dwelling Scarab larvae by the Black-backed Magpie, Gymnorhina tibicen (Lantham)., 1981). The Magpies' senses of smell, vibrotactile, sight and hearing were each tested in isolation with the stimulus present and a duplicate where the sense was masked. Hearing and sight were also compared with each other after each of the individual sense tests. Floyd & Woodland (1981) concluded that smell and vibrotactile senses did not play an important role in how the Magpies found the scarab larvae and that they most likely used the sounds produced by the burrowing scarabs to locate them within different substrates. The birds may also have the opportunity to use visual cues of the burrowing larvae when available.

The sensory perception stimuli used in the experiments in this thesis were designed to replicate the stimuli the parrots might encounter while foraging in their wild habitat. Red-crowned parakeets and Antipodes Island parakeets were given the option of four different stimuli in each of the four sensory tests. They were given four different colours of seed mixture (red, green, blue and yellow) based on different colours encountered in the birds' natural diet. In the taste experiment the birds were given the option of four different concentrations of sugar water (low, equivalent to honeydew and high) along with a control stimulus of unsweetened water. These sugar concentrations were based on the sugar levels of honeydew produced by scale insect throughout the year. In the experiments to assess smell, the birds were given the option of four different scents that make up some part of the bird's natural diet, these include scale insect, flax flowers, seed mixture and carrion of a wood pigeon. For the sound experiment the birds were given a choice between live and dead mealworms in two different substrates (bran flakes or leaf litter). The dead mealworms were offered to see if the birds were attracted by the sounds produced by the live mealworms or if they were more strongly attracted to the smell of the mealworms.

1.5 Behavioural characteristics

Choice experiments rely on the active participation of the animals in the experiment. The degree of this interaction can be influenced by several behavioural characteristics. Thus, the analysis of choice experiments that compare different species should consider the effect of temperament differences on the results. For the purposes of this thesis, I will use the term "animal temperament" to describe these behavioural characteristics.

1.5.1 Temperament

The word temperament is often used by many animal researchers to avoid using the term "personality" as this is thought to be an anthropomorphic term, as personality is seen as a human term (Gosling, 2001). An animal's temperament can be defined as "the individual character of one's physical constitution permanently affecting the manner of acting, feeling and thinking" (Sykes, 1982). Variations within an animal's temperament have been studied and multiple traits have been identified. Réale et al. (2007) suggested dividing temperament traits into five new categories based on the ecological situation in which the trait was measured in; 1) Shyness-boldness in which an individual's reaction to a dangerous or risky situation is measured but not the individual's response to a new situation. Terms such as 'tameness' and 'fearfulness' have been used in the same context but when looking at human reactions; 2) Exploration-avoidance considers the individual's response to a new environment, food source or novel objects. The new situation may be considered 'risky' to an animal if there is a chance that something bad may occur if the explored the new item (i.e. attacked by a predator).

3) General activity level of an individual can interfere with the measurements of temperament when looking at exploration and boldness. Réale et al. (2007) proposes that activity level be measured in a non-threatening and a non-novel environment as it will remove any exploration-avoidance behaviours. The last two categories are expressed in a social context rather than an individual context; 4) The level of aggressiveness is measure as an individual's reaction towards another member of the same species or conspecifics; 5) Sociability is the reaction of an individual in the presence or absence of conspecifics excluding aggressive behaviour. Unsociable individuals will avoid contact with another individual but sociable animals will seek out other members of the same species (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). These categories should only be used as a working tool as some have very limited criteria which may not be easy to abide by in some situations.

The categories, created by Réale et al. (2007), allow temperament to be measured by correlated behavioural or physiological traits. For example, the exploration rate of a laboratory rodent can be measured by the total distance covered and the amount of times it displayed exploratory behaviours including sniffing or rearing. Therefore, temperament can be readily characterised by physiological, hormonal or behavioural indices that are measurable within a specific ecological situation. These definitions and categories that Réale et al. (2007) proposed have been used by others to create their own definition of a variety of terms used to describe animal personalities and temperament (Stamps & Groothuis, 2010; Dingemanse, et al., 2007; Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Sih & Bell, 2008).

Individuals can be classified along a continuum of a certain temperament traits with an extreme trait at either end. Boldness measures the reaction of individuals to a risky or dangerous situation with the boldest animals who take the most risks being at one end of the continuum and the shyest animals who take the least amount of risks at the opposite end. Both extremes are still considered the same behaviour, i.e. two different expressions of boldness, rather than two completely different traits (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Most animals will show a variable amount of behavioural responses from shy to bold. Temperament phenotypes are affected by selection and will be either favoured or selected against depending on the ecological condition the population experiences. This selection generally leads to a variety of phenotypes being present within the same population. Temperament phenotypes should be separated from an animal's motivational sates (e.g. hunger level), and ability traits (e.g. cognitive or perception ability) although the interaction between these behaviours are involved in the expression of a certain behavioural pattern.

1.5.2 Personality

While some researchers suggest avoiding the term personality for animal studies, there is a growing body of behavioural literature which seeks to define individual personality traits in animals. Personality can be defined as "a set of individual differences that are affected by the development of an individual" (McAdams & Olson, 2010). These differences can be behavioural or physiological and the differences between members of the same species can be common in standard conditions across groups of the same age and sex (Stamps, J. A., 2007). However, these individual differences have been mostly neglected as having limited biological relevance and are usually seen as either a result of inaccurate measurements or a sign of non-adaptive variation (Groothuis & Carere, 2005). The scientific community is still debating whether a human term like "personality" can be transferred onto the behavioural observations of animals (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). This attribution of human characteristics onto something non-human is known as personification and can cause anthropomorphic biases when it comes to interpreting the behavioural analysis of animals such as fish or birds.

However, people who intensively work with or care for small groups of the same species will perceive different personalities within the group. This has been interpreted as anecdotal evidence that suggests inter-individual variation in behaviour may be present in other animals (Groothuis & Carere, 2005). Scientific research into animal personalities is still a relatively new field compared to other behavioural studies such as reproduction and effects of stress. One major problem with behavioural and physiological research is that they usually focus on the differences between populations or treatments but fail to follow the individuals for a long enough period of time in order to accurately measure any behavioural variations that could be attributed to personality (Groothuis & Carere, 2005).

Due to the intensive field work conducted by many ethologists and ecologists, there is a wide range of knowledge about the variety of behaviour that occurs under natural conditions in several bird species (Groothuis & Carere, 2005). Some personality traits have been intensively studied including neophobia and exploration in relation to other behaviours such as innovation and opportunism. Innovation is defined as “a process that results in new or modified learned behaviour and introduces novel behavioural variants into a population’s repertoire” (Ramsey, Bastian, & van Schaik, 2007). Opportunism is “the tendency to exploit an opportunity or a favourable set of circumstances that is accessible to the animal” (Mcfarland, 2006)) (Lefebvre, Whittle, Lascaris, & Finkelstein, 1997). A number of different bird species have been used in personality studies including great tits (*Parus major*) (Groothuis & Carere, 2005), ravens (*Corvus corax*) (Stöwe & Kotrschal, 2007), barnacle geese (*Branta leucopsis*) (Kurvers, et al., 2009) and many species of warblers (Mettke-Hormann, Ebert, Schmidt, Steiger, & Stieb, 2005).

Groothius & Carere (2005) found that variation in selection pressures both in time and in space might be the mechanism that maintains the different behaviour profiles found within some populations of great tits. Stöwe & Kotrschal (2007) found that individual ravens differ in their behavioural phenotypes. The effects of personality traits in barnacle geese was investigated by Kurver et al. (2009) and the results showed that the overall movement patterns of an individual bird could potentially be shaped by the personality trait of the other members of the group and the movement patterns of the whole group of barnacle geese could be shaped by the mixture of different personality traits present. Mettke-Hofmann et al. (2009) looked at the personality traits of two closely related species of warblers and found that the resident Sardinian warblers were overall less neophobic and more explorative than the garden warblers which lead Mettke-Hofmann et al. (2005) to hypothesise that there were different personality traits amongst the resident Sardinian warblers however it was not clear whether there were any differences in migratory garden warblers. Mettke-Hofmann et al. (2005) suggested that the different lifestyles of the two warbler species might require some difference in the organisation of behaviours which might account for the lack of personality traits in the garden warblers.

The presence of different personality traits in a variety of bird species shows that the environment in which individuals adapt to and live in, has an influence on their overall personality traits, whether it’s the ability to move to new environment or being able to use the different personalities in the group to benefit each other.

For my study, I want to look into the different personalities shown by both the individual birds and the differences in their behavioural responses between the two closely related species, the red-crowned parakeets and Antipodes Island parakeets. This is to see what effect differences in environment and ecology will have on the personalities shown in the experiments.

A popular way to measure personality in many species is to conduct what is known as an “open field” or “novel environment” test which examines the behavioural responses of individuals when exposed to a new environment and whether these behaviours change if the individual is exposed repeatedly to the novel environment (Jones, 1977a; Jones, 1977b; Jones, 1978). A number of different species have been studied using this method of measuring personality including day old domestic poultry chickens (*Gallus gallus)*. Open field tests have been used to measure what the effect of repeated exposure and familiar cues or items have on behavioural traits like neophobia and exploration (Jones, 1977a; Jones, 1977b; Jones, 1978).

These experiments showed that the environment in which these birds lived in had an effect on their personality whether it was a positive or negative response to the novel environment or open field test. Those with bolder, highly neophillic personalities will respond in a positive way to a new environment as they are able to take advantage of what this new environment might contain whereas the shyer, highly neophobic personalities may not be as quick to take advantage of new environments.

A novel environment test was used for the experiments conducted in this study as I was interested in the effect that repeat testing had on the personality traits of two closely related parakeet species.

1.5.3 Problems with Evaluating Animal Personality

One of the major problems when it comes to analysing animal personality or temperament is that often the same trait can be analysed by a wide variety of people from different fields of science using different a number of different methods of testing. This may lead to a number of different interpretations about the same behavioural trait (Réale, Reader, Sol, McDougall, &

Dingemanse, 2007). There is also the problem that sometimes the testing protocol has been designed in a way that makes it difficult to understand what behaviour is being measured.

The most criticised personality test is the novel environment tests as it thought to force locomotion behaviour by provoking some animals escape response, which may be a measure of an unrelated behaviour. However, the novel environment test has been used to examine the effect of repeated exposure to a novel environment and how it effects the behavioural responses of some animals including domestic chickens (Jones, 1978; Jones, 1977a; Jones, 1977b). Although it has been criticised as forcing locomotion it is still a valid way to measure the effect of novelty and how animals respond to a new environment and how different personality traits differ in their responses. However, one must first understand what the behaviours that are being shown are linked to whether it be fear or exploration. This has been done in domestic chickens and other poultry birds which have linked freezing and periods of no movement to a state of fear whereas behaviours such a walking, pecking and other vocalisation have been linked to exploration (Jones, 1978; Jones, 1977a; Jones, 1977b).

Another problem that scientists have when evaluating animal personalities is the controversy around the use of human terms including ‘anxiety’ and ‘fear’. The concern is there may be some alternative interpretation that presents with similar physiological mechanisms to fear and anxiety in humans. (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). However, there have been many studies showing that animals do show some similar characteristics of what is known as fear or anxiety in humans including blood cortisol levels and explorative or neophobic responses (Kitaysky, Wingfield, & Piatt, 1999; Barry, Malison, Held, & Parrish, 1995; Cockrem, 2007).

Difficulties with following and marking individuals for a long-term period has led to most personality studies using one measure per individual observed or an average value taken from several observations rather than looking at the overall individual differences (Díaz-Uriarte, 2002). This averaging or short term analysis may result in no significant differences between the individuals due to the short duration of testing. To gain the full picture of an animal’s personality the studies should be carried out over a longer period to be able to pick up any of the subtle differences between individuals. However, this is often not accomplished due to the lack of resources and funding most researchers face in this scientific field of study.

1.6 Dimensions of Animal Personality

1.6.1 Activity Level

The activity levels of some animals are affected by several factors including habitat that they live in and the food they eat. The type of habitat that the animal lives in will influence its overall activity levels (Mettke-Hofmann, Winkler, & Leisler, 2002; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Blondel, Chessel, & Frochot, 1988). Studies have shown that species that live in complex or constantly changing environments will have a very active lifestyle as they will be constantly adapting to changes in their environments (Mettke-Hofmann, Winkler, & Leisler, 2002). Simple habitats such as open woodland will have relatively stable environments and will not encourage the species that inhabit them to be very active as they will not need to adapt to the changes in their environment. Island species will be affected by changes to their environment as these are often unstable (e.g. food shortages, extreme weather, seasonal variation) and species may be seen as more active compared to their mainland relatives as they need to adapt quickly to the changes that are a part of island life.

Another factor that influences the activity levels of some species is the food sources that they use, how easily these can be found and how abundant the food is (Mettke-Hofmann, Winkler, & Leisler, 2002). Food sources such as pollen, nectar, buds and nuts are difficult to find in the wild so the animals who consume these foods must spend more time searching for them as compared to animal who feeds on readily available and easy to find grasses, seeds and leaves (Mettke-Hofmann, Winkler, & Leisler, 2002). Animals that feed on hard to find food items will be more active as they must search longer to find their food when compared to animals who feed on easy to find food items.

Antipodes Island parakeets feed on grass and other vegetation, and therefore I hypothesise the birds will be highly explorative and show high levels of activity. This behaviour seems likely as they would have to spend more time foraging for food as resources are variable on islands and it is hard to obtain vegetation of some plants. The red-crowned parakeets on the other hand would be expected to be less active and spend less time exploring the options as they are a forest dwelling species that have a relatively constant food resource of berries, fruits and flowers.

1.6.2 Neophobia and Exploration Behaviours

Neophobia is described as the fear of new things including objects or environments and is one way scientists have looked into the personality of many different species including birds and some species of fish (Corey, 1978; Biondi, Bo, & Vassallo, 2010; Greenberg, 1983). Animals who are neophobic will show avoidance behaviours such as retreating towards a safe environment or will not interact with the new object or environment at all. Many studies have used this behaviour to get some idea of the animal personalities in different species of birds and other animals (Biondi, Bo, & Vassallo, 2010; Mettke-Hofmann, et al. 2005; Mettke-Hofmann, Winkler, & Leisler, 2002; Stöwe & Kotrschal, 2007; Fox & Millam, 2004).

Mettke-Hofmann et al. (2002) investigated the effect of ecological factors on the exploration and neophobia in 76 different species of parrots. Each species was put through one exploration test and one neophobia test to see if differences in ecology had any effect (Mettke-Hofmann, Winkler, & Leisler, 2002). The results found that birds that inhabit a complex environment (including forest edges and islands) or feed on the buds of plants had the shortest latency to approach the novel item. The species with the longest latency to approach were those who had a diet that consisted of a larger amount of seeds or flowers (Mettke-Hofmann, Winkler, & Leisler, 2002). Birds that feed on nuts or are found on islands had the longest duration of exploration, which might be due to the difficulty when it comes to the large spatial and seasonal variation of food sources on many offshore islands (Mettke-Hofmann, Winkler, & Leisler, 2002; O'Hara, Schwing, Federspiel, Gajdon, & Huber, 2016).

The novel object test showed a high level of neophobia in birds that have a diet that consists of a high proportion of insects (Mettke-Hofmann, Winkler, & Leisler, 2002). This result was also found by Greenberg (1983) who investigated the role that neophobia had on the degree of foraging specialization of Chestnut-sided warblers (*Denodroica pensylvanica*) and Bay-brested warblers (*D. castanea*). Greenberg (1983) found that the birds were more neophobic when presented with large, clustered red leaves and opaque or long yellow spines. This might be a response to the aposematic or warning colours (Greenberg, 1983; Coppinger, 1969). The birds might know that red or yellow coloured food items (such as some species of insects) are potentially toxic or dangerous and should be avoided. This avoidance behaviour would be shown by a high level of neophobia in birds as shown by Greenberg (1983) and Mettke-Hofmann et al. (2002).

Species that live in habitats with a higher risk of predation, including forests, will show more neophobia towards new environments than species that originate on islands (Greenberg, 1983; Glickman & Sroges, 1966). The plasticity of island birds may have been a result of lower predation risk which would be shown by a low level of neophobia and high levels of exploration/long exploration durations (Greenberg, 1983; Mettke-Hofmann, Winkler, & Leisler, 2002; Terborgh & Faaborg, 1973; Yeaton & Cody, 1973).

In this study the Antipodes Island parakeets are predicted to be the more neophilic of the two species tested as they evolved on islands that lack major predators and have shown similar characteristics to that of the known neophilic Kea, however the birds used in this study have come from a captive environment which may alter their responses. Antipodes Island parakeets also feed on tussock grasses and other vegetation in a highly variable island environment which will increase their need to explore new options more readily. The red-crowned parakeets on the other hand are predicted to be more neophobic as they evolved as a forest dwelling species that has major predators including mustelids and possums present in their environment. The red-crowned parakeets also feed on fruits, berries and flowers that are relatively evenly distributed throughout most forests and are usually highly abundant so the birds would not need to explore new food options often so will be predisposed to showing some restraint or neophobia towards new objects or environments.

1.6.3 Boldness-Shyness Continuum

Most behaviour that can be measured can be categorised along an axis or continuum from one extreme to the other. This can be easily seen when measuring the level of risk that an individual will take in a certain situation. Individuals that take the most risk (neophilic) will be at the bold end of the continuum and those who take the least amount of risk (neophobic) will be at the opposite end, with all other individuals falling somewhere in between these two extremes (Wilson, Clark, Coleman, & Dearstyne, 1994; Wilson, Coleman, Clark, & Biederman, 1993). According to Wilson et al. (1994) the shy-bold continuum is a "fundamental axis of behavioural variation in humans and at least some other animals" a number of human psychologists agree with this statement when it comes to humans but not so much in terms of animals. This shy-bold continuum is very similar to how neophobia is measured in some animals with individuals having their own level of neophobia/neophilia relative to each other and will also fall into a continuum as well with the neophilic individuals at one end and the neophobic individuals at the other end.

There are three major issues to this statement that have yet to be addressed (Wilson, Coleman, Clark , & Biederman, 1993). The first is that this continuum has never been studied in the wild using the natural populations of the test species. All studies that have been conducted so far have used either wild caught individuals or laboratory bred animals (Wilson, Coleman, Clark, & Biederman, 1993; Carere & van Oers, 2004). The second problem is that there is a lack of evolutionary perspective as no studies have tried to predict and test the adaptive patterns of the shy-bold continuum that might be affected by natural selection (Wilson, Coleman, Clark , & Biederman, 1993). The final problem is that due to the fact that a large amount of research into the shy-bold continuum has been done solely on humans and only a small number of mammals, the distribution of shyness and boldness amongst other taxa if still largely unknown.

Psychologists have measured the shyness and boldness of humans using their response to a new or novel object and this has been used to measure the same thing in non-human animals including birds and some fish (Wilson, Coleman, Clark , & Biederman, 1993). Pumpkinseed sunfish (*Lepmis* gibbosus) were tested to see what effect different capturing techniques had on the boldness or shyness of individual fish (Wilson, Coleman, Clark , & Biederman, 1993). The bolder trapped sunfish fish acclimated quicker to the new environment and were more explorative than the shy seined sunfish. Individual pumpkinseed sunfish did show a bold-shy continuum with some fish being bolder or shyer that others along with different rates of acclimation and explorative behaviours (Wilson, Coleman, Clark , & Biederman, 1993).

Based on the results shown by Wilson et al. (1993) there should be some kind of shy-bold continuum shown by the birds used in this study. It is predicted that the Antipodes Island parakeets will be the bolder individuals as they are an island species that has had no major predators present and have been seen displaying similar behaviours to that of the Kea and the Red-crowned parakeets will be the shyer individuals being forest dwelling species that has had to take predators into account when decided where to forage other daily tasks. If there is a shy-bold continuum present in this study the Antipodes Island parakeets will be at bold end of the continuum and the Red-crowned parakeets will be at the shy end of the continuum.

1.6.4 Effects of Captivity on Sensory Preferences and Personality

There is limited information available of the effect of captivity on the sensory preference of animals. Experiments using wild-caught animals that are temporarily placed into a captive or laboratory settings are usually short lived and there has been little research looking at the dietary changes in animals once they are placed into captivity. It is therefore unknown how captivity has affected the sensory preferences of the birds used in this study. Theoretically, if animals are kept for generations in captivity there will be a removal of selection pressure from sensory physiology which may tend to weaken ecological correlates to sensory choices. However, evidence for this is entirely lacking.

Most of the studies looking into the personalities of different animals, including a number of different bird species, have been conducted using wild caught animals that have been placed into a captive or laboratory setting for a period of time (Butler, Whittingham, Quinn, & Cresswell, 2006; Drent, van Oers, & van Noordwjk, 2003; Herborn, Heidinger, Alexander, & Arnold, 2014; Herborn, et al., 2010; Morand-Ferron, Cole, Rawles, & Quinn, 2011; McCowan, Rollins, & Griffith, 2014). The effect of being placed into captivity for even a short period of time has been shown to have some effect on the types of personalities and behaviours shown in a number of different species (Butler, Whittingham, Quinn, & Cresswell, 2006; Drent, van Oers, & van Noordwjk, 2003;

Herborn, Heidinger, Alexander, & Arnold, 2014; Herborn, et al., 2010; Morand-Ferron, Cole, Rawles, & Quinn, 2011; McCowan, Rollins, & Griffith, 2014). It is thought that by taking an animal from a wild habitat with its inherent risks to survival and social pressures and moving it into a homogenous or constant captive environment this may prevent some animals displaying their "natural" behaviours.

