Investigating sex-specific crypsis as a driver of sexual dichromatism in titipounamu (*Acanthisitta chloris*)

Jessica K. Peart

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Abstract

While sexual selection is often the evolutionary force behind sexual dichromatism in birds, natural selection acting on one or both sexes can also drive sex differences in colouration. This can occur if males and females use different foraging habitats with different background environments, requiring sex-specific plumage colouration to be cryptic against their respective foraging backgrounds and thus reduce predation risk. Sexual dichromatism in titipounamu (*Acanthisitta chloris*) could be driven by sex-specific needs for crypsis against their respective foraging backgrounds; previous research found that the green males spend more time foraging in amongst leaves and small branches, whereas the brown females spend more time foraging on trunks. However, that research focused on a population in atypical, primary succession forest and only considered titipounamu colour from a human visual perspective. Green plumage might also be less cryptic than is often assumed due to its ultraviolet reflectance and signalling properties. To determine whether this crypsis hypothesis holds true for titipounamu in their typical habitat and from the visual perspective of their avian predators, I investigated 1) sex differences in titipounamu foraging behaviour in a complex, native forest; 2) compared titipounamu colour to their background environment using relevant visual perception models and calibrated digital photography; and 3) whether either sex was compensating for more conspicuous colour through increased anti-predation behaviours through focal bird nest observations. Despite finding some sex differences in where titipounamu forage, I found no differences in how likely either sex was to be observed foraging against green or brown backgrounds. I also found that neither sex was cryptically coloured in their natural habitat from an avian visual perspective and could be distinguished from their background environment. While I found some evidence that titipounamu are cryptically patterned, this did not differ between sexes nor background substrate. Lastly, neither sex displayed more anti-predation behaviours at the nest, suggesting that neither sex is compensating more than the other for conspicuous colouration. Thus, my results suggest

that it is unlikely that titipounamu sexual dichromatism is driven by the need to be cryptic against different background environments. Rather, it could be driven by various aspects of sexual selection. This thesis highlights the importance of studying cryptic colour from the perspective of potential predators and challenges assumptions about crypsis, sexual dichromatism and green colouration in birds.

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Preface

My city of residence and work, Auckland, went into two lockdowns during 2021 to slow the spread of COVID-19 throughout New Zealand. The first, in February, resulted in a field trip being delayed as I could not leave Auckland to visit my field site. The second lockdown, starting on the 17th of August, lasted for 107 days. This extended lockdown meant that I was unable to collect spectrophotometry samples from the museum, meaning I could not use any spectrophotometry data from my project (we were unable to procure a spectrophotometer to take into the field to measure live birds). It also meant that any further attempts to calibrate the ultraviolet camera were impossible.

Table of contents

Chapter 1

General introduction

1.1. The importance of colour for animal signalling

The role of colour in animal signalling has long since fascinated biologists, inspired by the incredible diversity of colouration, patterning and ornamentation found across the animal kingdom (Amundsen, 2000; Caro, 2017; Darwin, 1871; Wallace, 1868). Considerable research has been dedicated to understanding the evolution and function of colouration in animals, resulting in a wealth of hypotheses and case studies almost as diverse as animal colouration itself (Caro, 2017; Kirkpatrick et al., 1990; Selander, 1972; Shultz & Burns, 2017). This research has shown that one of the main functions of colouration is to allow for communication and signalling between individuals (Caro, 2005). More well-known examples include ways that animals use extravagant colours and patterns to increase their attractiveness to potential mates; for example, male peacocks (*Pavo cristatus*) with more elaborate and bright trains may be more attractive to females (Gadagkar, 2003). Colour can also be used an honest signal of quality to attract mates, as the brightness or hue of coloured patches is often influenced by factors such as health, genetics, or dominance. A study of multiple indices of individual health in the king penguin (*Aptenodytes patagonicus*) found that beak colouration and auricular patch size were honest signals for physiological qualities such as body condition, metabolic rate, immunity, and stress responses (Viblanc et al., 2016). Likewise, colour can also be used to deter rivals and enforce social hierarchies through warning displays and aggression. For example, conspicuous eye colour of large Trinidadian guppies (*Poecilia reticulata*) is used as honest signal of aggressive motivation towards smaller conspecifics (Heathcote et al., 2018). Other studies have found that colour can be used to communicate information about relatedness or compatibility between