Most studies using wild-caught animals allow the individuals to have some habituation or settling period before testing begins, this is thought to allow the animals to become stable within the new environment and hopefully allow them to behave similarly to their wild counter-parts. Ekman & Hake (1990) found that the greenfinch (*Carduelis chloris*) took approximately one month to stabilize their behaviours when placed into a captive environment and estimated that birds with a similar body mass would require the same amount of settling period, this has been used in similar experiments on a wide range of passerine species (Ekman & Hake, 1990; Lilliendahl, 1998; Lillendahl, 2000; van der Veen & Sivars, 2000). Butler et al. (2006) investigated the effect of different settling periods on the foraging behaviour and overall individual differences on wild-caught chaffinches to figure out if there was a minimum settling period required for a chaffinch to have before it will start behaving similarly to wild chaffinches. Butler et al. (1990) found that some individual birds were more likely to forage during the trials regardless of their time in captivity prior to the start of testing. This may be due to their different personality types as the "bolder" individuals would be more inclined to forage and adapt to the new captive environment when compared to "shy" individuals (Wilson, Coleman, Clark , & Biederman, 1993; Butler, Whittingham, Quinn, & Cresswell, 2006).

Personality in animals has been shown to have some level of heritability in a number of species including birds. A study conducted on great tits by Drent, van Oers, & van Noordwjk (2003) found that there was a strong response to selection of certain copying behaviours or personality types after the fourth generation of captive great tits and that the laboratory conditions of their experiment and many other studies may be overestimating the natural heritabilities of certain personality types. They concluded this may be due to the reduction of environmental challenges faced by individuals in captivity (Drent, van Oers, & van Noordwjk, 2003; Riska, Prout, & Turelli, 1989).

Captivity has also been shown to have an effect on the reproduction of some animal species (McCowan, Rollins, & Griffith, 2014). Animals in captivity are not usually subjected to predation and will often have constant access resources such as food and mates. This constant environment may allow the bolder individuals to mate more successfully and produce a higher number of offspring compared to shy individuals (Roberts, Taylor, & Garcia de Leaniz, 2011;

McPhee, 2003; McCowan, Rollins, & Griffith, 2014). In a study conducted by McCowan, Rollins and Griffith (2014) showed that more explorative or bolder male great tits had more nestlings and a greater number of breeding attempts than less explorative or shy males. Bolder and more explorative males are seen to be better providers for their offspring and will therefore increase the likelihood of their offspring and genes making it to the next generation.

Captivity may allow those animals with personality attributes that maximise their reproductive success under captive conditions (e.g. more explorative/bolder males) to produce more offspring carrying those same traits and can therefore limit the amount of variation in terms of personality types seen in many captive animals (van Oers, de Jong, van Noordwjk, Kempenciers, & Drent, 2005; Price, 1970; McCowan, Rollins, & Griffith, 2014).

By using captive birds in this study we may have reduced the amount of personality differences seen between individual birds of both species as the original breeding populations may have been dominated by the bolder individuals being more reproductively successful and therefore perpetuating those characteristics.

1.7 Aims

The aim of this study was to investigate and describe the sensory preferences of Red-crowned parakeets and Antipodes Island parakeets within four different sensory options. I hypothesised that the ecological differences in habitat and diet of each species would have an effect on the overall behaviour or preferences shown, but that individual personality and the captive origin of the birds may also play a role.

Bibliography

Ackerman, J. S. (1978). Leonardo's Eye. *Journal of the Warbug and Courtauld Institues, 41*, 108-146.

Altmann, J. (1974). Observational study of behavior. *Behaviour, 49*(3), 227-266.

Bang, B. G., & Cobb, S. (1968). The Size of the Olfactory Bulb in 108 Species of Birds. *The Auk, 85*, 55-61.

Barry, T. P., Malison, J. A., Held, J. A., & Parrish, J. J. (1995). Ontogeny of the cortisol stress response in larval rainbow trout. *General comparative endocrinology, 97*(1), 57-65.

Beason, R. C. (2001). What Can Birds Hear? *21st Vertebrate Pest Conference* (pp. 92-96). California: USDA National Wildlife Research Centre- Staff Publications.

Bennett, A. T., & Cuthill, I. C. (1994). Ultraviolet vision in birds: what is its function? *Vision research, 34*(11), 1471-1478.

Benus, R. F., Bohus, B., Koolhaas, J. M., & van Oortmerssen, G. A. (1991). Heritable variation for agression as a reflection of individual coping strategies. *Experientia, 47*, 1008-1019.

Biondi, L. M., Bo, M. S., & Vassallo, A. I. (2010). Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (Milvago chimango). *Animal Cognition, 13*(5), 701-710.

Blondel, J., Chessel, D., & Frochot, B. (1988). Bird Species Impoverishment, Niche Expansion and Density Inflation in Mediterranean Islands Habitats. *Ecology, 69*(6), 1899-1917.

Boon, W. M., Kearvell, J. C., Daugherty, C. H., & Chambers, G. K. (2001). Molecular systematics and conservation of kakariki (Cyanoramphus spp.). *Science for Conservation, 176*, 1-46.

Bowmaker, J. K., & Martin, G. R. (1985). Visula pigments and oil droplets in the penguin, Spheniscus humboldti. *Journal of Comparative Physiology A, 156*(1), 71-77.

Breedlove, S. M., Watson, N. V., & Rosenzweig, M. R. (2010). General Principles of Sensory Processing, Touch and Pain. In S. M. Breedlove, N. V. Watson, & M. R. Rosenzweig, *Biological Psychology* (6th ed., pp. 216-217). Sunderland, Massachusetts: Sinauer Associates, Inc.

Butler, S. J., Whittingham, M. J., Quinn, J. L., & Cresswell, W. (2006). Time in captivity, idividual differences and foraging behaviour in wild-caught chaffinches. *Behaviour, 143*, 535-548.

Cannon, W. B. (1929). *Bodily changes is pain, fear, hunger and rage.* New York, New York, USA: Appleton.

Carere, C., & van Oers, K. (2004). Shy and bold great tits (Parus major): body temperature and breath rate in response to handling stress. *Physiology & Behavior, 82*, 905-912.

Cockrem, J. F. (2007). Stress, corticosterone response and avian personalities. *Journal of Ornithology, 148*(2), 169-178.

Colville, T. P., & Basseri, J. M. (2001). Avian Anatomy and Physiology. In T. P. Colville, & J. M. Basseri, *Clinical Anatamony and Physiology for Veterinary Technicians* (Third ed., pp. 357-360). St. Louis, Missouri: Mosby.

Cooney, C. R., Bright, J. A., Capp, E. J., Chira, A. M., Hughes, E. C., Moody, C. J., . . . Thomas, G. H. (2017). Mega-evolutionary dynamics of the adaptive radiation of birds. *Nature, 542*(7641), 344-347.

Coppinger , R. P. (1969). The effect of experience and novelty on avian feeding with reference to the warning coloration of butterflies, i. Reactions of wild-caught Blue Jays to novel insects. *Behaviour, 35*, 45-60.

Corey, D. T. (1978). The Determinants of Exploration and Neophobia. *Neuroscience & Biobehavioural Reviews, 2*, 235-253.

Corfield, J. R., Kolominsky, J., Craciun, I., Mulvany-Robbins, B. E., & Wylie, D. R. (2016). Is Cerebellar Architecture Shaped by Sensory Ecology in New Zealand Kiwi (Aptyerx mantelli). *Brain, behaviour and evolution, 87*(2), 88-104.

Corfield, J. R., Wild, J. M., Hauber, M. E., Parsons, S., & Kubke, M. F. (2007). Evolution of brain size in the Palaeognath lineage, with an emphasis on New Zealand ratites. *Brain, Behavior and Evolution, 71*(2), 87-99.

Cunningham, S. J., Corfield, J. R., Iwaniuk, A. N., Castro, I., Alley, M. R., Birkhead, T. R., & Parsons, S. (2013). The anatomy of the bill tip of kiwi and associated somatosensory regions of the brain: comparisons with seabirds. *PloS one, 8*(11), e80036.

Deeb, S. S. (2004). Molecular genetics of colour-vision deficiencies. *Visual Neuroscience, 21*, 191-196.

Deschner, T., Kratzsch, J., & Hohmann, G. (2008). Urinary C-peptide as a method for monitoring body mass changes in captive bonobos (Pan paniscus). *Hormones and Behaviour, 54*, 620-626.

Diamond, J., & Bond, A. B. (1991). Social Behaviour and Ontogeny of Foraging in the Kea (Nestor notabilis). *Ethology, 88*, 128-144.

Díaz-Uriarte, R. (2002). Incorrect analysis of crossover trials in animal behaviour research. *Animal Behaviour, 63*(4), 815-822.

Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personailities in a fluctuating environment. *Proceedings of the Royal Society of London, Series B: Biological Sciences, 271*(1541), 847-852.

Dingemanse, N. J., Wrighr, K., Kazem, A. J., Thomas, D. K., Hickling, R., & Dawney, N. (2007). Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology, 76*(6), 1128-1138.

Domann, N., Voets, T., & Nilius, B. (2008). TRPs in Our Senses. *Current Biology, 18*(18), R880-R889.

Dooling, R. J. (1980). Behvaiour and psychophysics of hearing in birds. In A. N. Popper, R. R. Fay, A. N. Popper, & R. R. Fay (Eds.), *Comparative studies of hearing in vertebrates* (pp. 261-288). New York: Springer-Verlag.

Dooling, R. J. (1982). Auditory perception in birds. In D. E. Kroodsma, E. H. Miller, D. E. Kroodsma, & E. H. Miller (Eds.), *Acoustic communication in birds* (pp. 95-130). New York: Academic Press.

Dooling, R. J. (1986). Perception of vocal signals by the budgerigar (Melopsittacus undulatus). *Experimental Biology, 45*, 195-218.

Drent, P. J., van Oers, K., & van Noordwjk, A. J. (2003). Realized heritability of personalities in the great tit (Parus major). *Proceedings of the Royal Society of London B: Biological Sciences, 270*(1510), 45-51.

Ebenhard, T. (1995). Conservation breeding as a tool for saving animal species from extinction. *Trends in Ecology & Evolution, 10*(11), 438-443.

Ekman, J. B., & Hake, M. K. (1990). Monitoring starvation risk: adjustments of body reserves in greenfinches (Carduelis chloris L) during periods of unpredictable foraging success. *Behavioural Ecology, 1*, 62-67.

Elliott, G., Dilks, P., & O'Donnell, C. (1996). The ecology of yellow-crowned parakeets (Cyanoramphus auriceps) in Nothofagus forest in Fiordland, New Zealand. *New Zealad Journal of Zoology, 23*, 249-265.

Engel, G., & Schmale, A. H. (1972). Conservation-withdrawal: A primary regulatory process for organic homeostasis. *Physiology, Emotion, and Psyuchosomatic Illness Ciba Foundation Symposium VIII* (pp. 57-95). Amsterdam: Elsevier.

Fay, R. R., & Popper, A. N. (2000). Evolution of hearing in vertebrates: the inner ears and processing. *Hearing research, 149*(1), 1-10.

Feenders, G., Klaus, K., & Bateson, M. (2011). Fear and exploration in european starlings (Sturnus vulgaris): A comparison of hand-raised and wild-caught birds. *PLoS One, 6*(4), e19074.

Floyd, R. B., & Woodland, D. J. (1981). Localization of soil dwelling Scarab larvae by the Black-backed Magpie, Gymnorhina tibicen (Lantham). *Animal Behaviour, 29*, 510-517.

Forshaw, J. M. (1978). *Parrots of the World* (third ed.). New Jersey, Unites States of America: Princeton University Press.

Fox , R. A., & Millam, J. R. (2007). Novelty and individual differences influence neophobia in orange-winged Amazon parrots (Amazona amazonica). *Applies Animal Behaviour Science, 104*, 107-115.

Fox, R. A., & Millam, J. R. (2004). The effect of early environment on neophobia in orange-winged Amazon parrots (Amazona amazonica). *Applied Animal Behaviour Science, 89*, 117-129.

Gajdon, G. K., Fijin, N., & Huber, L. (2004). Testing social learning in a wild mountain parrot, the kead (Nestor notabilis). *Learning & Behaviour, 32*(1), 62-71.

Gaze , P. D., & Cloud, M. N. (1983). Honeydew and its importance to birds in Beech Forests of South Island, New Zealand. *New Zealand Journal of Ecology, 6*, 33-37.

Giurfa , M., Nunez, J., Chittka, L., & Menzel, R. (1995). Colour preferences of flower-naive honeybees. *Journal of Comparative Physiology A, 177*(3), 247-259.

Gleich, O., & Manley, G. A. (1988). Quantitative morphological analysis of the sensory epithelium of the starling and pigeon basilar papilla. *Hearing research, 34*(1), 69-85.

Gleich, O., Dooling, R. J., & Manley, G. A. (2005). Audiogram, body mass, and basilar papilla length: correlations in birds and predicions for extinct archosaurs. *Naturwissenschaften, 92*(12), 595-598.

Glickman, S. E., & Sroges, R. W. (1966). Curiosity in zoo animals. *Behaviour, 22*, 151-188.

Goldsmith, T. H. (1980). Hummingbirds see near ultraviolet light. *Science , 207*(4432), 786-788.

Goldsmith, T. H., & Butler, B. K. (2005). Color vision of the budgerigar (Melopsittacus undulatus): hue matches, tetrachromay, and intensity discrimination. *Journal of Comparative Pysiology A, 191*(10), 933-951.

Goldstein, E. (2009). *Senstation and Perception.* Cengage Learning .

Gosling, S. D. (2001). From Mice to Men: What Can We Learn About Personality From Animal Research? *Psychological Bulletin, 127*(1), 45-86.

Greenberg, R. (1983). The role of neophobia in determining the degree of foraging specialisation in some migrant warblers. *The American Naturalist, 122*(4), 444-453.

Greene, T. (1998). Foraging Ecology of the red-crowned parakeet (Cyanoramphus novaezelandiae novaezelandiae) and yellow-crowned parakeet (C. auriceps auriceps) on Little Barrier Island, Hauraki Gulf, New Zealand. *New Zealad Journal of Ecology , 22*(2), 161-171.

Greene, T. (1999). Aspects of the ecology of Antipodes Island Parakeet (Cyanoramphus unicolor) and Reischek's Parakeet (C. novaezelandiae hochstetteri) on Antipodes Islands, October-November 1995. *Notornis, 46*, 301-310.

Greene, T. C. (2003). Breeding biology of red-crowned parakeets (Cyanoramphus novaezelandiae novaezelandiae) on Little Barrier Island, Hauraki Gulf, New Zealand. *Notornis, 50*, 83-99.

Gregory, R. L. (1997). Knowledge in Perception and Illusion. *Philosophical Transactions: Biological Science, 352*(1358), 1121-1127.

Groothuis, T. G., & Carere, C. (2005). Avian Personalities: characterization and epigenesis. *Neuroscience and Biobehavioural Reviews, 29*, 137-150.

Gsell, A. C., Hagelin, J. C., & Brunton, D. H. (2012). Olfaction Sensitivity in Kea and Kaka. *Emu, 112*, 60-66.

Gumbert, A. (2000). Colour choices by bumble bees (Bombus terrestris): innate preferences and generalization after learning. *Behavioural Ecology, 48*(1), 36-43.

Hagelin, J. C. (2004). Observations on the Olfactory ability of the Kakapo Strigpos habroptilus, the critically endangered parrot of New Zealand. *Ibis, 146*, 161-164.

Hart, N. S. (2001). The visual ecology of avian photoreceptors. *Progress in retinal and eye research, 20*(5), 675-703.

Healy, S., & Guilford, T. (1990). Olfactory-bulb size and nocturnality in birds. *Evolution*, 339-346.

Heather, B. D., & Robertson, H. A. (2005). Antipodes Island Parakeet Cyanromphus unicolor. In B. D. Heather, & H. A. Robertson, *The Field Guide to the Birds of New Zealand* (pp. 136 - 139). Auckland: Penguin Books .

Heffner, H. E., & Heffner, R. S. (2007). Hearing Ranges of Laboratory Animals. *Journal of the American Association for Laboratory Animal Science, 46*(1), 20-22.

Heffner, R. S., & Heffner, H. E. (1993). Degenerate hearing and sound localistion in naked mole rats (Heterocephalus glaber), with an overview of the central auditory structures. *Journal of Comparative Neurology, 331*(3), 418-433.

Henry, J. P., & Stephens, P. M. (1977). *Stress, health and the social environment: A sociobiologic approach to medicine.* Berlin, Germany: Springer Science & Business Media.

Heppner, F. (1965). Sensory Mechanisms and Envrionmental Clues Used by American Robins in Locating Earthworms. *The Condor, 67*(3), 247-256.

Herborn, K. A., Heidinger, B. J., Alexander, L., & Arnold, K. E. (2014). Personality predicts behavioural flexibility in a fluctuating, natural environment. *Behavioural Ecology, 25*(6), 1374-1379.

Herborn, K. A., Macleod, R., Miles, W. T., Schofield, A. N., Alexander, L., & Arnold, K. E. (2010). Personality in captivity reflects personality in the wild. *Animal Behaviour, 79*, 835-843.

Higgins, P. (1999). Order Psittaciformes. In P. Higgins, & P. Higgins (Ed.), *Handbook of Australian, New Zealand and Antartic Birds; Vol. 4 Parrots to Dollarbirds* (Vol. 4, pp. 25-504). Melbourne, Australia: Oxford University Press.

Higgins, P. (1999a). Order Psittaciformes. In P. Higgins, & P. Higgins (Ed.), *Handbook of Australian, New Zealand and Antarctic Birds; Vol. 4 Parrots to Dollarbirds* (Vol. 4, pp. 25-504). Melbourne, Australia: Oxford University Press.

Holyoak, D. T. (1973). Comments on Taxaonomy and Relationships in the Parrot subfamilies Nestorinae, Loriinae and Platycercinae. *Emu, 73*, 157-176.

Ings, T. C., Raine, N. E., & Chittka, L. (2009). A population comparison of the strength and persistence of innate colour preference and learning speed in the bumble bee Bombus terrestris. *Behavioural Ecology and Sociobiology, 63*(8), 1207-1218.

Jones, R. B. (1977a). Open-field responses of domestic chickens in the presence or absence of familiar cues. *Behavioural Processes, 2*, 315-323.

Jones, R. B. (1977b). Repeated exposure of the domestic chick to a novel environment: Effects on behavioural responses. *Behavioural Processes, 2*, 163-173.

Jones, R. B. (1978). Activities of chicks in their home cages and in an open field. *British Poultry Science, 19*, 725-730.

Jordan, L. A., & Ryan, M. J. (2015). The sensory ecology of adaptive landscapes. *Biology Letters, 11*(5), 20141054.

Kasumyan, A. O., & DÖving, K. B. (2003). Taste preferences in fishes. *Fish and fisheries, 4*(4), 289-347.

Kearvell, J. C., & Briskie, J. V. (2003). Similarity of chatter calls between Orange-fronted Parakeet Cyanoramphus malherbi and Yellow-crowned Parakeet C. auriceps. *Ibis, 145*, 333-336.

Kelber, A., Vorobyev, M., & Osorio, D. (2003). Animal Colour Vision - Behavioural tests and Physiological concepts. *Biological Reviews, 78*(1), 21-118.

Kemp, M. (1977). Leonardo and the Visual Pigment. *Journal of the Warbug and Courtauld Institutes, 40*, 128-149.

Kim, L. C., Garner, J. P., & Millam, J. R. (2009). Preferences of Orange-winged Amazon parrots (Amazona amazonica) for cage enrichment devices. *Applied Animal Behaviour Science, 120*(3), 216-233.

Kitaysky, A. S., Wingfield, J. C., & Piatt, J. F. (1999). Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. *Functional Ecology, 13*(5), 577-584.

Koolhaas, J. M., Korte, S. m., de Boer , S. F., van der Vegt, B. J., Van Reenen , H., Hopster, H., . . . Blokhuis, H. J. (1999). Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews, 23*, 925-935.

Korte, S. M., Ruesink, W., & Blokhuis, H. J. (1999). Heart rate variability during manual restraint in chicks from high- and low-feather pecking lines of laying hens. *Phsyiology & Behavior, 65*, 649-652.

Kurvers, R. H., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S. E., Ydenberg, R. C., & Prins, H. H. (2009). Personality differences explain leadership in barnacle geese. *Animal Behaviour, 78*(2), 447-453.

Laule, G. E. (2003). Positive reinforcement training and environmental enrichment: enhancing animal wellbeing. *Journal of American Veterinary Medical Association, 223*(7), 969-973.

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

Lillendahl, K. (2000). Daily accumulation of body reserves under increased predation risk in captive greenfinches Carduelis chloris. *Ibis, 142*, 587-595.

Lilliendahl, K. (1998). Yellowhammers get fatter in the presence of predotors. *Animal Behaviour, 55*, 1335-1340.

Lunau, K. (1990). Colour saturation triggers innate reactions to flower signals: flower dummy experiments with bumblebees. *Journal of Comparative Physiology A, 166*(6), 827-834.

Lunau, K., Wacht, S., & Chittka, L. (1996). Colour choices of naive bumble bees and their implications for colour preception. *Journal of Comparative Physiology A, 178*(4), 477-489.

Maloney, R. F., & McLean, I. G. (1995). Historical and experimental learned predator recognition in free-living New-Zealand robins. *Animal Behaviour, 50*(5), 1193-1201.

Martin, G. R., Wilson, K. J., Wild, J. M., Parsons, J. M., Kubke, M. F., & Corfield, J. (2007). Kiwi forego vision in the guidance of their nocturnal activities. *Plos one, 2*(2), e198.

Mather , J. A., & Anderson, R. C. (1993). Personalities of octopuses (Octopus rubescens). *Journal of Comparative Psychology, 107*, 336-340.

McAdams, D. P., & Olson, B. D. (2010). Personality Development: Continuity and Change Over the Life Course. *Annual Review of Psychology, 61*, 517-542.

McCann, C. (1963). External features of the tongues of New Zealand Psittaciformes. *Notornis, 10*(7), 326-345.

McCann, C. (1964). Observations on the tongues of some New Zealand Birds. *Notornis, 11*(1), 36-45.

McCowan, L. S., Rollins, L. A., & Griffith, S. C. (2014). Personality in captivity: More exploratory males reproduce better in aviary conditions. *Behavioural Processes, 107*, 150-157.

Mcfarland, D. (2006). *A Dictionary of Animal Behaviour.* Oxford: OUP Oxford.

McLean, J. (1911). Bush Birds of New Zealamd Part 1. *Emu, 11*(1), 1-17.

McPhee, M. E. (2003). Effects of captivity on repsonse to a novel envrionment in oldfield mouse (Peromyscus poltonotus subgriseus). *International Journal of Comparative Psychology, 16*(2).

Medler, K., & Kinnamon, S. C. (2004). Transduction Mechanisms in Taste Cells. In S. Fringe, & J. Bradley, *Transduction Channels in Sensory Cells* (pp. 153-155). Germany: Wiley-VCH.

Mettke-Hofmann, C., Winkler, H., & Leisler, B. (2002). The significance of ecological factors for exploration and neophobia in parrots. *Ethology, 108*(3), 249-272.

Mettke-Hormann, C., Ebert, C., Schmidt, T., Steiger, S., & Stieb, S. (2005). Personality traits in resident and migratory warbler species. *Behaviour, 142*(9-10), 1357-1375.

Montgomerie, R., & Weatherhead, P. J. (1997). How robins find worms. *Animal Behaviour, 54*, 143-151.

Morand-Ferron, J., Cole, E. F., Rawles, J. E., & Quinn, J. L. (2011). Who are the innovators? A field experiment with 2 passerine species. *Behavioural Ecology, 114*, 405-412.

Newberry, R. C. (1995). Environmental enrichment, increasing the biologial relevance of captive environments. *Applied Animal Behaviour Science, 44*, 229-243.

O'Hara, M., Huber, L., & Gajdon, G. K. (2015). The advantage of objects over images in discrimination and reversal learning by kea, Nestor notabilis. *Animal Behaviour, 101*, 51-60.

O'Hara, M., Schwing, R., Federspiel, I., Gajdon, G. K., & Huber, L. (2016). Reasoning by exclusion in the kea (Nestor notabilis). *Animal cognition, 19*(5), 965-975.

Okanoya, K., & Dooling, R. J. (1987). Hearing in passerine and psittacine birds: a comparative study of absolute and masked auditory thresholds. *Journal of Comparative Physiology, 101*(1), 7-15.

Olsson, P., Lind, O., & Kelber, A. (2015). Bird colour vision: behavioural thresholds reveal receptor noise. *The Journal of Experimental Biology, 218*, 184-193.

Parrish, J. W., Ptacek, J. A., & Will, K. L. (1984). The detection of near-ultraviolet light by nonmigratory and migratory birds. *The Auk*, 53-58.

Pevsner, J. (2002). Leonardo da Vinci's contributions to neuroscience. *TRENDS in neuroscience, 25*(4), 217-220.

Price, E. (1970). Different reactivity of wild and semi-domestic deermice (Peromyscus maniculatus). *Animal Behaviour, 18*, 747-752.

Pumphrey, R. J. (1948). The sense organs of birds. *Ibis, 90*(2), 171-199.

Pumphrey, R. J. (1961). Part II. Sensory Organs: Hearing. In A. J. Marshall, *Biology and Comparative Physiology of Birds* (Vol. 2, pp. 69-86). New York & London: Academic Press.

Rahbek, C. (1993). Captive Breeding - a useful tool in the preservation of biodiversity? *Biodiversity and Conservation, 2*, 426-437.

Ramsey, G., Bastian, M. L., & van Schaik, C. (2007). Animal innovation defined and operationalized. *Bheavioral and Brain Sciences, 30*(4), 393-407.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews, 82*(2), 291-318.

Riska, B., Prout, T., & Turelli, M. (1989). Laboratory estimates of heritability and genetic correlations in nature. *Genetics, 4*(5), 865-871.

Roberts, L. J., Taylor, J., & Garcia de Leaniz, C. (2011). Environmental envrichment reduces maladaptive risk-taking in slamon reared for conservation. *Biological Conservation, 144*(7), 1972-1979.

Robertson, H. A., Dowding, J. E., Elliott, G. P., Hitchmough, R. A., Miskelly, C. M., O'Donnell, C. F., . . . Taylor, G. A. (2013). Consevation Status of New Zealand Birds, 2012. Wellington, New Zealand . Retrieved 02 12, 2017, from http://www.doc.govt.nz/Documents/science-and-technical/nztcs4entire.pdf

Roper, T. J. (2003). Olfactory discrimination in Yellow-backed Chattering Lories Lorius garrulus flavopalliatus: first demonstration of oflaction in Psittaciformes. *Ibis, 145*(4), 689-691.

Saito, N. (1980). Structure and Function of the Avian Ear. In A. N. Popper, & R. R. Fray, *Comparative Studies of Hearing in Vertebrates* (pp. 241-260). New York, USA: Springer.

Schacter, D., Gilbert, D., Wegner, D., & Hood, B. (2011). *Psycology.* Worth Publishing .

Schwartzkopff, J. (1955). On the hearing of birds. *The Auk*, 340-347.

Sih, A., & Bell, A. M. (2008). Insights for behavioural ecology from behavioural syndromes. *Advances in the Study of Behaviour, 38*, 227-281.

Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters, 15*(3), 278-289.

Stamps, J. A. (2007). Growth-mortality tradeoffs and 'personality traits' in animals. *Ecology Letters, 10*, 355-363.

Stamps, J., & Groothuis, T. G. (2010). The development of animal personality: relevance, concepts and perspectives. *Biological Reviews, 85*(2), 301-325.

Stiles, F. G. (1976). Taste Preferences, Colour Preferences and Flower Choice in Hummingbirds. *The Condor, 78*(1), 10-26.

Stöwe, M., & Kotrschal, K. (2007). Behavioural phenotypes may determine whether social context facilitates or delays novel object exploration in ravens (Corvus corax). *Journal of Ornithology, 148*(2), 179-184.

Suzuki, T. K. (2017). On the origin of Complex Adaptive Traits: Progress Since the Darwin Versus Mivart Debate. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*.

Sykes, J. B. (1982). The Concise Oxford Dictionary of Current English. Oxford: Oxford University press.

Terborgh, J., & Faaborg, J. (1973). Turnover and ecological release of the avifauna of Mona Island, Puerto Rico. *Auk, 90*, 190-197.

Triggs, S., & Daugherty, C. (1996). Conservation and genetics of New Zealand parakeets. *Bird Conservation International, 6*, 89-101.

van der Veen, I. T., & Sivars, L. E. (2000). Causes and consequences of mass loss upon predator encounter: fedding interruption, stress or fit-or-flight? *Functional Ecology, 14*, 638-644.

van Oers, K., de Jong, G., van Noordwjk, A. J., Kempenciers, B., & Drent, P. J. (2005). Contribution of genetics to the study of animal personalities: a review of case studies. *Behaviour, 142*, 9-10.

Vaquero-Alba, I., McGowan, A., Pincheira-Donoso, D., Evans, M. R., & Dall, S. R. (2016). A quantitative analysis of objective feather color assessment: Measurements in the Laboratory do not reflect true plumage color. *The Auk, 133*(3), 325-337.

Verbeek, M. E., Drent, P. J., & Wiepkema, P. R. (1994). Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour, 48*, 1113-1121.

Vorobyev, M., Osorio, D., Bennett, A. T., Marshal, N. J., & Cuthill, I. C. (1998). Tetrachromacy, oil droplets and bird plumage colour. *Journal of Comparative Physiology - A Sensory, Neural, and Behavioral Physiology, 183*, 621-633.

Warham, J., & Bell, B. (1979). The birds of Antipodes Island, New Zealand. *Notornis, 26*(2), 121-169.

Weathers, W. W., Buttemer, W. A., Hayworth, A. M., & Nagy, K. A. (1984). An Evaluation of Time-Budget Estimates of Daily Energy Expenditure in Birds. *The Auk, 101*(3), 459-472.

Webb, N. V., Famula, T. R., & Millam, J. R. (2010). The effect of rope colour, size and fray on environmental enrichment device interaction in male and female Orange-winged Amazon parrots (Amazona amazonica). *Applied Animal Behaviour Science, 124*(3), 149-156.

Wein, A., Gajdon, G. K., & Schwing, R. (2015). Picture-Object Recognition in Kea (Nestor notabilis). *Ethology, 121*(11), 1059-1070.

Wells, D. L. (2009). Sensory stimulation as environmental enrichment for captive animals: a review. *Applied Animal Behaviour, 118*, 1-11.

Wenzel, B. M., & Sieck, M. H. (1972). Olfactory Perception and Bulbar Electrical Activity in Several Avian Species. *Physiology and Behavior*, 287-293.

West, R., Tisdall, C., & Aviss, M. (1995, March). *Captive management plan antipodes island parakeet (Cyanoramphus unicolor).* Retrieved from Department of Conservation: http://www.doc.govt.nz/Documents/science-and-technical/TSOP07.pdf

Wilkie, E. S., Vissers, P. M., Debipriya, D. A., DeGrip, J. W., Bowmaker, K. J., & Hunt, M. D. (1998). The molecular basis for UV vision in birds: spectral characteristics, cDNA sequences and retianl localistion of the IV-sensitive visual pigment of the biderigar (Melopsittacus undulatus). *Biochemical Journal, 330*(1), 541-547.

Wilson, D. S., Clark, A. B., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution, 9*(11), 442-446.

Wilson, D. S., Coleman, K., Clark , A. B., & Biederman, L. (1993). Shy bold continuum in pumpkinseed sunfish (Lepomis gibbosus) - an ecological study of psychological trait. *Journal of Comparative Psycology, 107*, 250-260.

Wolf, L. L., Hainsworth, F. R., & Gill, F. B. (1975). Foraging Efficiencies and Time Budget in Nectar-Feeding Birds. *Ecology, 56*(1), 117-128.

Yeaton, R., & Cody, M. (1973). Competitive release in island song sparrow populations. *Theoretical Population Biology, 5*, 42-58.

Zhao, G. Q., Zhang, Y., Hoon, M. A., Chandrashekar, J., Erlenbach, I., Pyba, N. J., & Zuker, C. S. (2003). The Receptors for Mammalian Sweet and Umami Taste. *Cell, 115*, 255-266.

Chapter Two: Methods

"Where we're going, we don't need roads."- Back to the Future (1985).

2.1 Approvals

The birds used in these experiments were from captive facilities and were all captive bred. The local Iwi (Rangitāne o Manawatū) along with the Department of Conservation (Authorisation Number: 43198-RES) and Massey University Animal Ethics committee (MUAEC Protocol 15/22) have approved this study.

2.2 Animals

2.2.1 Species

Two closely related species were used in this study; Red-crowned parakeets (*Cyanoramphus novaezelandiae*) and Antipodes Island parakeets (*Cyanoramphus unicolor*). Five individuals from each species (10 birds in total) were used in these experiments. The small sample size was due to availability from the captive facility.

Table 2.1 Background information about the birds used in the experiments. Shows the species, age, gender, captive time and origin of the birds for all 10 birds.

Bird ID	**Species**	**Age**	**Gender**	**Captive time**	**Origin**
A	Antipodes Island	1 year	Unknown	1 year	Victoria Esplanade
B	Antipodes Island	1 year	Unknown	1 year	Victoria Esplanade
C	Antipodes Island	1 year	Unknown	1 year	Victoria Esplanade
D	Antipodes Island	1 year	Unknown	1 year	Victoria Esplanade
E	Antipodes Island	2 years	Unknown	2 years	Victoria Esplanade
F	Red-crown	2 years	Unknown	2 years	Kowhai Park Gardens
G	Red-crown	2 years	Unknown	2 years	Kowhai Park Gardens
H	Red-crown	2 years	Unknown	2 years	Kowhai Park Gardens
I	Red-crown	2 years	Unknown	2 years	Kowhai Park Gardens
J	Red-crown	2 years	Unknown	2 years	Kowhai Park Gardens

2.2.2 Source Aviary

All birds were sourced from the Victoria Esplanade gardens in Palmerston North, New Zealand. The Red-crowned parakeets were moved from the Kowhai Park Gardens in Fielding, New Zealand to the Victoria Esplanade prior to when testing occurred.

2.3 Housing Management and Transport

Experiments were conducted at the Ecology Department at Massey University's Turitea campus in Palmerston North, New Zealand. The birds were transported in well ventilated transport boxes and keep in these boxes between tests in accordance to Massey University Ethics Committee guidelines. Diets of the birds used in this study were not changed for this study.

2.4 Equipment

2.4.1 Testing Box

The testing box (Figure 2.1), was a custom built clear perspex box (1x1x1m) with three hinged sections on the lid to allow for removal of the birds using a hand net after testing. The outside of the perspex was covered with a layer of black plastic to ensure that the birds were not distracted in the testing room. This also allowed for real time observations to be made while the researcher was in the room, avoiding the confounding effect of the observer on the birds. The box had a line of air holes for ventilation; these were covered with a thin black mesh to remove the bird’s ability to see through the perspex.

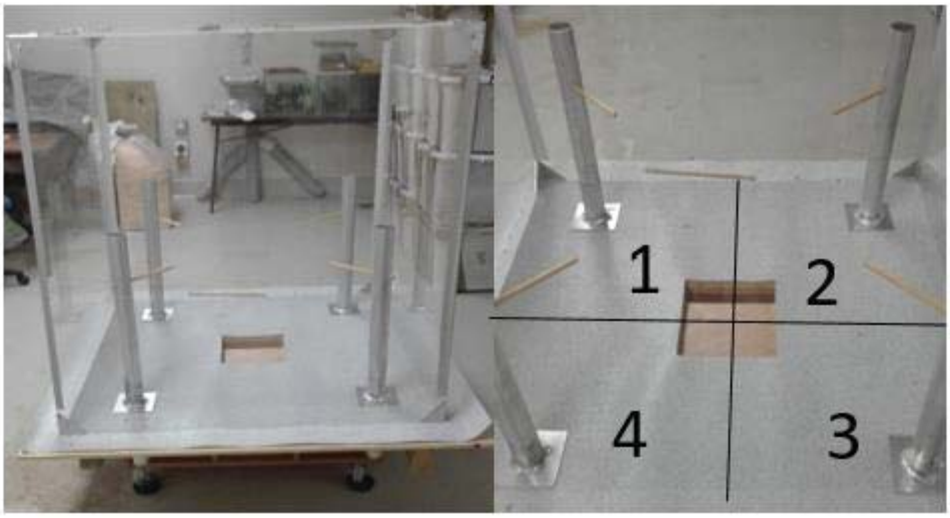


Figure 2.1 Testing box with testing apparatus based on Gsell, Hagelin & Brunton (2012). Quadrats were numbered one to four starting from the top left and moving clockwise around the box.

The base of the box was made from plain plywood and had four stainless steel poles (0.5m tall and 0.045m in diameter) in each corner situated 0.2m away from both walls. Each pole had a wooden perch (0.15m long) positioned 0.13m from the top of the pole to give the birds a place to perch and to allow access to the top of the poles which held the different stimuli during testing. A piece of rope was wrapped around all the poles making a connection between then enabling the birds to easily move from one pole to another without flying or returning to the ground. In the centre of the wooden base was an entry hole (0.2m x 0.2m) where a small wooden box (0.23m x 0.23m x 0.2m) was slid underneath. This box was where the birds were placed and then released into the large perspex box.

2.4.2 Cameras

Behaviours in the testing box were recorded with a GoPro camera (Hero 3+ Silver, Model number CHDHN-302, Resolution 960p at 60fps) suspended above the testing box. Footage was also watched in real time via a Logitech HD webcam (C615, Part number PN960-000738, Resolution 1080pHD) attached to the side of the testing box.

2.5 Experimental Design

Each bird was given a choice between four different sensory options, these were placed in the top of each of the four metal poles using small plastic cups that fit flush with the top of the metal pole.

Some of the options were able to be accessed directly by the birds (colour and taste experiments) but others were obscured with a black mesh to block any visual signals (sound and smell experiments) and to stop the birds from removing the objects. Each experiment was run four times with each individual bird and the position of the sensory options was randomised to prevent the birds from learning any placement patterns. This was also designed to show any orientation preferences of the individual birds. Each bird was put through all experiments 16 times with one repeat per day. Each bird had food withheld for one hour before testing to encourage the birds to participate in the testing. After testing was completed the bird's food was returned.

Each bird was tested four times per sensory modifier to give a total of 20 trials for Antipodes Island parakeets (five individuals) and 16 trials for the Red-crowned parakeet (four individuals).

2.5.1 Taste

For the taste experiment three different concentrations of nectar or sugar water were offered along with plain water for the control. The Antipodes Island Parakeets trials were prepared using Topflite Wild Bird Nectar Powder (raw sugar, dextrose, honey powder, pollen, ornithon/multi-vitamins) (Topflite, Oamaru, New Zealand). The Red Crowned Parakeets trials were prepared using Best Birds Lorikeet wet mix (wheat, rice, glucose, corn, fruit maize, soya protein isolate, non-fat dairy solids, honey, calcium and magnesium carbonates, vitamins and minerals) (Best Bird, Brooklands Pet Products, New Plymouth, New Zealand). Two different types of nectar powder were used as the Topflite nectar powder became unavailable at local supermarkets and pet shops.

These different concentrations were selected based on three different concentrations of sap from scale insects (Superfamily: *Coccoidea*) found in Beech forests throughout the year (Gaze & Cloud, 1983). The concentrations selected were low (25g nectar mix per 100g of water), honeydew (50g nectar mix per 100g of water) and high (75g nectar mix per 100g of water).

2.5.2 Colour

In the colour experiment the birds were offered four different coloured softfood mixtures (Best Bird 1st Choice Conditioning and Rearing Bird diet, Brooklands Pet Products, New Plymouth, New Zealand). The colours were chosen to approximate colours that would naturally occur in their diet (Greene, 1998; Greene, 1999; Higgins, 1999; Warham & Bell, 1979). The colours were red (representing flowers and berries), green (representing leaves and grasses), yellow representing (flowers, berries, leaves and grasses) and blue (representing a small portion of flowers and berries). Colours were produced using 5mls of food colouring; Green (Batch number 490085), Yellow (Batch number 561095) and Pillar Box Red (Batch number 547085) Queen Liquid Food Colouring (Queen Fine Foods, Alderley, Queensland, Australia) and Blue (Batch number 195125) Hansells Liquid Food Colouring (Hansells Food Group, Penrose, Auckland, New Zealand).

2.5.3 Olfaction

For the olfactory experiment the birds were offered four different smells, all of which were chosen as an analogue of part of the natural diet (Greene, 1998; Greene, 1999; Higgins, 1999; Warham & Bell, 1979). The options presented to the birds were Scale insects (*Hemiptera: Sternorrhyncha)*, New Zealand flax/Haraheke flowers (*Phormium tenax)* (Figure 2.2), parrot seed mixture (oats, sunflower seeds, canary seeds, barley, wheat, whole maize, white French millet, safflower, linseed, rape and peanuts; Topflite parrot seed) and pectoral muscle from New Zealand Wood Pigeon (Kereru *Hemiphaga novaeseelandiae)* this was to simulate carrion. The muscle tissue was sourced from a wild bird euthanized at Wildbase Hospital, Massey University due to injuries a week before testing began.

Figure 2.2 Haraheke N.Z Flax (Phormium tenax) flowers.

2.5.4 Auditory

In the auditory experiment mealworms (*Tenebrio molitor)* were presented as they are known to produce sounds when they move in different substrates (Floyd & Woodland, Loclization of soil dwelling Scarab larvae by the Black-backed Magpie, Gymnorhina tibicen (Lantham), 1981). The birds were offered a choice between live mealworms in leaf litter, live mealworms in bran flakes, freshly killed mealworms (head capsule removed) in leaf litter and freshly killed mealworms in bran flakes. The freshly killed mealworms were offered to help differentiate if birds were attracted to these sensory options because of auditory or olfactory stimuli.

2.6 Testing Procedure

Birds were collected from the aviaries at the Victoria Esplanade at 7.30am on each day of testing. Testing only happened from Monday to Friday. Birds were transported in budgie show cages, similar to the one shown in Figure 2.3**,** as provided by the manager of the aviaries. Each bird was provided with water and food during the approximately five minutes' drive from the captive facility to Massey University.

Figure 2.3 Budgie Show cage in which the birds were transported and isolated in before testing. Photo sourced from www.kentcages.com/ShowCageBudgie.htm.

Once the birds reached the testing location, they were first identified using coloured nail polish on their right foot; an example is shown in Figure 2.4 (blue for Antipodes Island Parakeets and Red for Red-crowned Parakeets) and placed into separate cages**.** The order in which they were tested was recorded and the food was removed from the first bird at 9.00am with the next birds having their food removed at 20 minute intervals. This ensured that each bird had only one hour of food deprivation. Water was available to each bird throughout the experimental period.

Each test bird was placed into the small wooden box and placed under the opening in the base of the testing box. The lid was removed from the small box, releasing the bird into the testing box. Once the bird had left the holding box the lid was replaced closing over the hole to stop the birds from re-entering the holding box during the trial. Each bird was given 20 minutes to investigate the testing environment. After the 20 minutes had elapsed the bird was removed from the test box using a hand net and placed back into the transport box. Food was returned to each bird after they had completed the test. All birds were tested between 9am and 12pm each day of testing. After all the birds had completed the test, they were returned to their aviaries and collected again the next testing day.

Figure 2.4 Coloured nail identification mark used to identify each individual bird.

2.7 Variables Measured

For all four experiments video was analysed using the video analysis program B.O.R.I.S (Behavioural Observation Research Interactive Software, version 3.47, DOI: 10.1111/2041-210X.12584**).** All behaviours analysed are listed in table 2.1. Two types of behaviour were recorded; state (a behaviour that is measured over a duration of time) or event (a behaviour that happens instantaneously and is measured by a frequency rather than duration) (Altmann, 1974). Most behaviours were classified as state events and the duration for which they were observed was recorded in seconds. Event behaviours were recorded as frequency or count data. For every state behaviour the quadrat in which it was performed was also recorded. Data was analysed using the statistical package Rx64 3.3.1.