individuals; the highly variable facial plumage of juvenile cliff swallows (*Petrochelidon pyrrhonota*) may allow parents to identify their offspring to feed after the post-fledging juveniles form large crèches with other unrelated birds (Johnson & Freedberg, 2014). Colour can also be used to signal information to potential predators; aposematism is a mechanism with which species can advertise their unpalatability or toxic qualities through bright and conspicuous colouration (Banci et al., 2020). Other species mimic the colour and pattern of aposematic species, whether they possess the same harmful traits as their model or not (Vane-Wright, 1980). This takes advantage of predators' interpretation of warning colouration and offers anti-predator benefits to the mimic (MacDougal & Stamp Dawkins, 1998; Shine et al., 2001). While some species use colour to deter or disorientate their predators (Espinosa & Cuthill, 2014), others use colour to avoid detection altogether (Endler & Greenwood, 1988; Hall et al., 2013; Troscianko et al., 2016). The need for concealment is an important evolutionary driver of animal colouration (Caro, 2005); camouflage is often selected for in prey species to reduce predation (Duarte et al., 2017; Ruiz-Rodríguez et al., 2013; Simpson et al., 2020), but also in predator species to allow them to track and ambush their prey (Pembury Smith & Ruxton, 2020). Background matching is a common adaptation in which the colour of a species closely resembles that of the environment they inhabit, making it challenging for them to be distinguished by predators or prey (Caro, 2005; Cuthill et al., 2005; Murali et al., 2021). For example, black-tailed gull (*Larus crassirostris*) eggs that most closely colour matched their nest background had the greatest chance of surviving to hatching compared to more contrasted eggs (Lee et al., 2010). A close pattern match of an animal to their background can also provide camouflage (Cuthill et al., 2005; Price et al., 2019a; Ramírez-Delgado & Cueva del Castillo, 2020). An example of cryptic patterning is disruptive colouration, which occurs when adjacent high contrast patches create the illusion of false edges on an animal's body, blending their form into their background (Cuthill et al., 2005; Espinosa & Cuthill, 2014; Stevens et al., 2006). For example, the bright yellow and brown banding on the orb web spider *Argiope keyserlingi* increases prey capture rates, concealing the spider through disruptive colouration (Herberstein et al., 2006). While these

examples have only touched on some of the proposed functions of animal colour, it is clear that colour has an important and diverse function in mediating interactions between animals, impacting both survival and reproductive fitness (Osorio & Vorobyev, 2008). Thus, colouration is an intriguing field in which to explore animal evolution and behaviour. Birds (Aves) are particularly interesting group in which to study colour as they have a vast and diverse array of colourful traits that are used for a myriad of different functions, often with fascinating evolutionary history (Amundsen, 2000; Stoddard & Prum, 2011).

1.2. How bird colour is produced

The colours of birds are diverse not only in appearance, but also in how they are created (Shawkey & D'Alba, 2017). Bird colour is typically produced through a combination of structural colour and pigmentation (Shawkey et al., 2009). Structural colouration is the term used to describe colour that is produced when nano-scale reflective tissues in bird feathers scatter light (Fu et al., 2016; Hill, 2006). The architecture of these nanostructures can be very diverse, producing a wide range of colours that vary depending on the arrangements of different materials (Srinivasarao, 1999). For example, amorphous assortments of air and keratin in feather barbs are responsible for producing blue and ultraviolet colours (Auber, 1957; Shawkey et al., 2009). Structural colouration is also often responsible for iridescence, as well as white and violet colour (Shawkey & D'Alba, 2017). Pigmentation is another widespread mechanism of bird colouration, responsible for a broad range of hues (Hill, 2006; Thomas et al., 2014). Pigments are deposited in feathers or skin and reflect only certain wavelengths depending on their underlying chemistry (Britton, 1995; Hill, 2006; Shawkey & D'Alba, 2017). Some pigments can be obtained through diet while others are produced endogenously (Hill, 2006). Melanin, which is also responsible for colour in human skin, provides black, brown, and yellow colours and is also involved in most bird patterns (Galván et al., 2017; Swan, 1974). Carotenoid-based colour is also common, formed by red, yellow,

and orange pigments that are incorporated into feathers or skin from the birds' diet. Some bird groups also have their own unique pigments (McGraw & Nogare, 2004; Negro et al., 2009; Rimington, 1939). Parrots, for example, produce their striking red, orange, and yellow plumage through a suite of unique pigments called psittacofulvins (Berg & Bennett, 2016). Combinations of structural colour, overlayed with various pigments, are responsible for many of the colours displayed by birds, particularly green colouration (Shawkey & D'Alba, 2017). However, the appearance of these colours can vary to receivers with different visual capabilities (Osorio & Vorobyev, 2008).

1.3. Colour vision in birds

The diverse range of colourful signals that birds use is reflected in their visual capabilities; birds have some of the most advanced colour vision in the animal kingdom (Hart, 2001; Kelber, 2019). Like humans, birds have three types of single cone through which to distinguish short, medium, and long wavelengths of light with the human visible light spectrum, between around 400 and 700nm. However, most birds also have a fourth shortwave sensitive single cone that allows them to see within the ultraviolet (UV) spectrum (Cuthill et al., 2000). This fourth photoreceptor occurs in two distinct classes: violet sensitive (VS), with a maximum absorbance (λ_{max}) of 402–426 nm and ultraviolet sensitive (UVS) with a λ_{max} of 355–380 nm (Ödeen & Håstad, 2013). This photoreceptor difference allows birds with UVS vision (including Psittaciformes and many Passeriformes) to be more sensitive to UV light than VS birds, especially as birds with VS vision (including many birds of prey) typically also have increased UV absorbance of the cornea and lens (Aidala et al., 2012; Carvalho et al., 2011; Lind et al., 2014). Additionally, bird cones also include an oil droplet typically pigmented with carotenoids, which can shift the peak sensitivities of the cone and may enhance colour vision (Vorobyev, 2003). Birds also have a double cone photoreceptor type, which may be used for colour discrimination, polarized light detection and luminance

detection (Günther et al., 2021; Pignatelli et al., 2010). Additional differences in visual acuity and eye positioning may also affect how colour and pattern is discriminated by birds (Kelber, 2019). Considering the vision of birds is important when studying colour, as viewing birds from a human perspective can misrepresent or overlook aspects of colouration that may have vital evolutionary or functional roles (Renoult et al., 2017). This may be particularly important for understanding colour that is selected through interactions with other birds, such as sexual dichromatism (Bennett et al., 1994).