For the data analysis, the behaviours have been grouped into different categories in order to analyse specific questions of this study that looks into the behavioural responses towards the novel environment of the testing apparatus. The behaviours were also grouped into locations in which they occurred in the testing box to look into the spatial distribution of the birds in the testing box. These were categorised into whether they were performed in the top half of the box (Up), in the bottom half of the box (Down) or whether they can occur in all locations of the box (Either) as listed in table 2.1. These behaviours were also categorised into whether they were an active or inactive behaviours to look at the amount of time the birds spent being active or inactive throughout the study. Active behaviours were walking on the rope or on the ground and flying around the box. Inactive behaviours were standing on the rope, on the ground or on the pole, along with chewing behaviours (at the cup/mesh, rope, pole, opening and air holes), investigating the options at the top of the pole, hanging from the rope and grooming behaviours. These behaviours were categorised into different groups depending on what question was being looked at, although they are still the same behaviours regardless of how they were categorised.

Table 2.2 Behaviours recorded in the video analysis of sensory choice experiments. Types of behaviours analysed (state/event), description of behaviours and the location within the box where the behaviours occurred (up, down or either).

Behaviour	**Description**	**State/Event**	**Location**
Grooming/Preening	Preening or grooming feathers.	State	Either
Chewing at Rope	Chewing at the rope around the pole	State	Up
Chewing at Cup/Mesh	Chewing at the mesh covering the cup in the sound and smell test or at the cup itself in all four experiments.	State	Up
Standing on the Rope	Sitting on the rope or perch in the top half of the box.	State	Up
Investigating	Bird is looking into the cup at the top of the pole.	State	Up
Walking on Rope	Bird walking along the rope from one pole to another.	State	Up
Standing on Pole	Bird sitting on top of the pole itself.	State	Up
Flying	Bird flying around the box.	State	Up
Hanging	Bird hanging upside down from one of the ropes connected to the poles.	State	Up
Chewing at Air Holes	Attempting to chew at the air holes on the bottom of each of the four walls.	State	Down
Chewing at Opening	Pulling up the flooring around the opening where the birds emerged.	State	Down
Walking on Ground	Walking along the ground in the test box.	State	Down
Standing on the ground	Standing on the ground of the box.	State	Down
Peck	Pecking at something in the box	Event	Either
Choice	Bird visited all four of the options presented and can then be seen as choosing to investigate that option as they know what is in each.	Event	-
Latency to emerge	Bird left the small holding box and entered the testing box.	Event	-
Drink/Eat	Bird drank or ate from one of the options in the colour or taste experiments.	Event	-

2.8 Data Analysis

All data were extracted from B.O.R.I.S and analysed using R statistical software (Rx64 3.3.1). Due to the external constraints on the numbers of species and individuals available for testing, detailed statistical analyses could not be done, therefore we present descriptive statistics of the results in this thesis. Graphs were created using the R package ggplot2.

2.8.1 Spatial Orientation

The testing box was divided into four different quadrats with one of the options given in each as shown in Figure 2.5. The top left corner was quadrat one (42^{0}NE), top right was quadrat two (26^{0}NE), bottom right was quadrat three (19^{0}N) and quadrat four was the bottom left corner of the box (28^{0}NE). The quadrat numbers were always kept in the same position with only the options given in each changing throughout the trials.

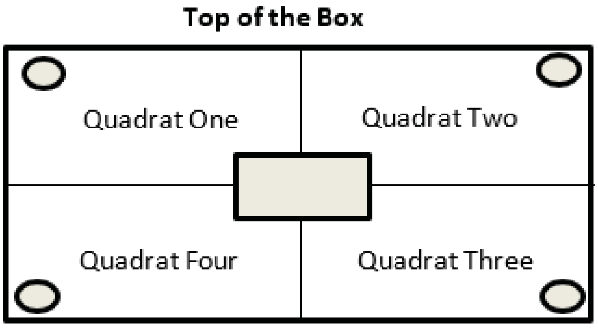


Figure 2.5 Base of testing box showing the position of each of the four quadrats, the position of the opening where the birds emerged from in the middle of the box and the positon of each of the poles in the four quadrats.

2.8.2 Height Preference

The testing box was split into two different levels, on the ground or on the top/rope. This allowed for further analysis of location to explore whether or not there were any preference for being up high or on the ground of the test box. State behaviours were categorised according to where in the test box they were performed. Up behaviours included: standing on the rope or perch, walking along the rope, standing on top of the pole, hanging upside down from the rope, chewing at the mesh or cup, chewing at the rope and flying. Down behaviours included: standing on the ground, walking on the ground, chewing at the small opening where the birds came out, chewing at the air holes along the bottom of the walls and chewing at the pole itself. Other behaviours recorded were behaviours that could be performed on both levels including grooming or preening and the point events that were scored as frequencies: pecking, drinking or eating at one of the options.

2.8.3 Emergence Time

The time taken for each bird to emerge from the small holding box into the testing box was recorded. If the bird did not emerge the trial was declared invalid and the data was removed from further analysis.

2.8.4 Active vs. Inactive Behaviours

All of the behaviours were categorised as active or inactive behaviours. Active behaviours included walking on the ground and rope and flying around the testing box. Inactive behaviours included standing on the ground, rope or pole, hanging upside down from the rope, chewing at the various surfaces (cup or mesh, pole, opening, rope and air holes) and grooming or preening.

2.8.5 Activity/Time Budget

The amount of time each individual bird spent performing each of the state behaviours was recorded as a proportion of time and was averaged over all 16 trials.

2.8.6 Choice Selection

Each of the four experiments had four different options available to each bird. The four options were arranged in a new order for each of the four repetitions and remained in that order for all birds on that repetition. For each trial the birds were given 20 minutes to explore and interact with the options given to them. If a bird visited all four of the options, the subsequent visits were identified as the bird making a choice to revisit this option as they were now aware of what was on offer in each of the four poles.

Each bird was tested four times per sensory modality, for a total of 16 trials of each individual bird. 80 trials for Antipodes Island parakeets (five individuals) and 64 trials for the Red-crowned parakeet (four individuals) were analysed.

Chapter Three: Results

“Carpe diem. Seize the day, boys. Make your lives extraordinary”- Dead Poets Society (1989)

A total of 144 trials were successfully recorded consisting of 16 trials of each of the five Antipodes Island parrots and 16 trials with each of the four red-crowned parakeets. One red-crowned parakeet (Bird I) did not engage in any of the 16 trials as it did not emerge from the holding box, this bird has been excluded from further analysis.

3.1 Quality control measures/Assessment of possible confounding factors

3.1.1 Spatial Distribution

The times spent in different quadrats are shown in Figure 3.1 for individual birds (3.1a) and both species (3.1b). This shows that there are not only individual tendencies but there is also a species tendency in certain quadrats.

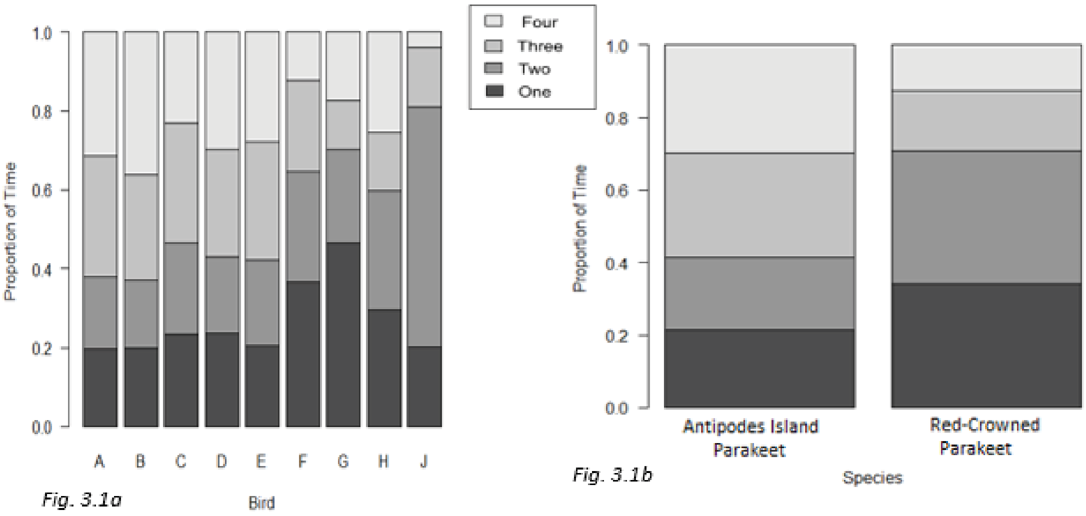


Fig. 3.1a

Fig. 3.1b

Figure 3.1 Proportion of time spent in each quadrat by each individual bird or species averaged over all trials. Figure 3.1a shows the time spent in each quadrat by individual birds averaged over all 16 trials. Birds A to E are Antipodes Island Parakeets and Birds F to J are Red-Crowned Parakeets. Figure 3.1b shows time spent in each quadrat averaged for each species over all 16 trials.

The Antipodes Island parakeets (bird A to E) showed a tendency for quadrats three and four, spending most of their time in these two quadrats. On the other hand, the Red-Crowned parakeets (bird F to J) showed the opposite pattern and spent more time in quadrats one and two. If there was nothing influencing the birds to spend more time in one quadrat more than the others, then they were expected to spend 25% of their time in each of the quadrats. Figures 3.1a and 3.1b show that this is not the case in both the individual birds and in the species as a whole. Birds A to E (Antipodes Island parakeets) showed a similar pattern to what was expected (25% of time spent per quadrat) as they spent between 20-30% on average in each of the four quadrats. Birds F to J (Red-crowned parakeets) spent more than the expected 25% in quadrats one and two (mean of 30-60%) this is especially shown by bird J who spent the majority (60%) of its time in quadrat two. This pattern of quadrat differences is also seen at the species level with the Antipodes Island parakeets spending between 20-30% of their time in each of the four quadrats and only spending slightly more time in quadrats three and four. Red-crowned parakeets on the other hand spent more time in quadrats one and two (mean of 35%) as shown in Figure 3.1b. This might be influenced by the large amount of time bird J spent in quadrat two when compared to the other Red-crowned parakeets. The effect of this spatial preference is unlikely to affect the choice experiments as I rotated the position of the sensory options between trials (see Chapter 2 for details).

3.1.2 Height Preference

The Antipodes Island parakeets tended to spend more time up high than on the ground spending an average of 59% in the top half of the box and 41% in the bottom half of the box. The Red-crowned parakeets did not show a clear preference for the top or bottom half of the box as they spent 42% of the total time in the top half and 41% of their time in the bottom half. These spatial preferences can be seen in Figure 3.2. Based on these results it can be concluded that the height preferences of the species are unlikely to affect the outcome of the choice experiments.

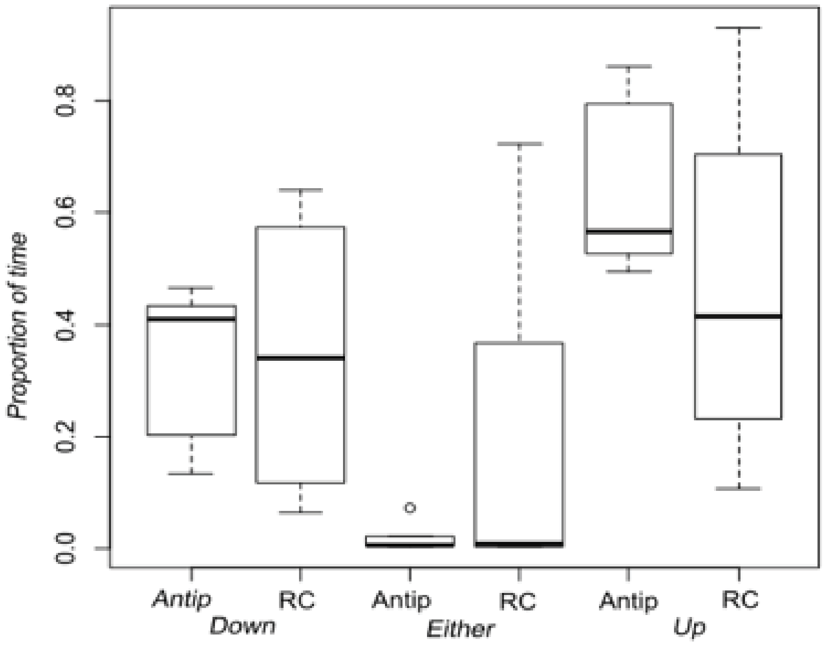


Figure 3. 2 The proportion of time spent up or down for each species averaged over all the 16 trials. Antip = Antipodes Island Parakeets. RC = Red-Crowned Parakeets.

3.1.3 Emergence Time

Figure 3.3 shows the average time taken for each species to emerge from the holding box. Both the Antipodes Island parakeets and the Red-crowned parakeets took 5 seconds on average to emerge from the holding box.

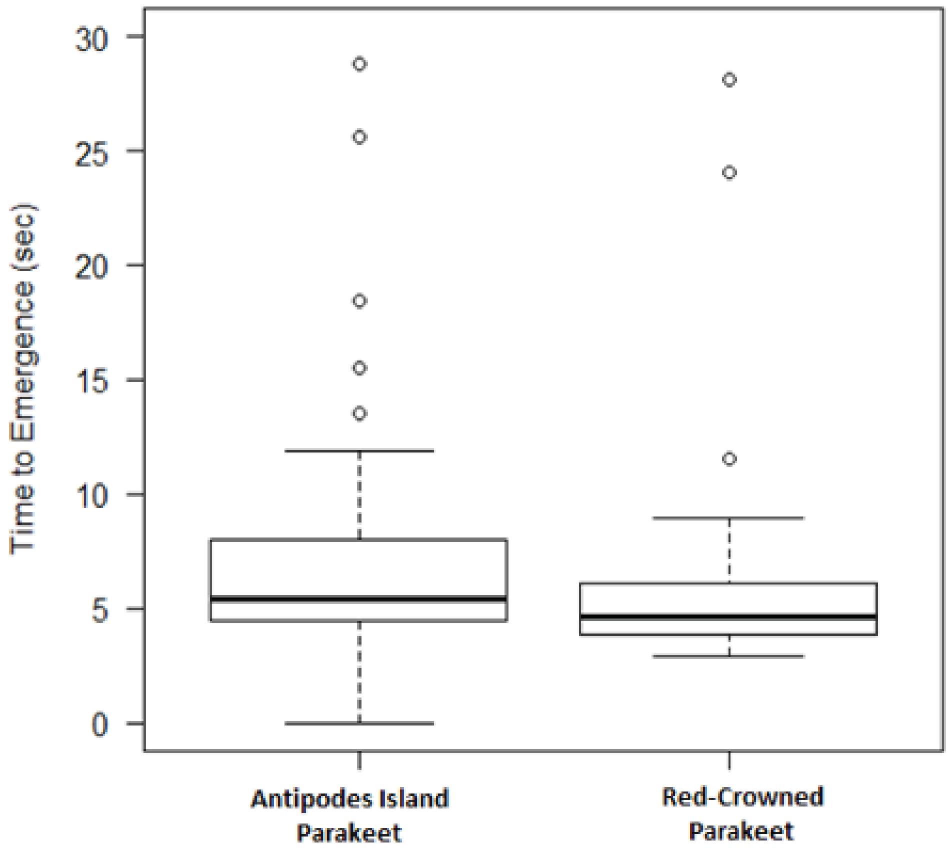


Figure 3. 3 The mean time taken for each species to emerge from the holding box. Along with the maximum and minimum emergence times with both the upper and lower quartiles shown as well. The circles above the boxes are the outliers.

Bird H only emerged for five of the sixteen trials. One Red-crowned parakeet (bird I) did not leave the box during any of the trials and was subsequently excluded from the analysis. Following the exclusion of this bird from the data, I concluded that emergence time would not affect the results of the choice experiments.

Analysis of the emergence times for individual Antipodes Island parakeets shows that most of the individuals had a mean emergence time between five and seven seconds with only one individual taking longer (mean of 23.5 seconds) as shown in table 3.1a.

Table 3.1a Emergence time (s) summary data for the Antipodes Island Parakeets (Antip) calculated for each individual bird over the number of trials they emerged. Rank for each bird is calculated using the median emergence time for each individual bird.

Bird ID	Species	Number of trials emerged	Median	Mean	Rank
A	Antip	15	7.1	23.5	4th
B	Antip	16	5.1	7.3	2nd
C	Antip	16	5.6	6.2	3rd
D	Antip	16	4.7	5.3	1st
E	Antip	16	5.1	7.5	2nd

Analysis of the emergence times for individual red-crowned parakeets shows each individual bird had a variety of mean emergence times. Only two individuals emerged with a mean time of five seconds as shown in table 3.1b. This shows a difference between individual birds and their mean emergence time.

Table 3.1b Emergence time (s) summary data for the Red-crowned Parakeets (RC) calculated for each individual bird over the number of trials they emerged. Rank for each bird is calculated using the median emergence time for each individual bird.

Bird ID	Species	Number of trials emerged	Median	Mean	Rank
F	RC	16	5.0	5.0	3rd
G	RC	16	4.4	5.2	2nd
H	RC	5	28.1	60.5	4th
J	RC	16	4.3	13.5	1st

3.1.4 Active vs. Inactive Behaviours

The amount of time each species spent performing behaviours that can be classified as active behaviours (walking on the ground or on the rope and flying) compared to inactive behaviours (standing on the ground, the rope or on the pole, hanging upside down from the rope) can shed some light on the overall activity levels of the two different species.

Figure 3.4 shows that the Antipodes Island parakeets spent an average of 9% of trial time performing active behaviours. The Red-crowned parakeets spent a mean of 4% of their time performing active behaviours. These findings show that the species differences in active behaviour could affect the outcome of the choice experiments and that inter-species comparisons of sensory choices may be confounded. Accordingly, we present results of the two species separately in the following results.

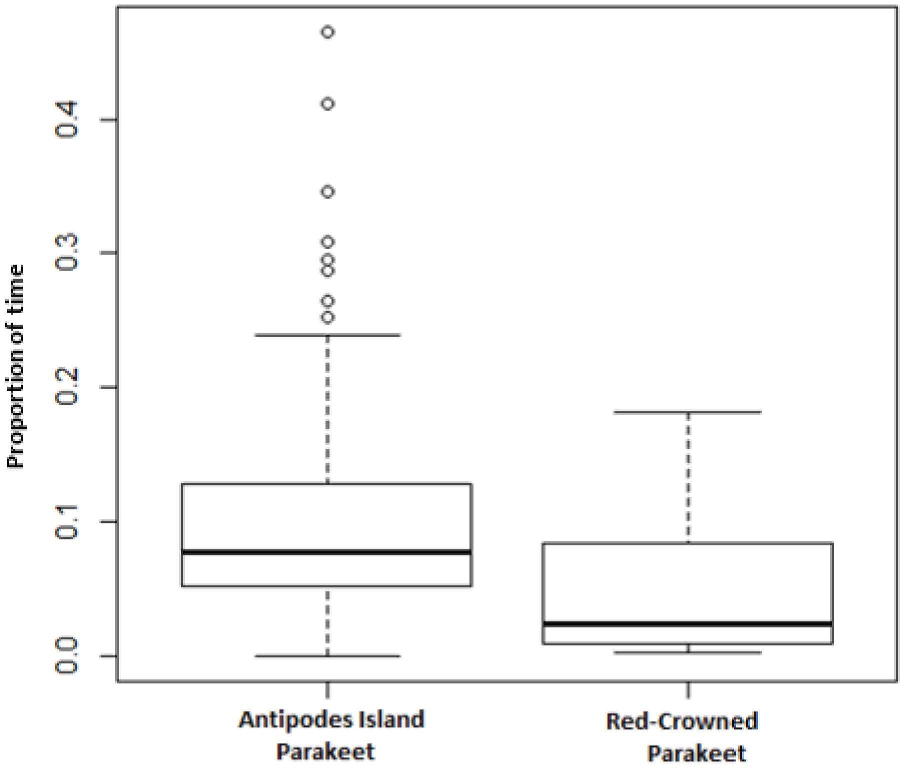


Figure 3.4 The average proportion of time both species spent performing active behaviours over all 16 trials. Along with the maximum and minimum time spent preforming active behaviours. Both the upper and lower quartiles are shown as well. The circles above the boxes are the outliers.

3.1.5 Average over all Trials

The average levels of activity were also different between the individuals of both species with bird A being the most active (mean = ~15%) out of all Antipodes Island parakeets and bird E (mean = ~ 6%) being the least active of all Antipodes Island parakeets. For the Red-crowned parakeets bird G was the most active (mean = ~9%) and bird F spending most of its time performing inactive behaviours (mean = ~5%) as shown in Figure 3.5a & 3.5b.

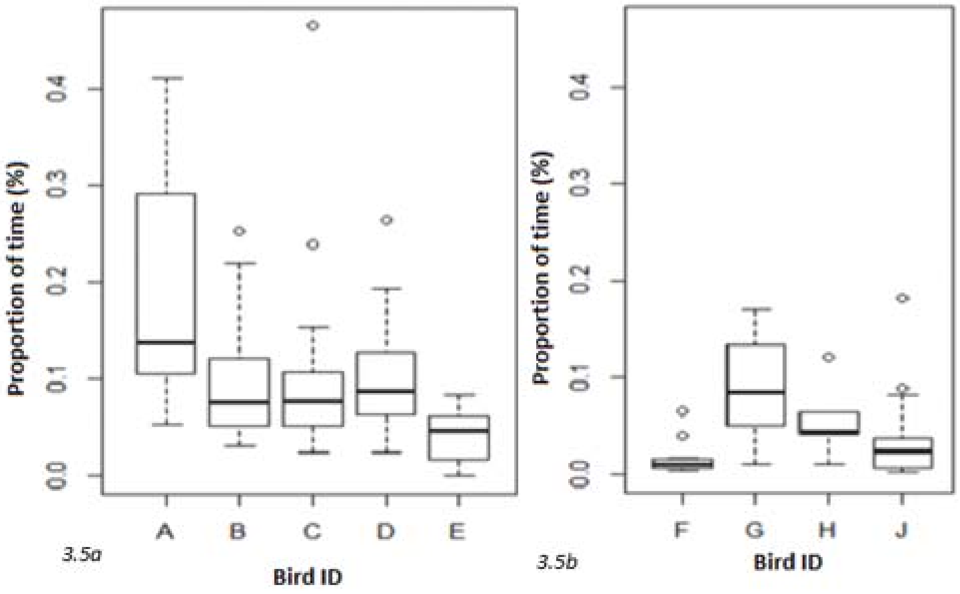


Figure 3. 5 The average proportion of time each individual bird spent performing active behaviours. 3.5a are Antipodes Island Parakeets. 3.5b are Red-crowned Parakeets.

Figures 3.6a & 3.6b show the percentage of time each individual bird spent performing “active” behaviours over each of the 16 trials. These figures show that there does not seem to be a pattern in terms of active behaviour and most birds showed a random level of “active” behaviours throughout all of the trials.

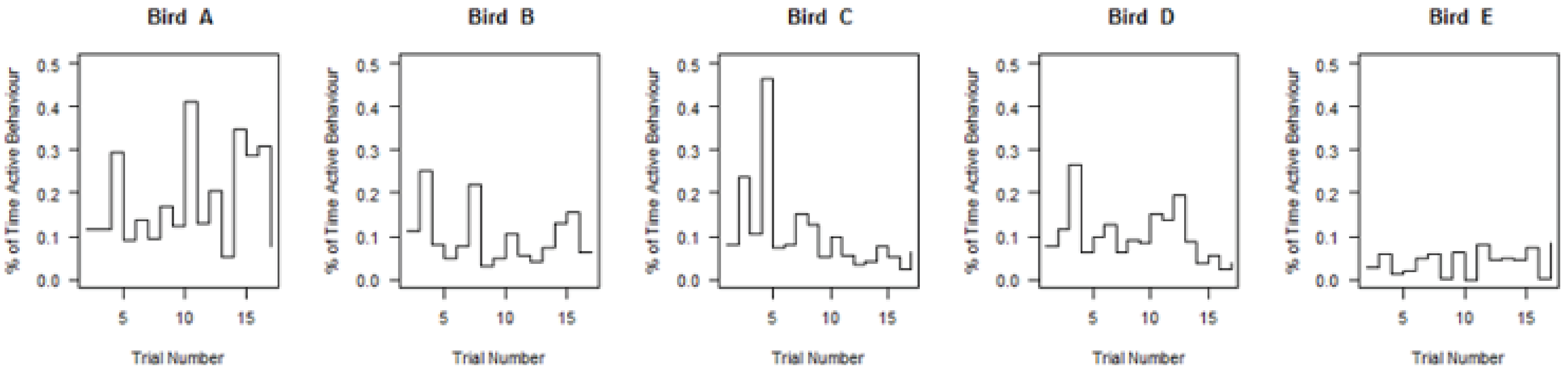


Fig 3.6a

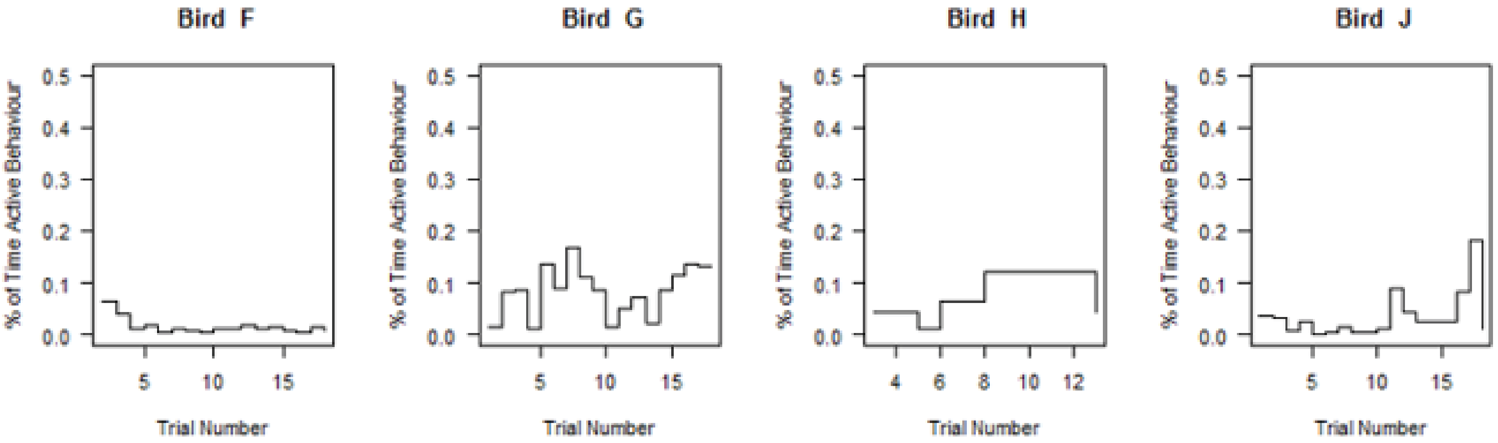


Fig 3.6b

Figure 3. 6 Change in individual bird's activity level for the Antipodes Island Parakeets (3.6a) and Red-crowned Parakeets (3.6b), shown as the percentage of time spent performing active behaviours over all the 16 trials

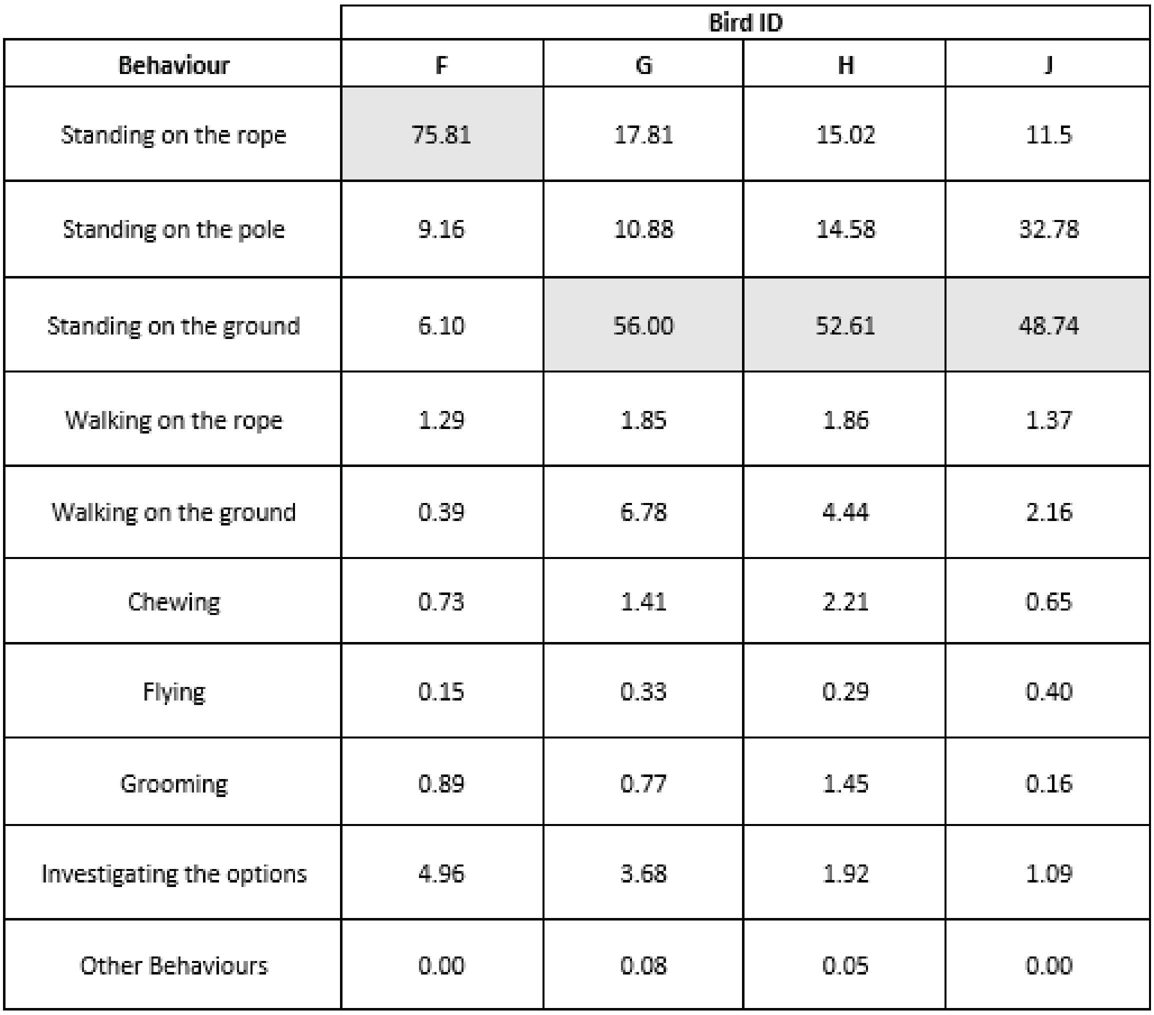
3.1.6 Activity Budget

Tables 3.2a & 3.2b show the proportion of time each individual spent performing each behaviour and gives the activity budget for each bird over all 16 trials. Table 3.2a shows that the Antipodes Island parakeets spent more time performing a number of different behaviours whereas the red-crowned parakeets spent most of their time standing on the ground as shown by table 3.2b. The Antipodes Island parakeets had a maximum mean of 48% of the trial performing one behaviour (bird E standing on the ground). The red-crowned parakeets spent a mean of at least 50% of the trial performing only one behaviour. On the basis of these findings, I conclude that species differences in the amount of time performing each behaviour will affect the outcome of the choice experiments and that inter-species comparisons of sensory choices will be confounded and the two species therefore are not able to be compared at the species level.

Table 3.2a Mean time individual Antipodes Island Parakeets spent performing the behaviours observed in the box over all 16 trials shown as a percentage of their total time. Other includes those behaviours that were recorded as a point behaviour and includes pecking and drinking or eating behaviours along with out of frame behaviour for Bird D only.

	Bird ID				
Behaviour	**A**	**B**	**C**	**D**	**E**
Standing on the rope	15.92	15.02	23.50	17.23	47.47
Standing on the pole	3.84	3.52	5.61	3.25	19.53
Standing on the ground	28.2	33.46	14.00	24.89	11.59
Walking on the rope	6.11	3.34	7.80	5.61	4.05
Walking on the ground	14.64	7.92	4.18	6.53	1.15
Chewing	14.27	20.33	24.94	21.93	7.53
Flying	0.46	0.23	0.30	0.31	0.15
Grooming	3.12	4.93	2.19	6.00	0.56
Investigating the options	11.19	10.34	16.39	11.07	7.22
Other Behaviours	0.51	0.37	0.65	2.78	0.08

Table 3.2b Average time individual Red-crowned Parakeets spent performing the behaviours observed in the box over all 16 trials. Other includes those behaviours that were recorded as a point behaviour and includes pecking and drinking or eating behaviours.



	Bird ID			
Behaviour	**F**	**G**	**H**	**J**
Standing on the rope	75.81	17.81	15.02	11.5
Standing on the pole	9.16	10.88	14.58	32.78
Standing on the ground	6.10	56.00	52.61	48.74
Walking on the rope	1.29	1.85	1.86	1.37
Walking on the ground	0.39	6.78	4.44	2.16
Chewing	0.73	1.41	2.21	0.65
Flying	0.15	0.33	0.29	0.40
Grooming	0.89	0.77	1.45	0.16
Investigating the options	4.96	3.68	1.92	1.09
Other Behaviours	0.00	0.08	0.05	0.00

Figures 3.7a & 3.7b show the activity budget as a stacked bar graph which shows the proportion of time each individual bird performed each behaviour once they had emerged from the holding box. These graphs allow for easier interpretation of the results. Bird I has been removed from this graph as it did not emerge from the holding box during any of the trials. The Antipodes Island parakeets (Figure 3.7a) spread their time across all of the behaviours. The Red-crowned parakeets (Figure 3.7b) seemed to spend the majority of their time standing on the rope, the ground or on a pole with approximately 50% of their total time spent performing these behaviours. 81.52% of bird J's time was spent either standing on the ground (48.74%) or standing on top of the pole (32.78%).

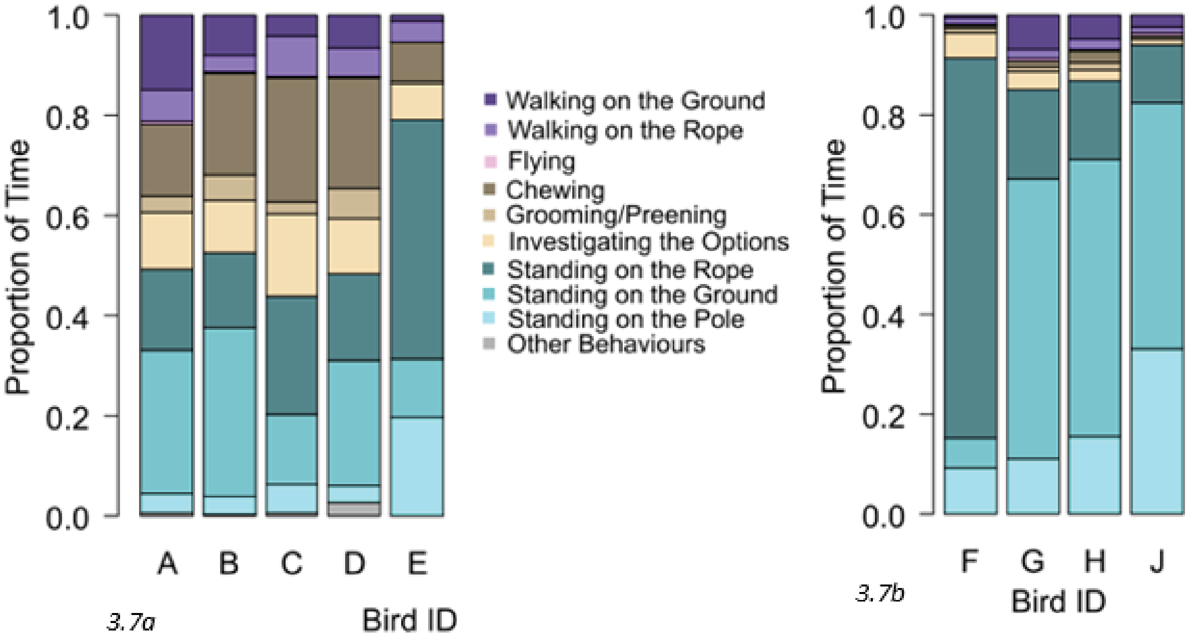


Figure 3.7 Activity Budget for each individual shown by the proportion of time the individual spent performing each behaviour once they had emerged from the holding box. Other behaviours includes hanging from the rope, out of frame (for bird D only) and point behaviours such as pecking and drinking or eating.

Antipodes Island Parakeets were shown to have a higher proportion of time spent chewing on objects; the rope, the cup or mesh that covered it in some tests (sound and smell), the pole, at the ventilation holes at the bottom of the walls or the opening where the birds emerged from.

3.2 Inter-Species Differences in Choice Behaviour

3.2.1 Species Differences

Table 3.3 Number of trials in which a choice was made in Antipodes Island and red-crowned parakeets in each of the four sensory tests.

	Colour		**Taste**		**Smell**		**Sound**	
	Antipodes Island Parakeet	Red-crowned Parakeet	Antipodes Island Parakeet	Red-crowned Parakeet	Antipodes Island Parakeet	Red-crowned Parakeet	Antipodes Island Parakeet	Red-crowned Parakeet
Choice	19 95%	6 46%	18 94%	5 42%	19 95%	9 64%	18 90%	9 64%
No choice	1 5%	7 54%	1 5%	7 58%	1 5%	5 36%	2 10%	5 36%
Total	20	13	19	12	20	14	20	14
Fishers exact test	*p = 0.003		*p = 0.002		p = 0.061		p = 0.097	

A total of 132 choices were recorded during the trials. Antipodes Island parakeets were significantly more likely ($\chi^2 = 25.85$, df = 1, $p = 0.0001$) to make a choice (74/79 valid trials) than red-crowned kakariki (29/53 valid trials) which had an effect on the choice trials and limited what inter-species comparisons could be made in sensory choices. This inter-species behavioural difference persisted throughout all choice experiments but was edged out of significance for smell and sound as more red-crowned parakeets made choices in these trials (Table 3.3). One Antipodes Island parakeet (bird A) did not participate in the first taste trial as it did not emerge from the holding box. This accounts for the total of 19 in the taste modality. One of the Red-crowned parakeets (Bird H) only emerged from the holding box for five out of the sixteen trials. Bird H participated in one colour trial, two sound trials and two smell trials and did not participate in any of the taste trials. This accounts for the different totals for the Red-crowned parakeets as there were only 13 trials for colour, 14 trials for both sound and smell and only 12 trials for taste all together.

3.2.2 Duration of Investigative Behaviours

The Antipodes Island parakeets made more choices over all sensory modalities (93.7% of trials) than the Red-crowned parakeets (54.7% of trials). Figure 3.8 shows the proportion of time each species spent investigating all the options given to them averaged over all 16 trials. The Antipodes Island Parakeets showed a longer duration of investigative behaviour compared to non-investigative behaviour. The Red-crowned parakeets did not show any clear differences between investigative and non-investigative behaviours. I conclude that species differences in active behaviour affected the outcome of the choice experiments and inter-species comparisons of sensory choices were confounded.

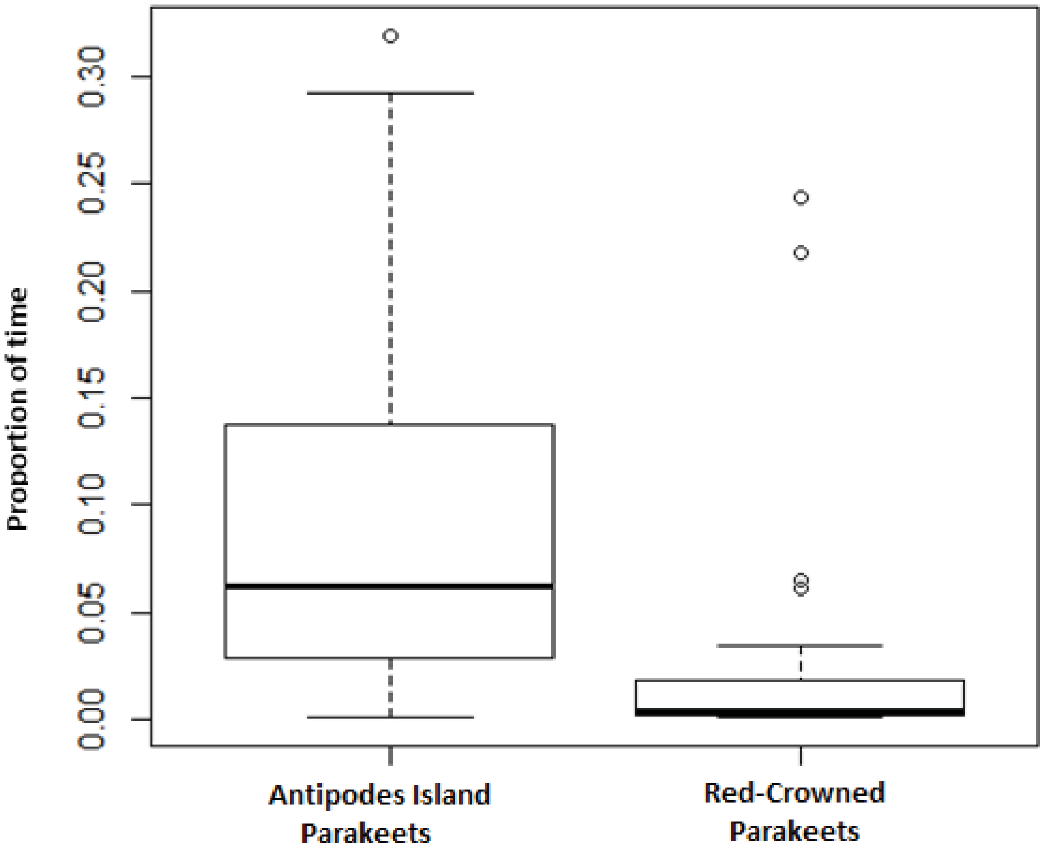
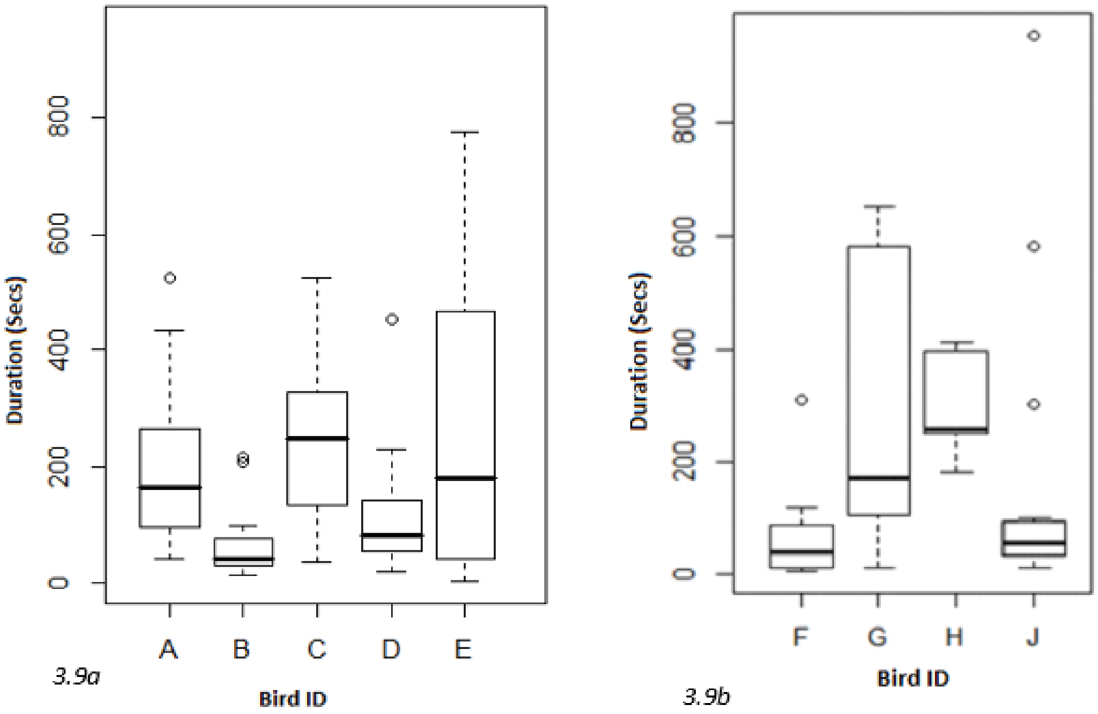


Figure 3.8 Average proportion of time both species spent investigating all four options available to them.