1.4. Drivers of sexual dichromatism

Sexual dichromatism is a specific type of sexual dimorphism in which males and females display different colourations and patterns. These often extravagant differences in bird colouration between sex have fascinated biologists since Darwin, leading to significant debate and hypotheses about how this widespread phenomena could have evolved (Badyaev & Hill, 2003; Darwin, 1871; Kimball & Ligon, 1999; Martin & Badyaev, 1996; Matysioková et al., 2017; Wallace, 1868; Wallace, 1891). What makes sexual dichromatism so interesting is that for it to arise, different selection pressures must be acting on each sex within the same species (Badyaev & Hill, 2003). Theories surrounding the evolutionary drivers of sexual dichromatism vary, including combinations of sexual selection, social selection, and various forms of natural selection (Badyaev & Hill, 2003; Baker & Parker, 1979; Darwin, 1871; Kirkpatrick et al., 1990; Shultz & Burns, 2017; Wallace, 1868; Wallace, 1891).

1.4.1. Sexual selection

Sexual dichromatism is often driven by sexual selection, where traits that increase reproductive success are selected for through aiding in attracting or monopolising access to

the potential mates (Andersson & Simmons, 2006). As colour is often involved in signalling and mate choice, sexual selection often drives sex differences in colouration (Shultz & Burns, 2017; Soler & Moreno, 2012). While there are many examples of sexual selection in birds, one of the most prominent examples is the birds of paradise (Paradisaeidae), many species of which display exaggerated colourful traits in the males, while females are more muted by comparison (Irestedt et al., 2009). Sexual selection can drive sexual dichromatism as one sex, often the male, often experiences higher competition for mating opportunities than the other (Andersson & Simmons, 2006). Females tend to invest more in each reproductive event, as they have a limited number of gametes and offspring they can produce per season (Robert, 2017). Males often invest less in each reproductive bout, able to produce many less costly gametes and potentially mate with multiple females per season, making females the limiting sex in terms of reproduction (Selander, 1972). This inequality in investment means that females tend to be more selective with which males they mate with as they have limited opportunities to produce quality offspring. Thus, there is often strong selection for males that can display their quality or successfully attract females through certain traits, including colouration. However, sex roles can also be reversed (Amundsen, 2000; Tobias, Montgomerie & Lyon, 2012). Males may be choosy when selecting a female mate in species where males invest heavily in reproduction through parental care, or in breeding systems where males must produce highly competitive sperm or invest in mate guarding (Emlen & Wrege, 2004; Fryxell et al. 2019). For example, male wattled jacanas (*Jacana jacana*) provide most of the parental care for chicks which reduces their opportunities for further reproduction (Emlen & Wrege, 2004). Thus, females that are more competitive and attractive to males are selected for, resulting in female wattle jacanas being much larger than males, as well as displaying colourful facial ornamentation and wing spurs.

Intra- and inter-specific competition for ecological resources or access to the other sex seems to drive similar trait expression as sexual selection, such as costly signals, displays and aggressiveness (LeBas, 2006). As colour is often a signal of individual quality, social

selection can also drive sexual dichromatism if it acts upon the sexes differently. For example, only male house sparrows display a black bib on their breast and white bars on their wings (Bókony et al., 2006; Nakagawa et al., 2007). The size of the black bib signals the individual status or dominance rank, with birds with larger bibs having greater fighting and territory defence success. More conspicuous wing bars were also related to defence success (Bókony et al., 2006). Thus, male colouration may be used by house sparrows to assess whether to engage in or escalate an aggressive encounter with another male. Interestingly, there was little evidence that bib size was attractive to females, suggesting this male-male competition is enough to drive the sex difference in colour in this species (Nakagawa et al., 2007).

1.4.2. Natural selection

Animal colouration is driven by a trade-off between conspicuousness and crypsis; an individual must be able to signal conspecifics (conspicuousness), but also conceal itself from potential predators and prey (crypsis) (Gomez & Théry, 2007). Signalling through colour is common in birds, with colourful traits often sexually selected (Osorio & Vorobyev, 2008). However, bright colouration can also make birds more conspicuous to their predators (Ruiz-Rodríguez et al., 2013). Thus, cryptic colouration may also be selected for, in which animals are coloured or patterned in ways that reduce visibility to predators by increasing how closely they match their background environments (Caro, 2005). Some species balance this trade-off by being completely cryptically coloured and using other adaptations to signal to mates and competitors, such as vocalisations (Barreira & García, 2019; Hagelin & Jones, 2007). However, in some birds, it can result in a mix of traits that allow them to be simultaneously cryptic to their predators and conspicuous to their conspecifics. In an analysis of neotropical birds, countershading was common, with birds having lighter undersides and darker dorsal regions to blend in with the light levels projected from above

and below (Gomez & Théry, 2007; Ruxton et al., 2004; Speed et al., 2005). However, birds often had small patches of conspicuous colour that could be used to signal other individuals without reducing overall crypsis. These patches can be in ventral, wing or tail locations that could be hidden from potential predators (Gomez & Théry, 2007; Gruson et al., 2021), or around the face and breast which are easily visible to nearby conspecifics, but less so to predators searching from below or above (Delhey, 2020; Simpson et al., 2020). Taking advantage of differences in visual capabilities may be another strategy to balance this trade off. Many passerines can see shorter wavelengths within the ultraviolet spectrum than their avian predators (Bennett & Cuthill, 1994; Håstad et al., 2005). For example, a study of songbirds found that colourful plumage patches were much more conspicuous to other songbirds with UVS vision than they were to VS avian predators such as raptors and corvids (Håstad et al., 2005).

In contrast to Darwin's theory on sexual selection driving sexual dimorphism in birds (Darwin, 1871), Wallace proposed the "female-crypsis" hypothesis (Wallace, 1868; Wallace, 1891). He suggested that crypsis is often selected for in female birds as they typically invest more into nest incubation and feeding offspring, which would make them and the nest vulnerable to detection from predators without some form of camouflage (Götmark et al., 1997; Martin & Badyaev, 1996). In role reversed systems or systems where colour is not strongly sexually selected, crypsis can be selected for in males as well (Slagsvold, Dale & Kruszewicz, 1995). This hypothesis can potentially work in conjunction with sexual selection when only one sex contributes to parental care, with the nesting parent being selected to become more cryptic to reduce nest predation, while the other is selected to become more conspicuous to attract mates (Martin & Badyaev, 1996; Soler & Moreno, 2012). For example, breeding female chaffinches (*Fringilla coelebs*) spend more time provisioning their offspring than males, resulting in a higher risk of predation and selection for cryptic colouration (Götmark et al., 1997).

There is evidence to suggest that ecological differences between the sexes can also drive sexual dichromatism; if males and females display different behaviours or use different habitats, they may be placed under different selective pressures (Selander, 1966; Slatkin, 1984). If each sex is seen against different coloured backgrounds, different types of cryptic colouration could be selected for in each sex, resulting in sexual dichromatism. While this has not been well studied in birds, it has been demonstrated in other taxa such as lizards (Medina, Losos et al., 2017; Orton & McBrayer, 2018), snakes (Forsman, 1995), and insects (Forsman & Appelqvist, 1999; Ramírez-Delgado & Cueva del Castillo, 2020). For example, female *Sphenarium* grasshoppers display high background colour matching, while males have dark patterning that may act to disrupt their edges, making them harder to distinguish to predators (Ramírez-Delgado & Cueva del Castillo, 2020). This sexual dichromatism is likely driven by differing natural selection pressures in the different microhabitat each sex utilises. The male grasshoppers are highly mobile and search through a variety of background types to find females (Thornhill & Alcock, 1983). This behaviour may result in selection for disruptive colouration, a camouflage that tends to be effective across a wider range of environments (Murali et al., 2021; Stevens & Cuthill, 2006; Stevens et al., 2006b). Alternatively, sex differences in foraging behaviour can result in the trade-off between crypsis and conspicuous being balanced through sexual dichromatism. In *Eclectus* parrots, males are green and cryptic, whereas females are bright red and highly conspicuous (Heinsohn, 2008). Intense female-female competition for cavity nesting sites has driven social selection for brightly coloured red plumage in females that can signal quality (Heinsohn, Murphy & Legge, 2003). Meanwhile, males do all the foraging to feed their offspring, often roaming large distances that make them vulnerable to predation (Heinsohn, 2008). However, their green plumage may help them be cryptic in their environment (Heinsohn, 2008; Heinsohn et al., 2005). Females spend most of their time hidden in their cavity nests and are therefore less vulnerable to predation, allowing selection for their bright plumage despite the costs of conspicuousness (Heinsohn et al., 2003). Thus, both the

behaviours of each sex and their environment can influence what selective forces are acting upon colouration, and therefore drive sexual dichromatism.