Individual birds show different amounts of investigative behaviour during the trials. Figures 3.9a & 3.9b show the duration each bird spent investigating the four options given to them over the 16 trials. Figure 3.8a shows that three of the Antipodes Island parakeets (Bird A, C and E) spent a greater proportion of the trial in investigative behaviours. Figure 3.8b shows two of the red-crowned parakeets (Bird G and H) spent a greater proportion of the trial in investigative behaviours. Within both species, these results suggest individual differences occur in the expression of this investigative behaviour.



3.9a

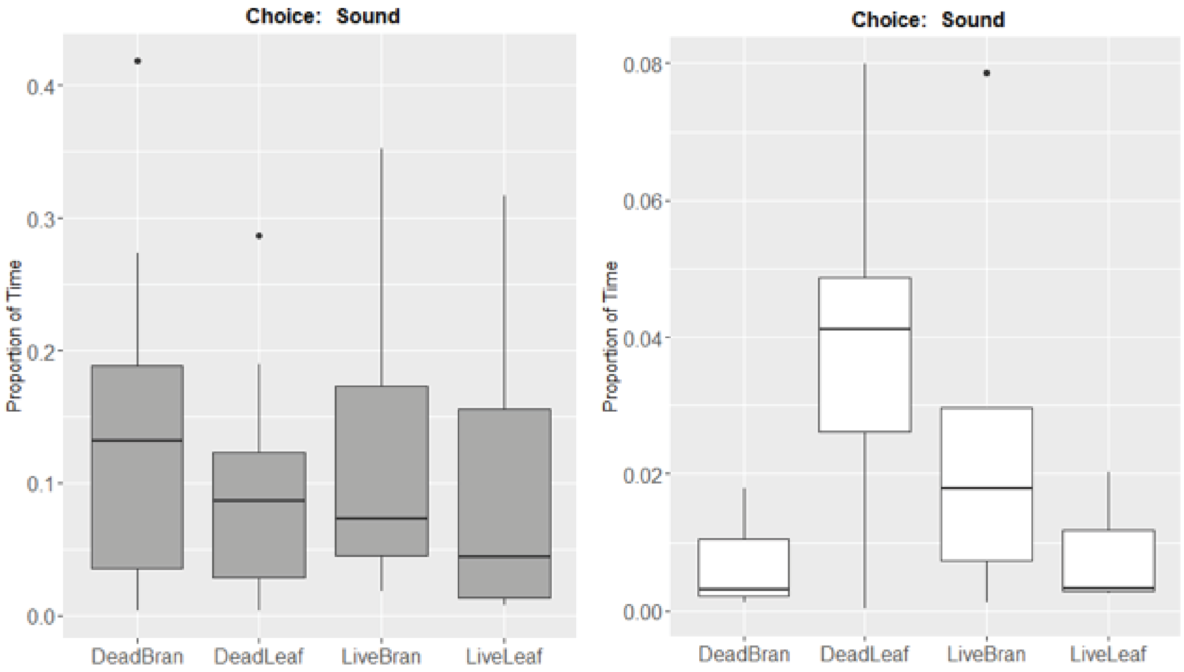
3.9b

Figure 3.9 Average time (seconds) taken for each bird to investigate all four options and therefore make a "choice". Also shown is the upper and lower quartiles and maximum and minimum time taken to investigate all four sensory options.

3.3 Choices between Sensory Stimuli

3.3.1 Sound

Due to the species difference in choice behaviour, no meaningful statistical comparisons were able to be made between the species, however Antipodes Island (figure 3.10a) and Red-crowned parakeets (figure 3.10b) appeared to show no clear preference for the live mealworms over the dead mealworms.



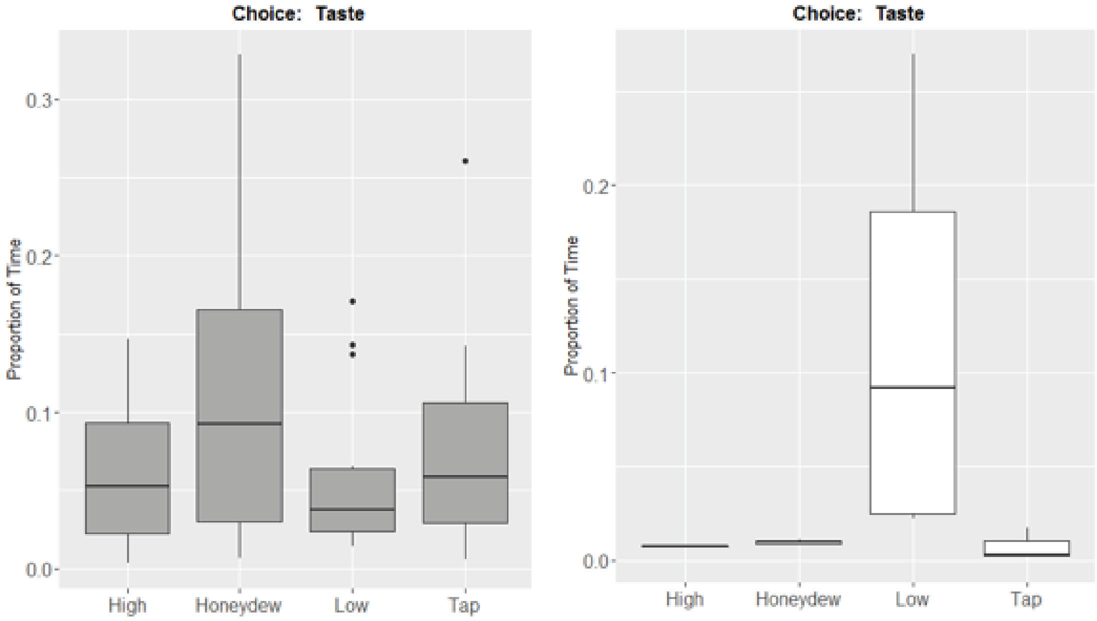
3.10a

3.10b

Figure 3.10 Proportion of time each species spent investigating each of the four sounds once they had made a "choice". The scents were either a live mealworm (Live) or a freshly killed (Dead) mealworm in either bran flakes (Bran) or leaf litter (Leaf). Shown by the median, upper and lower quartiles, the minimum and maximum values and the outliers (represented as dots).

3.3.2 Taste

Figure 3.11 shows the amount of time each species spent investigating the four sugar water concentrations after they had made a “choice”. Due to the species difference in choice behaviour, no meaningful statistical comparisons were able to be made between the species. The Antipodes Island parakeets showed no clear preference for sugar concentration and spent time investigating all four options provided (Figure 3.11a). The red-crowned parakeets showed a clear preference for the water with a low sugar concentration, spending on average of 9% of the proportionate trial time investigating this option (Figure 3.11b).



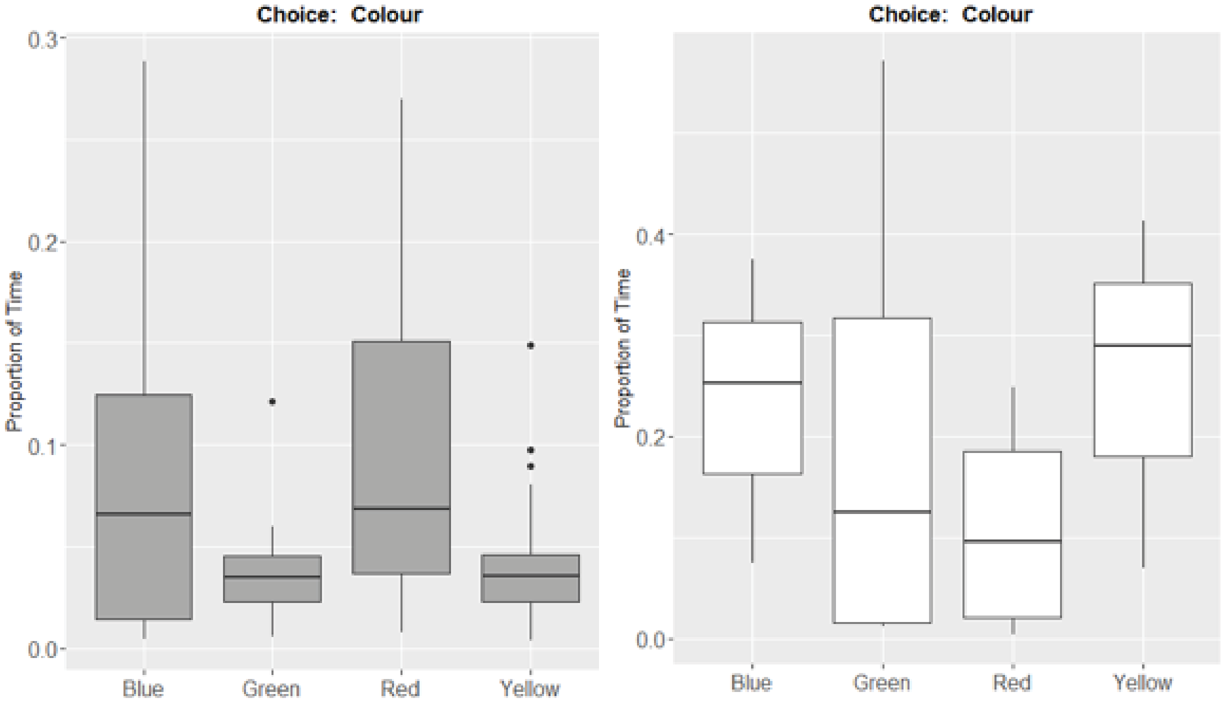
3.11a

3.11b

Figure 3.11 Proportion of time each species spent investigating each of the four different sugar water concentrations after they had made a "choice". High sugar concentration = 75g of nectar powder per 100g of water. Honeydew concentration = 50g of nectar powder per 100g of water. Low sugar concentration = 25g nectar powder per 100g of water. Tap = water from the tap. Shown by the median, upper and lower quartiles, the minimum and maximum values and the outliers (represented as dots).

3.3.3 Colour

The proportion of time spent by the birds investigating each of the four colours of wet-food mixture once they had visited all four, and could therefore be considered to make a “choice” is shown in figure 3.12a (Antipodes Island parakeets) and figure 3.12b (red-crowned parakeets). Due to the species difference in choice behaviour, no meaningful statistical comparisons were able to be made between the species. However, within each species, a visual appraisal of the box-whisker plots reveals no clear colour preferences between individuals.



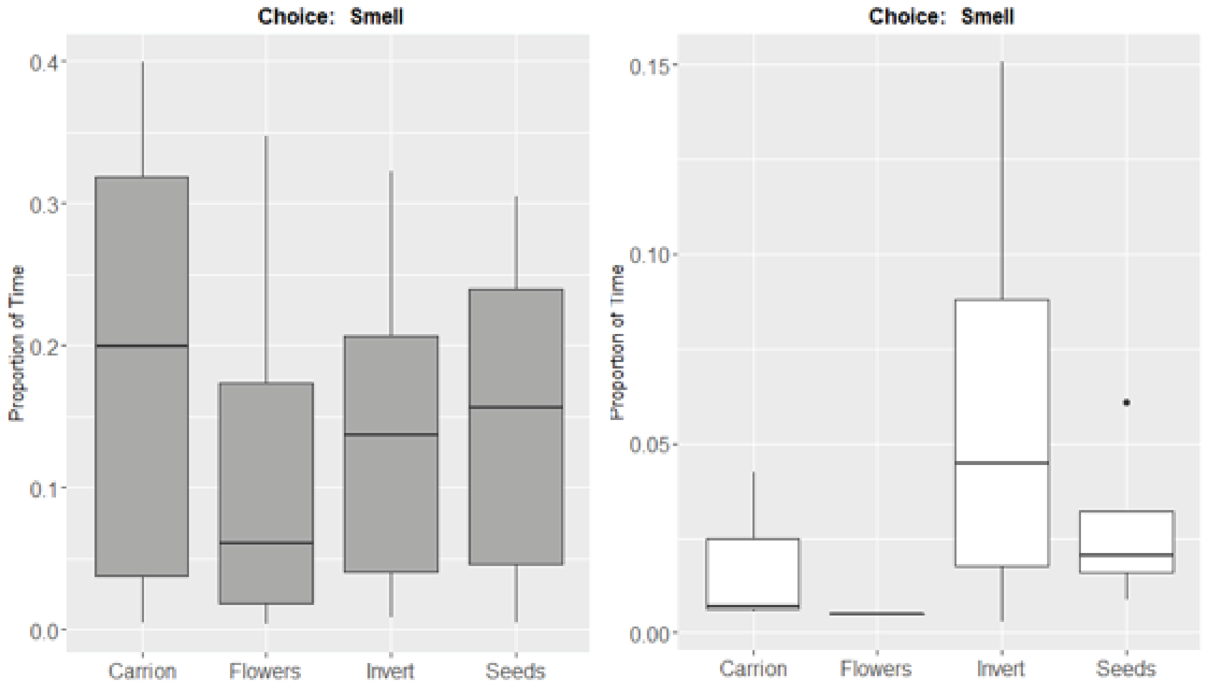
3.12a

3.12b

Figure 3.12 Proportion of time each species spent investigating each colour of wet food mixture after they had visited all four options and could be considered to have made a "choice". Shown by the median, upper and lower quartiles, the minimum and maximum values and the outliers (represented as dots).

3.3.4 Smell

Figure 3.13a&b shows the proportion of time each species spent investigating each scent after they were observed to make a “choice”. Due to the differences in choice behaviour, no meaningful statistical comparisons were able to be made between the species. The Antipodes Island parakeets (figure 3.13a) spent more time with the carrion (20% on average) than any of the other scent options. Red-crowned parakeets (figure 3.13b) showed a preference for the invertebrate scent, spending an average of 5% of their proportionate time investigating this option.



3.13a *3.13b*

Figure 3.13 Proportion of time each species spent investigating each scent after they had made a "choice". A piece of wood pigeon breast muscle was used for the carrion scent. New Zealand native flax (Phormium tenax) was used for the flower scent. Scale insects (Hemiptera: Sternorrhyncha) were used for the invertebrate (Invert) scent. Cockatiel and parrot seed mixture was used for the seed scent. Shown by the median, upper and lower quartiles, the minimum and maximum values and the outliers (represented as dots).

Chapter Four: Discussion

"So long and thanks for all the fish"- Hitchhiker's Guide to the Galaxy (2005).

The two species used in this study did not respond in similar ways to the testing apparatus that was used in the four sensory experiments. These results highlight that there are species differences in exploration, avoidance and temperament but it also means that the sensory perceptions of these two species cannot be directly compared. For the purpose of this discussion the two species will be compared in terms of their individual behavioural responses towards the same novel environment of the testing and the discussion on the sensory experiments will also be done with each species separately.

4.1 Behavioural responses to a novel environment

4.1.1 Antipodes Island Parakeets

In the wild, the Antipodes Island parakeets are an island species that live in a highly variable environment. According to the results of a study conducted by Mettke-Hoffman, Winkler and Leisler (2002), environmental factors lead to a low level of neophobia as the birds must find new food sources due to the seasonal variation of food and other resources on islands having a greater effect on the ecology of the species that inhabit them (Mettke-Hofmann, Winkler, & Leisler, 2002). However, the Antipodes Island parakeets used in my experiments were born in a captive facility and were not subjected to seasonal variation in their food sources and had relatively stable environmental conditions. Yet these birds still showed low levels of neophobia, which may be the result of some innate behaviours that would have originated in the source population of these captive birds. For example, the Antipodes Island parakeets as a species took on average 5 seconds to emerge from the holding box averaged over all 16 trials conducted.

The Antipodes Island parakeets were overall highly active during testing, on average they spent 9% of their time performing active behaviours (see chapter two: methods for description of active behaviours). Jones (1977) found that active behaviours including walking, pecking and vocalisation are signs of exploration in domestic chickens. It therefore may be concluded that the behaviours categorised as “active” can be seen as a sign of exploration in this study based on the results of other studies conducted (Jones, 1977; Jones, 1978).

The activity budget analysed for the five Antipodes Island parakeets used in this study showed that all birds spent most of their time performing numerous behaviours rather than just one or two. The Antipodes Island parakeets showed a high level of chewing of different objects making up the testing apparatus. This high level of chewing could be seen as explorative or investigative behaviours like that of the kea and other parrot species.

These results suggest that Antipodes Island parakeets have innate behavioural characteristics similar to kea, which are notoriously inquisitive, highly intelligent and have very little neophobia towards novel/new objects or environments (Greene T. , 1999). I suggest despite being reared in a stable captive environment with limited variety and readily available food resources, the Antipodes Island parakeets have retained the evolved behavioural traits of their island forebears that were the source population of these captive birds and captivity has not had any demonstrable effect on the heritability of these traits. This hypothesis would ideally be validated by conducting these experiments on free-living Antipodes Island parakeets as well.

Antipodes Island parakeets are naturally a ground dwelling parrot species that live in the tussocks fields on the Antipodes Islands (Higgins P. J., 1999b). In this study the birds were given the opportunity to spend their time either on the ground or up on the rope that connected the four poles. The Antipodes Island parakeets tended to spend more of their time up on the rope or poles than on the ground of the testing apparatus.

The birds used in this study were captive-bred and lived in an enclosure lacking their natural tussock fields and the ground was usually concrete with small patches of grass. These conditions might mean that these Antipodes Island parakeets were more inclined to spend time on the ropes of the testing apparatus due to the lack of a natural tussock environment. Alternatively, these Antipodes Island parakeets may have spent more time up on the rope and poles of the testing apparatus due to their curious nature. The birds could have been interested in what the poles contained and also trying to pull the rope from the poles as they showed a lot of chewing behaviours especially at the ropes or the cups/mesh present at the top of each pole. These results may suggest that some behaviours, such as spatial orientation, can be directly moderated by the individual bird's experiences in captivity rather than being an innate behavioural trait shaped by evolutionary forces. However, my evidence for this is tenuous in these experiments and further studies are required to explore this idea.

4.1.2 Red-Crowned Parakeets

In contrast, the red-crowned parakeets, being a forest dwelling species, might not be as willing to investigate a new environment as they live in a relatively stable environment where their food and other resources such as shelter and water tend to be constant in abundance and location. According to Mettke-Hofmann, Winkler and Leisler (2002) forest species should be reluctant to explore new or novel items and environments as they come from a stable environment not affected by seasonal changes of resources and weather conditions that make finding food difficult. Red-crowned parakeets are a forest dwelling species that ranges from the canopy to the forest floor where they feed on a relatively stable diet of fruits, berries and some invertebrates. These environmental conditions according to Mettke-Hoffman, Winkler and Leisler (2002) may lead to the red-crowned parakeets having a high level of neophobia or fear when presented with a novel object or environment.

Surprisingly, 4 out of 5 red-crowned parakeets emerged just as quickly from the holding box as the Antipodes Island parakeets. One bird refused to emerge in all trials and was removed from the data set. Other behavioural traits were suggestive of high levels of neophobia. For example, the red-crowned parakeets were less active over all 16 trials only spending a mean of 4% of their time in active behaviours. This low activity might be a sign of fear or stress similar to results from novel item or open field tests conducted by several researchers (Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Kitaysky, Wingfield, & Piatt, 1999; Cockrem, 2007). The activity budget shown by the red-crowned parakeets in this study showed greater than 50% of their time was spent standing on either the ground or the pole. This lack of movement could also be interpreted as a sign of distress or fear similar to the results shown from novel item and environment tests conducted on domestic chickens (Jones, 1978; Jones, 1977).

The red-crowned parakeets used in this study were born in the captive facility that they were sourced from and therefore are not under the same conditions faced by the wild populations. The conditions at the captive facility are stable in terms of food and other resources (e.g. water access and shelter availability) thus the birds do not face the same environmental conditions as the wild populations. The captive conditions the birds were raised in were similar to that used by the Antipodes Island parakeets, yet behavioural indicators of relative neophobia remain. This adds further evidence to the hypothesis that there are innate species dispositions in terms of neophobia and neophilia that are shaped by ancestral evolutionary forces which may be affected by the reproductive success of the source population of the red-crowned parakeets used in this experiment. In order to understand the degree of alteration that captive rearing environments can have on behavioural traits would require carrying out these experiments on free-living red-crowned parakeets to compare the results.

Being a forest dwelling species the red-crowned parakeets should not show a clear preference for vertical spatial orientation, translated here as being up or down in the testing apparatus as they range from the canopy to the floor of the forest. This lack of clear preference was shown in the experiments with the red-crowned parakeets not showing a clear preference for either "up” or “down”.

The red-crowned parakeets used in this study were captive bred which may have affected their spatial distribution as the captive environment they were sourced from lacks the wide range of vegetation and trees that they would occur in their natural habitat.