1.5. The function of green colour in birds

Green colouration is often assumed to be cryptic, and in many cases green colour does help animals blend in with their background environment. For example, in a study of neotropical birds, canopy-dwelling species were more frequently displayed green plumage than lower-dwelling species to increase camouflage with the foliage (Gomez & Théry, 2007). However, evolution of green colouration is not always driven by selection to be cryptic, but instead green pigmentation can provide protection from bacteria or signal quality (Blount & McGraw, 2008; Grande et al., 2004; Griggio et al., 2009; Siefferman & Hill, 2005). Green colouration is often produced through structural blue colour combined with pigments such as carotenoids, and given carotenoids are only obtained through diet, the intensity of green colouration can therefore provide honest signals about the quality of a potential mate or rivals (Blount & McGraw, 2008; Pike et al., 2009). In parrots, psittacofulvin pigments overlaying blue structural colour are used to produce green rather than carotenoids (Berg & Bennett, 2016), but as blue structural colour has also been associated with individual quality (Andersson, 1999; Fitzpatrick, 1998; Siefferman & Hill, 2005), green colouration in parrots could still be providing an honest signal of health. This means green colouration may be driven by social or sexual selection, not just for cryptic colouration. For example, parasite load has been found to decrease carotenoid-pigmentation in greenfinches (*Carduelis chloris*), suggesting that green colour could be used to judge the health and immunocompetence of individuals (Saks et al., 2003). Green pigmentation has also been associated with protecting feathers from bacterial degradation; carotenoid-pigmented feathers, as well as green parakeet (*Aratinga acuticaudata*) feathers (colour produced by yellow psittacofulvin pigment over blue structural colour) were less degraded by *Bacillus licheniformis* than white or melanin-

pigmented feathers in an *in vitro* experiment (Grande et al., 2004). Green pigments and blue structural colour also often reflect in the ultraviolet spectrum; while green may appear cryptic to us, it may not be for animals that can see UV light (Badyaev & Hill, 2000). UV signals are likely important for signalling in birds such as in sexual displays (Griggio et al., 2009; Hausmann et al., 2003). For example, in the *Eclectus* parrots discussed above, the green males appear cryptic to their predators with limited UV vision, but the UV reflectance of their green plumage allows them to be conspicuous to females (Heinsohn, 2008). We should therefore be cautious about assuming that the role of green plumage is solely for crypsis; it is important to explore and interpret plumage colour function using the target species visual capabilities. However, there are very few studies on the sexual dichromatism where at least one sex is green. Therefore, this thesis addresses this major gap by investigating sexual dichromatism in a small, green, and sexually dichromatic forest bird, the titipounamu (*Acanthisitta chloris*).

1.6. Why study titipounamu?

The titipounamu (*Acanthisitta chloris*), also known as riflemen, is a sexually dimorphic, green and brown forest bird that is endemic to New Zealand (Hunt & McLean, 1993). There are two subspecies, North Island *A. c. granti* and South Island *A. c. chloris.* In both sub-species, males are smaller than females, with smaller hind claws and less decurved beaks (Hunt & McLean, 1993; Sherley, 1993). Males also have solid green dorsal plumage, whereas the females have a dorsal plumage mottled with brown and greenish yellow (Figure 1). The evolution of this sexual dichromatism in titipounamu is somewhat of a mystery. They are, therefore, an interesting species in which to explore the concepts of sexual dichromatism and its evolutionary drivers. Many of the hypotheses that attempt to explain sexual dichromatism seem like unreasonable explanations for this species due to certain elements of their biology, such as their biparental care and cooperative breeding system, as well as

their cavity nesting traits (Sherley, 1990; Sherley, 1994; Sherley, 1990a). Interestingly, titipounamu are basal passerines, so may provide insights into the evolution of other birds (Barker et al., 2002).

Figure 1: North Island titipounamu (*Acanthisitta chloris granti*), showing the sex differences in plumage colouration.

1.6.1. Titipounamu biology

Titipounamu are New Zealand's smallest native birds, weighing between 5.5 and 7g (Sherley 1993). They display sexual dimorphism, with females being larger than males (Hunt & McLean 1993; Sherley 1994). This is thought to relate to the energetic needs of thermoregulation and egg production in females (Lill 1991; Sherley 1993). Females also have larger hind claws and more decurved bills than males, which could be related to differences in foraging environments between males and females (Hunt & McLean 1993); the females' large hind claws and decurved beak may allow them to forage more efficiently on trunks, while the smaller males may be more efficient in amongst small branches and leaves. Despite the sexually dichromatic dorsal plumages, both sexes have white ventral colouration. Carotenoid pigments have been found to contribute to their colouration (Thomas

et al., 2014). The plumage of both sexes has reflectance peaks in the ultraviolet spectrum (Withers, 2013).

Titipounamu are insectivores, feeding on a wide variety of invertebrates including beetles (Coleoptera) and moths (Lepidoptera) in both larval and adult stages, as well as arachnids (Higgins et al., 2001). They demonstrate a spiralling behaviour while foraging, starting at the base of tree trunks, and spiralling upwards to forage on insects on the trunk. However, they also glean insects from foliage. Previous work has found that males and females forage in different parts of the forest during the breeding season, with males spending more time foraging in the canopy amongst leaves and females spending more time on tree trunks (Hunt & McLean, 1993). Non-breeding adults spend a significant proportion of time in close proximity to each other while foraging. Titipounamu tend to stay within relatively small but exclusive home ranges, although they do not display much territorial behaviour, so these territories appear to be maintained through mutual avoidance (Cameron, 1990; Sherley, 1985).