4.2 Individual Variation in Temperament

Animal temperament is thought to be affected by selection pressures created by the environment in which the animals inhabit and some phenotypes will be favoured over others (Dingemanse, et al., 2007; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih & Bell, 2008; Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Stamps & Groothuis, 2010). Some research shows that there is a benefit to having a range of temperament phenotypes and personalities within a population as it provides some benefits to the population as well as the individuals.

The captive nature of these birds may also have an effect on the personality types or temperament phenotypes shown by the birds used in these experiments. Captivity has been shown to have an effect not only of the ability of the animals to display “normal” behaviours due to the constant homogenous environment but can also have an effect on the heritability of these different personality types (Ekman & Hake, 1990; Lilliendahl, 1998; Lillendahl, 2000; van der Veen & Sivars, 2000; Drent, van Oers, & van Noordwjk, 2003; Riska, Prout, & Turelli, 1989).

Depending on the wild source of the original captive population, some temperament phenotypes may have been lost as the individuals who possessed the phenotypes that were ill-suited to captivity may have not been able to successfully breed in a captive environment (Drent, van Oers, & van Noordwjk, 2003; Riska, Prout, & Turelli, 1989). Therefore, the captive population may have continued by the more dominant captive suited phenotypes leading to the loss of variation between the temperament phenotypes or personality types shown by the captive birds used in this study.

4.2.1 Antipodes Island Parakeets

The individual Antipodes Island parakeets used in this study had some variation in the measures that were analysed but overall the five birds used in this study showed similar responses to the novel environment of the testing apparatus. The main difference observed in terms of the temperament was activity levels, with bird E seeming to be the least active, whereas bird A could be seen as the most active and more likely to display several behaviours in the same amount of time as bird E.

This information could be used to create a boldness or neophobia continuum with bird A at the bold/neophilic end and bird Eat the shy/neophobic end with the others somewhere in between (Wilson, Clark, Coleman, & Dearstyne, 1994). However, there was no individual bird that could be counted as completely neophobic/shy as all of the birds participated in the experiments in some aspect and the within species continuum is therefore comparatively narrow when comparing the five birds to each other.

Overall the Antipodes Island parakeets were explorative and were very curious at what was being offered to them, they spent time chewing at the different surfaces of the testing apparatus (pole, rope, floor or cups in the poles). These behaviours are very similar to those seen by kea in the alpine regions of New Zealand (Higgins P. J., 1999b; Greene, 1999). The curious and highly explorative nature shown by the Antipodes Island parakeets in this study makes interpreting the results of the experiments in terms of their sensory preferences very difficult as they did not show a clear preference for any of the four options presented to them and were seen to be interested in almost everything that was present in the testing box.

In terms of temperament there is little evidence that suggests that the Antipodes Island parakeets have different temperaments as they were all active and explorative and responded in similar ways in regards to the novel environment. This high explorative and activity levels could be an innate behavioural response towards a novel environment from their island ancestry, as these birds are from a captive facility and do not face the same drastic changes in their environment (Greene, 1999; Higgins P. J., 1999b; Warham & Bell, 1979; Mettke-Hofmann, Winkler, & Leisler, 2002). However, this study only tested five birds which is a small subset of a population and may not show all of the temperament phenotypes that are present in the whole captive population.

4.2.2 Red-Crowned Parakeets

The red-crowned parakeets used in this study showed greater behavioural differences in their individual responses towards the novel environment of the testing apparatus. The extreme of this is a single bird that refused to emerge from the testing box, and had to be excluded from further analysis. The remaining individual birds were analysed using the different measures of this study showed some variation in behavioural responses. For example, Bird F was less active and spent more time standing in one place than other birds.

The red-crowned parakeets tended to clump on a boldness/neophobia continuum as three of the birds (bird G, H and J) had similar responses towards the novel environment of the testing apparatus. Bird I was the extremely neophobic or shy bird out of all the red-crowned parakeets used in this study, and bird F can be positioned between this bird and the others on the spectrum.

Overall, the red-crowned parakeets were not active preferring to spend more time standing in one spot and less time investigating the sensory options presented to them. In terms of temperament the birds differed in their responses but not enough for clear phenotypes to be seen. These similar responses towards a novel environment makes interpreting the results of the sensory experiments slightly difficult as the birds tended not to investigate any of the sensory options presented to them and therefore did not show any strong preferences.

4.3 Response to Sensory Stimuli

Although there were significant differences in the behavioural responses to the testing apparatus between the two species, 5/5 Antipodes Island parakeets and 4/5 red-crowned parakeets satisfied the criteria for making a sensory choice in at least one of the 16 trial conducted. For this threshold to be reached a bird had to first visit all four options presented to them, and only then was the sensory preference was able to be recorded. This threshold was reached in 74/79 trials with the Antipodes Island parakeets and 29/53 trials with the red-crowned parakeets.

4.3.1 Antipodes Island Parakeets

The Antipodes Island parakeets showed interest in most of the sensory options presented to them, this may be due to their curious and inquisitive nature. The clearest sensory choice from the Antipodes Island parakeets was in the olfactory tests, especially that of the carrion option. On the Antipodes Islands the Antipodes Island parakeets have been seen to scavenge on seabird carcasses along the coastline and have been known to actively hunt storm petrels (Higgins P. J., 1999b; Warham & Bell, 1979). These birds were raised in a captive environment and fed a diet of seed and fruit and no carrion. Despite this, a sensory preference for carrion suggests that there is an innate attraction to this odour that has perhaps been shaped by the limited food resources available to these bird’s ancestors that were part of the source population of the birds used in these experiments. Dietary differentiation leading to changes in morphology and physiology is a well established evolutionary paradigm (Cooney, et al., 2017; Suzuki, 2017).

There are no studies that have considered the olfactory responses and physiology of Antipodes Island parakeets or any members of the *Cyanoramphus* genus. The strong response of the Antipodes Island parakeets in this study suggests that they do have some ability to smell odours. However, it is unknown what their olfactory bulb to cerebral hemisphere ratio is and where they would fit within the known ratios of many bird species including the brown kiwi (Bang & Cobb, 1968; Corfield, Kolominsky, Craciun, Mulvany-Robbins, & Wylie, 2016; Corfield, Wild, Hauber, Parsons, & Kubke, 2007; Martin, et al., 2007).

4.3.2 Red-Crowned Parakeets

The red-crowned parakeets showed the most interest in the colour sensory test and only showed a slight interest in the remaining sense tests. The red-crowned parakeets were interested in all four of the colour options presented to them paying particular attention to the blue and yellow options compared to the yellow and green options. The natural diet of the red-crowned parakeet consists of mostly fruits and berries which in New Zealand forests are primarily red and occasionally blue, dark purple or black (Greene, 1998; Higgins P., 1999a). This preference towards colour more than other sensory options may have been retained from the source population and has not been affected by the captive environment faced by the birds used in this study.

This preference for colour in the red-crowned parakeets suggest a preference for visual stimuli and may be how these birds are foraging for their main source of food, fruits and berries (Greene, 1998; Higgins P., 1999a). It is known that most birds are tetrachromatic animals and are therefore able to see the full spectrum of visible colours (red to blue) (Vorobyev, Osorio, Bennett, Marshal, & Cuthill, 1998; Kelber, Vorobyev, & Osorio, 2003). Being a forest dwelling species the red-crowned parakeets might be heavily reliant on colour over smell or taste as it may be easier to obtain the ripeness of the fruit based on what colour its flesh is.

There is a potential problem when considering the temperament phenotypes of the red-crowned parakeets in this experiment, as only five individuals were used and only four of those individuals were analysed. This small sample size might be excluding the birds that have different phenotypes as it has been shown that some populations can have a number of different phenotypes present in a group (Kurvers, et al., 2009).

4.4 Effects of Captivity on Sensory Responses

All of the birds used in this study were born and raised in captive facilities. This creates a problem when analysing the sensory responses of these birds in these experiments as the choices were based on their wild diet. The results of this study may be confounded by the captive nature of these birds as they may show some behaviours or preferences that may differ from what wild birds of the same two species may show.

The curious nature of the Antipodes Island parakeets persisted even though they came from captive facilities. This shows that they may have retained some of their “wild” behavioural responses towards a novel environment. Although the birds used in this study were sourced from the same captive facility they still showed species differences in terms of their sensory preferences. One problem that may occur when using captive birds, including the birds used in this study, is the genetic variation between the individual birds. I suspect that the birds used in this study were all genetically very closely related which might not be showing the full spectrum of behavioural responses in the wider scope of both species.

Although there are problems with using captive birds, the results have shown some major differences between the two species. These differences can possibly be a sign that these behaviours or preferences may be innate to the species and will remain in captive bred birds.

4.5 Limitations of this Study

Although this study did show some differences in both the behavioural responses and sensory preferences of both species there are some limitations to this study. One problem with the experimental set up was that the sensory options were only presented on top of the poles which required the birds to be up on the rope for them to be able to investigate the different options. This may have led to a bias for birds spending more time up on the rope rather than on the ground as they might have preferred. This can be rectified if these experiments were to be repeated by have the sensory options available on both the ground and on the poles, therefore allowing the birds to spend more time on the ground if they preferred and still given them the opportunity to make a sensory choice.

Originally the test box was to be kept as a clear perspex, but in pilot trials the birds seemed to be more interested in what was in the room outside of the box rather than what was being offered to them inside of the box. This was corrected for by placing black plastic rubbish bags around the outside of the testing box to remove the distraction of the room for the birds. This fix however had its own problems as the black plastics bags made the walls reflective and the birds were seen looking at their own reflection on occasion. To completely remove the problems of outside distraction if this study were to be repeated would be to make the testing box from and opaque plastic or wood to remove any reflection caused by the plastic walls.

There are several ways in which these behavioural traits and sensory preferences of these two species could be tested that are different from the experiments used in this study. A simple experiment in the home facility of the captive birds would eliminate the effect of the novel environment and would focus on the sensory preferences the individual birds. If this method was to be used the birds would have to be separated from each other and allowed to habituate to their new environment before the sensory tests could begin to ensure the tests were not influenced by social dynamics, the novel environment or objects.

Another way these sensory experiments could be conducted on these two species is to test for only one sense at a time by isolating the other senses from the testing apparatus similar to how Floyd and Woodland (1981) and Montgomerie and Weatherhead (1997) studied the foraging tactics of the black-backed magpie and American robin (Floyd & Woodland, 1981; Montgomerie & Weatherhead, 1997). In order to fully examine the sense that is being tested the behavioural responses of the birds would need to be analysed further to ensure all behaviours correspond to either investigating or choice selection have been fully understood. This would look into the different level of attraction each of the senses being tested and if the birds are able to discriminate between those options that they prefer over those that have no use for them. Given my results, I would suggest that more investigative effort be put into odour for Antipodes Island parakeets and vision for red-crowned parakeets.

A way to potentially validate the results found in this study would be to investigate the same behavioural responses and sensory preferences using wild birds of the same species. This however has its own problems the biggest being access to a wild population of both species. The Antipodes Island parakeets are only found naturally in the wild on the Antipodes Island group which has strict visitor regulations and permit needs and is located 860km SE of Stewart Island (Greene, 1999; Higgins P. J., 1999b; Warham & Bell, 1979). The red-crowned parakeets on the other hand are found naturally on the mainland of New Zealand but their populations are limited outside of captive facilities however this makes them easier to obtain access to wild birds.

The main reason why captive birds were used in this study was the increased likelihood that the birds would participate in the experiments and not have any behavioural issues with being placed inside of the testing box. Wild birds on the other hand are suspected to show a high level of stress or fear during handling and might show a high level of distress when placed in the testing box (Feenders, Klaus, & Bateson, 2011). However, a study conducted by Feenders, Klaus and Bateson examined the responses of hand raised and wild caught starlings of similar age in response to both a novel environment and a novel object. They found that the wild caught starlings were faster to move once placed in the novel environment, which was interpreted as evidence of a high escape motivation, and no significant differences between the wild caught and hand raised starlings in response to a novel object or explorative behaviours (Feenders, Klaus, & Bateson, 2011). These results show that wild caught starlings could be used in laboratory studies without affecting the outcome in terms of stress or fear levels.

4.6 Environmental Enrichment Opportunities

The results of this study could potentially be used to help create an environmental enrichment programme for captive Antipodes Island and red-crowned parakeets as it shows that there were some differences between the species in terms of their responses to a novel environment and different sensory options.

The Antipodes Island parakeets showed a high level of activity and exploration when presented with a novel environment and showed the most interest in the olfactory sense test. Using these results an enrichment programme should include options with different scents possibly including carrion. These highly neophilic parrots should be given a large variety of objects that differ in colour, textures, smell and taste to keep them interested and entertained (Fox & Millam, 2007; Kim, Garner, & Millam, 2009; Webb, Famula, & Millam, 2010). An enrichment program could be adapted from the one that is given to captive kea in New Zealand. By creating an enclosure that closely matches that of their natural island habitat and offering the birds a place to burrow and tussocks or other grasses to hide in or eat it will give the birds the enrichment they need to keep them entertained and stimulated similar to that of their wild counterparts.

The red-crowned parakeets on the other hand showed little interest in any of the sensory options except for the colour experiment. Using these results an enrichment programme for the captive red-crowned parakeets should offer the birds a wide variety of coloured items in particular red or blue items as the birds used in this study were more interested in these two options. Captive red-crowned parakeets can also be enriched from an enclosure that has some different tiers of vegetation to allow them to behave in a similar way to the wild species found in the forests around New Zealand.

4.7 Conclusion

The results of this study showed that there were differences between the Antipodes Island and red-crowned parakeets when presented with a novel environment and four different sensory experiments. The Antipodes Island parakeets were the more active and explorative of the two species investigating most of the sensory options presented to them. In particular, the carrion scent, and spending most of their time performing various behaviours including walking and chewing that the different surfaces of the testing apparatus. The red-crowned parakeets showed the opposite response to the novel environment as they were less active, preferred to stand in one place and showed most interest in the colour experiment.

These results suggest that differences in the ecology of the two closely related species has led to some innate differences in the birds' sensory preferences and personalities. The Antipodes Island parakeets acted more like the curious kea and not like their close relatives the red-crowned parakeets. However, in terms of temperament there was not sufficient evidence to conclude that temperament phenotypes existed within each species. This may be due to the small sample size; a larger sample group could show more varied responses and phenotypes.

The captive nature of the birds might have affected the behavioural responses of the birds but using wild birds in this study was not feasible due to the problems with access and the time restrictions faced by this study. If this study was to be repeated and access to wild birds was possible it would be interesting to assess what effect captivity has had on the birds compared to their wild counterparts.

This study shows that ecological differences does have some effect on the way these birds react to the same novel environment and that these closely related species use different senses in foraging for food. The results also show that even though the birds were born and raised in the same captive facility with similar environmental conditions there are still some innate behaviours shown which shows that captivity does not always change the natural behaviours of the animals and that two closely related species that are raised in the same environment can act differently.

Bibliography

Ackerman, J. S. (1978). Leonardo's Eye. *Journal of the Warbug and Courtauld Institues, 41*, 108-146.

Altmann, J. (1974). Observational study of behavior. *Behaviour, 49*(3), 227-266.

Bang, B. G., & Cobb, S. (1968). The Size of the Olfactory Bulb in 108 Species of Birds. *The Auk, 85*, 55-61.

Barry, T. P., Malison, J. A., Held, J. A., & Parrish, J. J. (1995). Ontogeny of the cortisol stress response in larval rainbow trout. *General comparative endocrinology, 97*(1), 57-65.

Beason, R. C. (2001). What Can Birds Hear? *21st Vertebrate Pest Conference* (pp. 92-96). California: USDA National Wildlife Research Centre- Staff Publications.

Bennett, A. T., & Cuthill, I. C. (1994). Ultraviolet vision in birds: what is its function? *Vision research, 34*(11), 1471-1478.

Benus, R. F., Bohus, B., Koolhaas, J. M., & van Oortmerssen, G. A. (1991). Heritable variation for agression as a reflection of individual coping strategies. *Experientia, 47*, 1008-1019.

Biondi, L. M., Bo, M. S., & Vassallo, A. I. (2010). Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (Milvago chimango). *Animal Cognition, 13*(5), 701-710.

Blondel, J., Chessel, D., & Frochot, B. (1988). Bird Species Impoverishment, Niche Expansion and Density Inflation in Mediterranean Islands Habitats. *Ecology, 69*(6), 1899-1917.

Boon, W. M., Kearvell, J. C., Daugherty, C. H., & Chambers, G. K. (2001). Molecular systematics and conservation of kakariki (Cyanoramphus spp.). *Science for Conservation, 176*, 1-46.

Bowmaker, J. K., & Martin, G. R. (1985). Visula pigments and oil droplets in the penguin, Spheniscus humboldti. *Journal of Comparative Physiology A, 156*(1), 71-77.

Breedlove, S. M., Watson, N. V., & Rosenzweig, M. R. (2010). General Principles of Sensory Processing, Touch and Pain. In S. M. Breedlove, N. V. Watson, & M. R. Rosenzweig, *Biological Psychology* (6th ed., pp. 216-217). Sunderland, Massachusetts: Sinauer Associates, Inc.

Butler, S. J., Whittingham, M. J., Quinn, J. L., & Cresswell, W. (2006). Time in captivity, idividual differences and foraging behaviour in wild-caught chaffinches. *Behaviour, 143*, 535-548.

Cannon, W. B. (1929). *Bodily changes is pain, fear, hunger and rage.* New York, New York, USA: Appleton.

Carere, C., & van Oers, K. (2004). Shy and bold great tits (Parus major): body temperature and breath rate in response to handling stress. *Physiology & Behavior, 82*, 905-912.

Cockrem, J. F. (2007). Stress, corticosterone response and avian personalities. *Journal of Ornithology, 148*(2), 169-178.

Colville, T. P., & Basseri, J. M. (2001). Avian Anatomy and Physiology. In T. P. Colville, & J. M. Basseri, *Clinical Anatamony and Physiology for Veterinary Technicians* (Third ed., pp. 357-360). St. Louis, Missouri: Mosby.

Cooney, C. R., Bright, J. A., Capp, E. J., Chira, A. M., Hughes, E. C., Moody, C. J., . . . Thomas, G. H. (2017). Mega-evolutionary dynamics of the adaptive radiation of birds. *Nature, 542*(7641), 344-347.

Coppinger , R. P. (1969). The effect of experience and novelty on avian feeding with reference to the warning coloration of butterflies, i. Reactions of wild-caught Blue Jays to novel insects. *Behaviour, 35*, 45-60.

Corey, D. T. (1978). The Determinants of Exploration and Neophobia. *Neuroscience & Biobehavioural Reviews, 2*, 235-253.

Corfield, J. R., Kolominsky, J., Craciun, I., Mulvany-Robbins, B. E., & Wylie, D. R. (2016). Is Cerebellar Architecture Shaped by Sensory Ecology in New Zealand Kiwi (Aptyerx mantelli). *Brain, behaviour and evolution, 87*(2), 88-104.

Corfield, J. R., Wild, J. M., Hauber, M. E., Parsons, S., & Kubke, M. F. (2007). Evolution of brain size in the Palaeognath lineage, with an emphasis on New Zealand ratites. *Brain, Behavior and Evolution, 71*(2), 87-99.

Cunningham, S. J., Corfield, J. R., Iwaniuk, A. N., Castro, I., Alley, M. R., Birkhead, T. R., & Parsons, S. (2013). The anatomy of the bill tip of kiwi and associated somatosensory regions of the brain: comparisons with seabirds. *PloS one, 8*(11), e80036.

Deeb, S. S. (2004). Molecular genetics of colour-vision deficiencies. *Visual Neuroscience, 21*, 191-196.

Deschner, T., Kratzsch, J., & Hohmann, G. (2008). Urinary C-peptide as a method for monitoring body mass changes in captive bonobos (Pan paniscus). *Hormones and Behaviour, 54*, 620-626.

Diamond, J., & Bond, A. B. (1991). Social Behaviour and Ontogeny of Foraging in the Kea (Nestor notabilis). *Ethology, 88*, 128-144.

Díaz-Uriarte, R. (2002). Incorrect analysis of crossover trials in animal behaviour research. *Animal Behaviour, 63*(4), 815-822.

Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personailities in a fluctuating environment. *Proceedings of the Royal Society of London, Series B: Biological Sciences, 271*(1541), 847-852.

Dingemanse, N. J., Wrighr, K., Kazem, A. J., Thomas, D. K., Hickling, R., & Dawney, N. (2007). Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology, 76*(6), 1128-1138.

Domann, N., Voets, T., & Nilius, B. (2008). TRPs in Our Senses. *Current Biology, 18*(18), R880-R889.

Dooling, R. J. (1980). Behvaiour and psychophysics of hearing in birds. In A. N. Popper, R. R. Fay, A. N. Popper, & R. R. Fay (Eds.), *Comparative studies of hearing in vertebrates* (pp. 261-288). New York: Springer-Verlag.

Dooling, R. J. (1982). Auditory perception in birds. In D. E. Kroodsma, E. H. Miller, D. E. Kroodsma, & E. H. Miller (Eds.), *Acoustic communication in birds* (pp. 95-130). New York: Academic Press.

Dooling, R. J. (1986). Perception of vocal signals by the budgerigar (Melopsittacus undulatus). *Experimental Biology, 45*, 195-218.

Drent, P. J., van Oers, K., & van Noordwjk, A. J. (2003). Realized heritability of personalities in the great tit (Parus major). *Proceedings of the Royal Society of London B: Biological Sciences, 270*(1510), 45-51.

Ebenhard, T. (1995). Conservation breeding as a tool for saving animal species from extinction. *Trends in Ecology & Evolution, 10*(11), 438-443.

Ekman, J. B., & Hake, M. K. (1990). Monitoring starvation risk: adjustments of body reserves in greenfinches (Carduelis chloris L) during periods of unpredictable foraging success. *Behavioural Ecology, 1*, 62-67.

Elliott, G., Dilks, P., & O'Donnell, C. (1996). The ecology of yellow-crowned parakeets (Cyanoramphus auriceps) in Nothofagus forest in Fiordland, New Zealand. *New Zealad Journal of Zoology, 23*, 249-265.