Titipounamu are monogamous with almost no extra-pair paternity and display cooperative breeding at some nests (Preston et al., 2013). They also tend to live in kin neighbourhoods (Preston, Briskie & Hatchwell, 2016). Adult birds from previous clutches contribute to feeding of offspring, and sometimes unrelated birds will also contribute (Sherley 1993; Sherley 1994). Both parents contribute significantly to the care of young (Sherley, 1993). Males do most of the nest building (Sherley, 1994). Both parents will incubate eggs and feed young, but males contribute more than half of the feeding of chicks and fledglings. Titipounamu typically nest in enclosed cavities in trunks and branches of trees, but have relatively flexible nesting patterns, choosing to nest in other enclosed areas, such as nest boxes and tree fern skirts (Higgins et al., 2001; Moran et al., 2019; Sherley, 1985). As most of the native predators of titipounamu are avian species that rely mostly on vision to locate prey (Higgins et al., 2001), being hidden from sight in cavities while nesting is likely an effective strategy to reduce nest predation (Martin, Thomas, & Li, 1992), making Wallace's "female nest crypsis"

hypothesis unlikely (Wallace, 1868; Wallace, 1891). The high parental investment by males also violates the assumption of Wallace's hypothesis that females are providing most of the parental care. Because males spend so much time at the nest, we would expect them to be similarly coloured to females if Wallace's hypothesis was relevant to this species. Instead, they are not only differently coloured to females, but are potentially contrasted to the background colour of their nests while visiting which may make them visible to predators while at the nest. Hunt and McLean (1993) argue that sexual selection is also an unlikely cause of sex differences in colouration because titipounamu are monogamous, not particularly territorial or aggressive, and males are smaller than females (Cameron, 1990; Sherley, 1993). While sexual selection can drive sexual dichromatism in monogamous species, it is often less exaggerated (Dunn, Whittingham, & Pitcher, 2001; Kirkpatrick, Price, & Arnold, 1990).

1.6.2. Could sex-specific crypsis have driven titipounamu sexual dichromatism?

Previous research implied that titipounamu colour differences could be linked to crypsis (Hunt & McLean, 1993). Hunt and McLean (1993) found that titipounamu had different foraging niches during the breeding season when energy demand was high. Males (green) spent more time against green foliage backgrounds, whereas females (brown) spent more time foraging against brown tree trunks. Thus, these results suggest that because each sex matched their respective foraging environment, their sexual dichromatism could be driven by the need to be cryptic against their different foraging backgrounds. However, this hypothesis has some limitations. Firstly, Hunt and McLean's (1993) foraging and nesting observations of titipounamu were only done in a primary succession kānuka (*Kunzea* spp. complex) forest where birds were using artificial nest boxes. This environment and the behaviours of birds within it are unlikely to be representative of the complex native forest and natural nesting

habits with which titipounamu have evolved. Secondly, to identify whether titipounamu matched their background, they compared feathers to colour charts and made judgements based solely on human visual sensitivities. This is problematic as birds have different visual sensitivities to humans, including a single-cone photoreceptor that allows them to see in the ultraviolet range (Hart & Hunt, 2007). Titipounamu plumage has been found to have some UV reflectance (Withers, 2013), which could influence how cryptic they appear to other birds. As all of the predators that titipounamu evolved alongside are avian species who may see parts of the UV spectrum (Ödeen & Håstad, 2013), we cannot make conclusions about titipounamu colouration and how they are perceived by predators without factoring in the differences between avian and human visual systems.

Differences in foraging habitat were also only found in the breeding season in Hunt & McLean's (1993) study, which seems unusual if colour differences are driven by a need to be cryptic. Even if each sex is cryptic while foraging on different substrates, males would become highly conspicuous when feeding chicks at tree trunk nests (Higgins et al., 2001; Moran et al., 2019; Sherley, 1985). If crypsis is selected for in titipounamu to avoid predation, drawing attention to the nest seems counterintuitive as higher activity levels around nests has been linked to increase predation risk (Martin et al., 2000; Matysiokova & Remes, 2018; Skutch, 1949). Crypsis is also often selected for in female birds that spend a lot of time on the nest incubating eggs and chicks, as this is a vulnerable time for the female and the offspring (Martin & Badyaev, 1996). However, since titipounamu are cavity nesters, making them challenging to see while incubating, it seems unlikely that crypsis would be selected for to camouflage birds while on the nest (Sherley, 1994). These factors lead us to challenge the idea that titipounamu colouration is driven by a need to be cryptic against different backgrounds.

The ambiguity surrounding titipounamu colouration makes them an interesting species in which to study potential drivers of sexual dichromatism. Additionally, understanding the function of the green colouration in males may also contribute to challenging the assumption

that green colouration is always cryptic. To start to address the question of what drives the sexual dichromatism of titipounamu, this thesis aims to test the hypothesis that titipounamu sexual dichromatism is driven by the need for crypsis against the different foraging backgrounds of each sex. To achieve this, I will need to conduct a more thorough analysis of how closely titipounamu plumage colour matches with their background.

1.7.1 How can we measure bird colour?

To explore the drivers of sexual dichromatism, we must be able to quantify bird colour in a way that is reliable, repeatable, and accurate (Renoult et al., 2017). Additionally, any analysis needs to consider that bird vision differs significantly from our own. Considering the visual capabilities of birds is often important as the perception of conspecifics, competitors and predators can influence the evolution and function of different colourations (Bennett et al., 1994; Osorio & Vorobyev, 2008).

Colour chart systems were adopted by earlier researchers to make comparisons between different colours and categorise them (Hill, 2006; Villafuerte & Negro, 1998). This was an affordable and accessible way to measure colour but relied completely on subjective conclusions based on human vision. As the evidence for UV vision in birds started to grow, the use of this methodology was largely rejected in favour for an approach that could capture the full range of avian vision: spectrometric colour quantification, now the most standard tool in the study of colour (Johnsen, 2016; Yang et al., 2021; Zuk & Decruyenaere, 1994). Equipment such as spectrophotometers allow for reliable measurements of reflectance independent of lighting conditions or observer bias across the entire avian visual spectrum (Tella et al., 1998). Spectrophotometry requires a spectrometer, a light source and a probe (Hill, 2006). Light is directed from the light source down a probe onto the target area. The wavelengths that are reflected up the probe are measured by the spectrometer and recorded as spectral data. Analysing these reflectance measurements can be fairly simple with certain

software, including modelling the colour through an avian visual system (Maia et al., 2019). However, spectrophotometers can be expensive, inaccessible and cannot always be taken into the field (Hill, 2006). Measuring fine scale colours or patterns can also be quite difficult with a spectrophotometer probe, particularly around sensitive areas such as the eyes and face. While spectrophotometry is a practical and objective methodology overall, there are some contexts in which a different approach could be useful (Yang et al., 2021).

A more recent methodology for measuring colour is through calibrated digital photography (Johnsen, 2016; Troscianko et al., 2015; Yang et al., 2021). This requires using various image analysis software to extract colour data from standardized images (van de Berg et al., 2020). Standards of known reflectance are necessary to include in each image frame to allow for calibration of the image and the camera (Bergman & Beehner, 2008; Stevens et al., 2007). This is necessary as cameras vary in how sensitive they are to each wavelength of light and are often designed to produce images that are appealing to us, rather than images that are colour accurate to real life. The lighting environment and camera settings must also be kept consistent across the images to remove potential variation in colour (Troscianko et al., 2015). Images can then be calibrated using image analysis software, such as micaToolbox and QCPA framework (van de Berg et al., 2020), but other options include various R packages and the MATLAB computing platform (see Cadena et al., 2018, Chan et al., 2019 and Maia et al., 2019 for examples). The colour analyses available for images are diverse but include chromatic and achromatic colour comparison and pattern analyses (van de Berg et al., 2020). To account for the vision of the receiver or target species in colour analyses, it is possible to create species-specific visual models through which you can determine colour differentiation potential for different species. To do this for birds, you need to know the species' ocular media transmission (what wavelengths can pass through the lens and cornea), the absorption of the oil droplet pigments and the spectral sensitivities of the birds' photoreceptors, as well as the ratio of each type of photoreceptor arranged on the retina (Hart, 2002; Höglund et al., 2019; Lind et al., 2013). It is also valuable to know the

visual acuity of the species to account for the distance that the colour would be viewed from (Caves et al., 2018). This information has only been acquired for a handful of species, and often model species are selected as a proxy for the target species in colour analyses (Marshall & Stevens, 2014; Marshall et al., 2016).

A challenge of the photography method is that cameras typically function within the human visible spectrum to cater for our trichromatic vision. However, we know that many other animal groups have different visual capabilities compared to humans, including birds (Bennett & Cuthill, 1994). Therefore, if we are studying colouration within the context of signalling or camouflage, we must consider the visual capacity of the receiver species if we are to understand how those colourations are biologically important (Bennett et al., 1994; Osorio & Vorobyev, 2008). To model any animal with UV vision, you must have a camera that can take images within the ultraviolet spectrum (Troscianko et al., 2015). Thus, UV photography is often an important aspect to include in studies using digital photography. This can be achieved with a camera modified to capture light across the human visible and ultraviolet spectrums. Typically, two photographs are taken of a subject; one using a filter that only lets in the light from human visible spectrum, and another using a filter that allows only the ultraviolet wavelengths to be captured. These two images can then be combined and analysed using image analysis software to measure colour across the entire visual spectrum of the target species (van de Berg et al., 2020).

Overall, photography provides an accessible, non-invasive way of measuring animal colour, while also allowing for holistic colour and pattern sampling (van de Berg et al., 2020; Yang et al., 2021). Images also allow for new ways to incorporate pattern size and shape into colour analyses. Photography can also help to achieve direct comparisons of animals to the environment they are photographed in (Stevens et al., 2007). While this methodology may not be as well established as spectrophotometry, new resources and literature are increasingly being published (van de Berg et al., 2020; Cadena et al., 2018; Chan et al.,

2019; Maia et al., 2019). Thus, I intend to use photography to study titipounamu sexual dichromatism and model their colour from the perspective of their predators.