Engel, G., & Schmale, A. H. (1972). Conservation-withdrawal: A primary regulatory process for organic homeostasis. *Physiology, Emotion, and Psyuchosomatic Illness Ciba Foundation Symposium VIII* (pp. 57-95). Amsterdam: Elsevier.

Fay, R. R., & Popper, A. N. (2000). Evolution of hearing in vertebrates: the inner ears and processing. *Hearing research, 149*(1), 1-10.

Feenders, G., Klaus, K., & Bateson, M. (2011). Fear and exploration in european starlings (Sturnus vulgaris): A comparison of hand-raised and wild-caught birds. *PLoS One, 6*(4), e19074.

Floyd, R. B., & Woodland, D. J. (1981). Localization of soil dwelling Scarab larvae by the Black-backed Magpie, Gymnorhina tibicen (Lantham). *Animal Behaviour, 29*, 510-517.

Forshaw, J. (1978). Cyanoramphus. In J. Forshaw, *Parrots of the World* (pp. 2262-271). TFH Publications .

Fox , R. A., & Millam, J. R. (2007). Novelty and individual differences influence neophobia in orange-winged Amazon parrots (Amazona amazonica). *Applies Animal Behaviour Science, 104*, 107-115.

Fox, R. A., & Millam, J. R. (2004). The effect of early environment on neophobia in orange-winged Amazon parrots (Amazona amazonica). *Applied Animal Behaviour Science, 89*, 117-129.

Gajdon, G. K., Fijin, N., & Huber, L. (2004). Testing social learning in a wild mountain parrot, the kead (Nestor notabilis). *Learning & Behaviour, 32*(1), 62-71.

Gaze , P. D., & Cloud, M. N. (1983). Honeydew and its importance to birds in Beech Forests of South Island, New Zealand. *New Zealand Journal of Ecology, 6*, 33-37.

Giurfa , M., Nunez, J., Chittka, L., & Menzel, R. (1995). Colour preferences of flower-naive honeybees. *Journal of Comparative Physiology A, 177*(3), 247-259.

Gleich, O., & Manley, G. A. (1988). Quantitative morphological analysis of the sensory epithelium of the starling and pigeon basilar papilla. *Hearing research, 34*(1), 69-85.

Gleich, O., Dooling, R. J., & Manley, G. A. (2005). Audiogram, body mass, and basilar papilla length: correlations in birds and predicions for extinct archosaurs. *Naturwissenschaften, 92*(12), 595-598.

Glickman, S. E., & Sroges, R. W. (1966). Curiosity in zoo animals. *Behaviour, 22*, 151-188.

Goldsmith, T. H. (1980). Hummingbirds see near ultraviolet light. *Science , 207*(4432), 786-788.

Goldsmith, T. H., & Butler, B. K. (2005). Color vision of the budgerigar (Melopsittacus undulatus): hue matches, tetrachromay, and intensity discrimination. *Journal of Comparative Pysiology A, 191*(10), 933-951.

Goldstein, E. (2009). *Senstation and Perception.* Cengage Learning .

Gosling, S. D. (2001). From Mice to Men: What Can We Learn About Personality From Animal Research? *Psychological Bulletin, 127*(1), 45-86.

Greenberg, R. (1983). The role of neophobia in determining the degree of foraging specialisation in some migrant warblers. *The American Naturalist, 122*(4), 444-453.

Greene, T. (1998). Foraging Ecology of the red-crowned parakeet (Cyanoramphus novaezelandiae novaezelandiae) and yellow-crowned parakeet (C. auriceps auriceps) on Little Barrier Island, Hauraki Gulf, New Zealand. *New Zealad Journal of Ecology , 22*(2), 161-171.

Greene, T. (1999). Aspects of the ecology of Antipodes Island Parakeet (Cyanoramphus unicolor) and Reischek's Parakeet (C. novaezelandiae hochstetteri) on Antipodes Islands, October-November 1995. *Notornis, 46*, 301-310.

Greene, T. C. (2003). Breeding biology of red-crowned parakeets (Cyanoramphus novaezelandiae novaezelandiae) on Little Barrier Island, Hauraki Gulf, New Zealand. *Notornis, 50*, 83-99.

Gregory, R. L. (1997). Knowledge in Perception and Illusion. *Philosophical Transactions: Biological Science, 352*(1358), 1121-1127.

Groothuis, T. G., & Carere, C. (2005). Avian Personalities: characterization and epigenesis. *Neuroscience and Biobehavioural Reviews, 29*, 137-150.

Gsell, A. C., Hagelin, J. C., & Brunton, D. H. (2012). Olfaction Sensitivity in Kea and Kaka. *Emu, 112*, 60-66.

Gumbert, A. (2000). Colour choices by bumble bees (Bombus terrestris): innate preferences and generalization after learning. *Behavioural Ecology, 48*(1), 36-43.

Hagelin, J. C. (2004). Observations on the Olfactory ability of the Kakapo Strigpos habroptilus, the critically endangered parrot of New Zealand. *Ibis, 146*, 161-164.

Hart, N. S. (2001). The visual ecology of avian photoreceptors. *Progress in retinal and eye research, 20*(5), 675-703.

Healy, S., & Guilford, T. (1990). Olfactory-bulb size and nocturnality in birds. *Evolution*, 339-346.

Heather, B. D., & Robertson, H. A. (2005). Antipodes Island Parakeet Cyanromphus unicolor. In B. D. Heather, & H. A. Robertson, *The Field Guide to the Birds of New Zealand* (pp. 136 - 139). Auckland: Penguin Books .

Heffner, H. E., & Heffner, R. S. (2007). Hearing Ranges of Laboratory Animals. *Journal of the American Association for Laboratory Animal Science, 46*(1), 20-22.

Heffner, R. S., & Heffner, H. E. (1993). Degenerate hearing and sound localistion in naked mole rats (Heterocephalus glaber), with an overview of the central auditory structures. *Journal of Comparative Neurology, 331*(3), 418-433.

Henry, J. P., & Stephens, P. M. (1977). *Stress, health and the social environment: A sociobiologic approach to medicine.* Berlin, Germany: Springer Science & Business Media.

Heppner, F. (1965). Sensory Mechanisms and Envrionmental Clues Used by American Robins in Locating Earthworms. *The Condor, 67*(3), 247-256.

Herborn, K. A., Heidinger, B. J., Alexander, L., & Arnold, K. E. (2014). Personality predicts behavioural flexibility in a fluctuating, natural environment. *Behavioural Ecology, 25*(6), 1374-1379.

Herborn, K. A., Macleod, R., Miles, W. T., Schofield, A. N., Alexander, L., & Arnold, K. E. (2010). Personality in captivity reflects personality in the wild. *Animal Behaviour, 79*, 835-843.

Higgins, P. (1999). Order Psittaciformes. In P. Higgins, & P. Higgins (Ed.), *Handbook of Australian, New Zealand and Antartic Birds; Vol. 4 Parrots to Dollarbirds* (Vol. 4, pp. 25-504). Melbourne, Australia: Oxford University Press.

Higgins, P. (1999a). Order Psittaciformes. In P. Higgins, & P. Higgins (Ed.), *Handbook of Australian, New Zealand and Antarctic Birds; Vol. 4 Parrots to Dollarbirds* (Vol. 4, pp. 25-504). Melbourne, Australia: Oxford University Press.

Holyoak, D. T. (1973). Comments on Taxaonomy and Relationships in the Parrot subfamilies Nestorinae, Loriinae and Platycercinae. *Emu, 73*, 157-176.

Ings, T. C., Raine, N. E., & Chittka, L. (2009). A population comparison of the strength and persistence of innate colour preference and learning speed in the bumble bee Bombus terrestris. *Behavioural Ecology and Sociobiology, 63*(8), 1207-1218.

Jones, R. B. (1977a). Open-field responses of domestic chickens in the presence or absence of familiar cues. *Behavioural Processes, 2*, 315-323.

Jones, R. B. (1977b). Repeated exposure of the domestic chick to a novel environment: Effects on behavioural responses. *Behavioural Processes, 2*, 163-173.

Jones, R. B. (1978). Activities of chicks in their home cages and in an open field. *British Poultry Science, 19*, 725-730.

Jordan, L. A., & Ryan, M. J. (2015). The sensory ecology of adaptive landscapes. *Biology Letters, 11*(5), 20141054.

Kasumyan, A. O., & DÖving, K. B. (2003). Taste preferences in fishes. *Fish and fisheries, 4*(4), 289-347.

Kearvell, J. C., & Briskie, J. V. (2003). Similarity of chatter calls between Orange-fronted Parakeet Cyanoramphus malherbi and Yellow-crowned Parakeet C. auriceps. *Ibis, 145*, 333-336.

Kelber, A., Vorobyev, M., & Osorio, D. (2003). Animal Colour Vision - Behavioural tests and Physiological concepts. *Biological Reviews, 78*(1), 21-118.

Kemp, M. (1977). Leonardo and the Visual Pigment. *Journal of the Warbug and Courtauld Institutes, 40*, 128-149.

Kim, L. C., Garner, J. P., & Millam, J. R. (2009). Preferences of Orange-winged Amazon parrots (Amazona amazonica) for cage enrichment devices. *Applied Animal Behaviour Science, 120*(3), 216-233.

Kitaysky, A. S., Wingfield, J. C., & Piatt, J. F. (1999). Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. *Functional Ecology, 13*(5), 577-584.

Koolhaas, J. M., Korte, S. m., de Boer , S. F., van der Vegt, B. J., Van Reenen , H., Hopster, H., . . . Blokhuis, H. J. (1999). Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews, 23*, 925-935.

Korte, S. M., Ruesink, W., & Blokhuis, H. J. (1999). Heart rate variability during manual restraint in chicks from high- and low-feather pecking lines of laying hens. *Phsyiology & Behavior, 65*, 649-652.

Kurvers, R. H., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S. E., Ydenberg, R. C., & Prins, H. H. (2009). Personality differences explain leadership in barnacle geese. *Animal Behaviour, 78*(2), 447-453.

Laule, G. E. (2003). Positive reinforcement training and environmental enrichment: enhancing animal wellbeing. *Journal of American Veterinary Medical Association, 223*(7), 969-973.

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

Lillendahl, K. (2000). Daily accumulation of body reserves under increased predation risk in captive greenfinches Carduelis chloris. *Ibis, 142*, 587-595.

Lilliendahl, K. (1998). Yellowhammers get fatter in the presence of predotors. *Animal Behaviour, 55*, 1335-1340.

Lunau, K. (1990). Colour saturation triggers innate reactions to flower signals: flower dummy experiments with bumblebees. *Journal of Comparative Physiology A, 166*(6), 827-834.

Lunau, K., Wacht, S., & Chittka, L. (1996). Colour choices of naive bumble bees and their implications for colour preception. *Journal of Comparative Physiology A, 178*(4), 477-489.

Maloney, R. F., & McLean, I. G. (1995). Historical and experimental learned predator recognition in free-living New-Zealand robins. *Animal Behaviour, 50*(5), 1193-1201.

Martin, G. R., Wilson, K. J., Wild, J. M., Parsons, J. M., Kubke, M. F., & Corfield, J. (2007). Kiwi forego vision in the guidance of their nocturnal activities. *Plos one, 2*(2), e198.

Mather , J. A., & Anderson, R. C. (1993). Personalities of octopuses (Octopus rubescens). *Journal of Comparative Psychology, 107*, 336-340.

McAdams, D. P., & Olson, B. D. (2010). Personality Development: Continuity and Change Over the Life Course. *Annual Review of Psychology, 61*, 517-542.

McCann, C. (1963). External features of the tongues of New Zealand Psittaciformes. *Notornis, 10*(7), 326-345.

McCann, C. (1964). Observations on the tongues of some New Zealand Birds. *Notornis, 11*(1), 36-45.

McCowan, L. S., Rollins, L. A., & Griffith, S. C. (2014). Personality in captivity: More exploratory males reproduce better in aviary conditions. *Behavioural Processes, 107*, 150-157.

Mcfarland, D. (2006). *A Dictionary of Animal Behaviour.* Oxford: OUP Oxford.

McLean, J. (1911). Bush Birds of New Zealamd Part 1. *Emu, 11*(1), 1-17.

McPhee, M. E. (2003). Effects of captivity on repsonse to a novel envrionment in oldfield mouse (Peromyscus poltonotus subgriseus). *International Journal of Comparative Psychology, 16*(2).

Medler, K., & Kinnamon, S. C. (2004). Transduction Mechanisms in Taste Cells. In S. Fringe, & J. Bradley, *Transduction Channels in Sensory Cells* (pp. 153-155). Germany: Wiley-VCH.

Mettke-Hofmann, C., Winkler, H., & Leisler, B. (2002). The significance of ecological factors for exploration and neophobia in parrots. *Ethology, 108*(3), 249-272.

Mettke-Hormann, C., Ebert, C., Schmidt, T., Steiger, S., & Stieb, S. (2005). Personality traits in resident and migratory warbler species. *Behaviour, 142*(9-10), 1357-1375.

Montgomerie, R., & Weatherhead, P. J. (1997). How robins find worms. *Animal Behaviour, 54*, 143-151.

Morand-Ferron, J., Cole, E. F., Rawles, J. E., & Quinn, J. L. (2011). Who are the innovators? A field experiment with 2 passerine species. *Behavioural Ecology, 114*, 405-412.

Newberry, R. C. (1995). Environmental enrichment, increasing the biologial relevance of captive environments. *Applied Animal Behaviour Science, 44*, 229-243.

O'Hara, M., Huber, L., & Gajdon, G. K. (2015). The advantage of objects over images in discrimination and reversal learning by kea, Nestor notabilis. *Animal Behaviour, 101*, 51-60.

O'Hara, M., Schwing, R., Federspiel, I., Gajdon, G. K., & Huber, L. (2016). Reasoning by exclusion in the kea (Nestor notabilis). *Animal cognition, 19*(5), 965-975.

Okanoya, K., & Dooling, R. J. (1987). Hearing in passerine and psittacine birds: a comparative study of absolute and masked auditory thresholds. *Journal of Comparative Physiology, 101*(1), 7-15.

Olsson, P., Lind, O., & Kelber, A. (2015). Bird colour vision: behavioural thresholds reveal receptor noise. *The Journal of Experimental Biology, 218*, 184-193.

Parrish, J. W., Ptacek, J. A., & Will, K. L. (1984). The detection of near-ultraviolet light by nonmigratory and migratory birds. *The Auk*, 53-58.

Pevsner, J. (2002). Leonardo da Vinci's contributions to neuroscience. *TRENDS in neuroscience, 25*(4), 217-220.

Price, E. (1970). Different reactivity of wild and semi-domestic deermice (Peromyscus maniculatus). *Animal Behaviour, 18*, 747-752.

Pumphrey, R. J. (1948). The sense organs of birds. *Ibis, 90*(2), 171-199.

Pumphrey, R. J. (1961). Part II. Sensory Organs: Hearing. In A. J. Marshall, *Biology and Comparative Physiology of Birds* (Vol. 2, pp. 69-86). New York & London: Academic Press.

Rahbek, C. (1993). Captive Breeding - a useful tool in the preservation of biodiversity? *Biodiversity and Conservation, 2*, 426-437.

Ramsey, G., Bastian, M. L., & van Schaik, C. (2007). Animal innovation defined and operationalized. *Bheavioral and Brain Sciences, 30*(4), 393-407.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews, 82*(2), 291-318.

Riska, B., Prout, T., & Turelli, M. (1989). Laboratory estimates of heritability and genetic correlations in nature. *Genetics, 4*(5), 865-871.

Roberts, L. J., Taylor, J., & Garcia de Leaniz, C. (2011). Environmental envrichment reduces maladaptive risk-taking in slamon reared for conservation. *Biological Conservation, 144*(7), 1972-1979.

Robertson, H. A., Dowding, J. E., Elliott, G. P., Hitchmough, R. A., Miskelly, C. M., O'Donnell, C. F., . . . Taylor, G. A. (2013). Consevation Status of New Zealand Birds, 2012. Wellington, New Zealand . Retrieved 02 12, 2017, from http://www.doc.govt.nz/Documents/science-and-technical/nztcs4entire.pdf

Roper, T. J. (2003). Olfactory discrimination in Yellow-backed Chattering Lories Lorius garrulus flavopalliatus: first demonstration of oflaction in Psittaciformes. *Ibis, 145*(4), 689-691.

Saito, N. (1980). Structure and Function of the Avian Ear. In A. N. Popper, & R. R. Fray, *Comparative Studies of Hearing in Vertebrates* (pp. 241-260). New York, USA: Springer.

Schacter, D., Gilbert, D., Wegner, D., & Hood, B. (2011). *Psycology.* Worth Publishing .

Schwartzkopff, J. (1955). On the hearing of birds. *The Auk*, 340-347.

Sih, A., & Bell, A. M. (2008). Insights for behavioural ecology from behavioural syndromes. *Advances in the Study of Behaviour, 38*, 227-281.

Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters, 15*(3), 278-289.

Stamps, J. A. (2007). Growth-mortality tradeoffs and 'personality traits' in animals. *Ecology Letters, 10*, 355-363.

Stamps, J., & Groothuis, T. G. (2010). The development of animal personality: relevance, concepts and perspectives. *Biological Reviews, 85*(2), 301-325.

Stiles, F. G. (1976). Taste Preferences, Colour Preferences and Flower Choice in Hummingbirds. *The Condor, 78*(1), 10-26.

Stöwe, M., & Kotrschal, K. (2007). Behavioural phenotypes may determine whether social context facilitates or delays novel object exploration in ravens (Corvus corax). *Journal of Ornithology, 148*(2), 179-184.

Suzuki, T. K. (2017). On the origin of Complex Adaptive Traits: Progress Since the Darwin Versus Mivart Debate. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*.

Sykes, J. B. (1982). The Concise Oxford Dictionary of Current English. Oxford: Oxford University press.

Terborgh, J., & Faaborg, J. (1973). Turnover and ecological release of the avifauna of Mona Island, Puerto Rico. *Auk, 90*, 190-197.

Triggs, S., & Daugherty, C. (1996). Conservation and genetics of New Zealand parakeets. *Bird Conservation International, 6*, 89-101.

van der Veen, I. T., & Sivars, L. E. (2000). Causes and consequences of mass loss upon predator encounter: fedding interruption, stress or fit-or-flight? *Functional Ecology, 14*, 638-644.

van Oers, K., de Jong, G., van Noordwjk, A. J., Kempenciers, B., & Drent, P. J. (2005). Contribution of genetics to the study of animal personalities: a review of case studies. *Behaviour, 142*, 9-10.

Vaquero-Alba, I., McGowan, A., Pincheira-Donoso, D., Evans, M. R., & Dall, S. R. (2016). A quantitative analysis of objective feather color assessment: Measurements in the Laboratory do not reflect true plumage color. *The Auk, 133*(3), 325-337.

Verbeek, M. E., Drent, P. J., & Wiepkema, P. R. (1994). Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour, 48*, 1113-1121.

Vorobyev, M., Osorio, D., Bennett, A. T., Marshal, N. J., & Cuthill, I. C. (1998). Tetrachromacy, oil droplets and bird plumage colour. *Journal of Comparative Physiology - A Sensory, Neural, and Behavioral Physiology, 183*, 621-633.

Warham, J., & Bell, B. (1979). The birds of Antipodes Island, New Zealand. *Notornis, 26*(2), 121-169.

Weathers, W. W., Buttemer, W. A., Hayworth, A. M., & Nagy, K. A. (1984). An Evaluation of Time-Budget Estimates of Daily Energy Expenditure in Birds. *The Auk, 101*(3), 459-472.

Webb, N. V., Famula, T. R., & Millam, J. R. (2010). The effect of rope colour, size and fray on environmental enrichment device interaction in male and female Orange-winged Amazon parrots (Amazona amazonica). *Applied Animal Behaviour Science, 124*(3), 149-156.

Wein, A., Gajdon, G. K., & Schwing, R. (2015). Picture-Object Recognition in Kea (Nestor notabilis). *Ethology, 121*(11), 1059-1070.

Wells, D. L. (2009). Sensory stimulation as environmental enrichment for captive animals: a review. *Applied Animal Behaviour, 118*, 1-11.

Wenzel, B. M., & Sieck, M. H. (1972). Olfactory Perception and Bulbar Electrical Activity in Several Avian Species. *Physiology and Behavior*, 287-293.

West, R., Tisdall, C., & Aviss, M. (1995, March). *Captive management plan antipodes island parakeet (Cyanoramphus unicolor).* Retrieved from Department of Conservation: http://www.doc.govt.nz/Documents/science-and-technical/TSOP07.pdf

Wilkie, E. S., Vissers, P. M., Debipriya, D. A., DeGrip, J. W., Bowmaker, K. J., & Hunt, M. D. (1998). The molecular basis for UV vision in birds: spectral characteristics, cDNA sequences and retianl localistion of the IV-sensitive visual pigment of the biderigar (Melopsittacus undulatus). *Biochemical Journal, 330*(1), 541-547.

Wilson, D. S., Clark, A. B., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution, 9*(11), 442-446.

Wilson, D. S., Coleman, K., Clark , A. B., & Biederman, L. (1993). Shy bold continuum in pumpkinseed sunfish (Lepomis gibbosus) - an ecological study of psychological trait. *Journal of Comparative Psycology, 107*, 250-260.

Wolf, L. L., Hainsworth, F. R., & Gill, F. B. (1975). Foraging Efficiencies and Time Budget in Nectar-Feeding Birds. *Ecology, 56*(1), 117-128.

Yeaton, R., & Cody, M. (1973). Competitive release in island song sparrow populations. *Theoretical Population Biology, 5*, 42-58.

Zhao, G. Q., Zhang, Y., Hoon, M. A., Chandrashekar, J., Erlenbach, I., Pyba, N. J., & Zuker, C. S. (2003). The Receptors for Mammalian Sweet and Umami Taste. *Cell, 115*, 255-266.