1.8. Aims and overview

I aim to investigate whether the sexual dichromatism in titipounamu could be driven by a need to be cryptic in differing foraging environments. If crypsis were driving sexual dichromatism, I would expect to see that 1) there are differences in how each sex uses their forest habitat; 2) the plumage of each sex matches the colours or pattern of the environment they are using; and 3) that more conspicuous birds might modify their behaviour during periods of higher predation risk. To investigate whether titipounamu fulfil these conditions, I address three main questions:

1. Where do male and female birds spend their time foraging? Do they spend more time against backgrounds that they contrast with or match?

2. Are titipounamu cryptic? How well does the plumage of birds match the various types of background they interact with within a rich natural environment?

3. Do we see compensatory anti-predator behaviours at the nest in birds that are more conspicuous? Do birds that are more conspicuous (or in more conspicuous places) spend more time being vigilant against predators at the nest?

Chapter 2 focuses on the second question, exploring titipounamu foraging behaviours to identify any sex differences in where birds forage and the colour of backgrounds that they forage against. I predict that males and females will forage on different substrates and perch types as found in Hunt and McLean (1993). Females, with their large hind claws and decurved beaks, are likely to be slightly better adapted for foraging on vertical surfaces and probing under bark than males, and therefore I expect to observe them more frequently on trunks than males. Males, on the other hand, may forage more efficiently on small branches

in amongst leaves due their smaller size and hind claws. Given these perch differences, I predict that there will be significant differences in general background colour. Females spend more time against trunks and may therefore most often be seen against brown backgrounds. Males spend more time in amongst foliage and may therefore be seen more often against green backgrounds.

Chapter 3 addresses the first question through an in-depth analysis of titipounamu colour and how closely it matches with their background colours from an avian visual perspective, using digital imaging. I predict that females will be a closer match to their background than males. Potentially, the sexual dichromatism of titipounamu is driven by selection on specifically females to become more cryptic. As they are slightly larger and slower while producing eggs than males, natural selection may have driven them to become more camouflaged. Foraging on trunks may also leave females more exposed than males, who may be more challenging for a predator to locate while foraging amongst leaves. Thus, I expect that females are a close colour and pattern match to their backgrounds when modelled under an avian predator visual system, whereas males may be less closely matched due to reduced need for crypsis and potentially sexual selection. I also predict that female colour will match the colour of trunks and male colour will match green foliage colours, given previous work found that these are the foraging habitats each sex uses most often (Hunt & McLean, 1993).

In Chapter 4, I examine titipounamu nest behaviour to distinguish any sex differences that may indicate either sex is compensating for their potentially more conspicuous colouration. I originally predicted that males would be more conspicuous at cavity nests than females as their bright green dorsal plumage appears to contrast more with the typically brown nest substrates than female plumage does. However, Chapter 3 found that yellow-brown female plumage was more conspicuously coloured than males against green, but not brown backgrounds. Therefore, it is unclear which sex, if either, is more conspicuous at the nest. I predict that if one sex is more conspicuous, (Martin, Scott, & Menge, 2000; Matysiokova &

Remes, 2018; Skutch, 1949) we may expect to see this sex adopting some sort of anti-predation behaviour to compensate for their increased visibility to predators, as nest predation often increases with parental visibility around the nest (Martin et al., 2000; Matysiokova & Remes, 2018; Skutch, 1949). This could include increased vigilance before and after entering the nest, or through reducing the time they spend visible at the nest.

Finally, in the general discussion I synthesise the findings of these chapters and discuss what they mean in context of the evolution of titipounamu colour and in a more general sense, the evolution of green plumage, sexual dichromatism and how colouration can influence behaviours based on insights from this basal passerine.

This is a thesis by publication, so each data chapter is written as a standalone paper. Thus, there is some overlap and repetition of ideas across chapters to ensure they can be understood in isolation.

Chapter 2

Sex differences in foraging behaviours

2.1. Abstract

While sexual selection is often the evolutionary force behind sexual dichromatism in birds, natural selection acting on one or both sexes can also drive sex differences in colour. This can occur if males and females use different foraging habitats with different background environments, requiring different plumage colouration to be cryptic against their respective foraging backgrounds and thus reduce predation risk. Sexual dichromatism in titipounamu (*Acanthisitta chloris*) could be driven by differing needs for crypsis against their respective foraging backgrounds; previous work found that the green males spend more time foraging in amongst leaves and small branches, whereas the brown females spend more time foraging on trunks. However, that research focused on the South Island sub-species, outside of their typical mature, native forest habitat and did not consider the background colour that each sex was seen against while foraging. Thus, I aimed to provide a more accurate assessment of whether there are sex differences in titipounamu foraging behaviours using focal animal foraging observations in a complex, diverse forest habitat and taking consideration of the background colour focal birds are found against. My results demonstrate some support for sex differences in the choice of perch type within a complex forest, however I found no difference between the sexes in terms of the background colour preferentially used by titipounamu. This result suggests that, despite differences in perch use, titipounamu do not forage against backgrounds that closely match their colouration. This calls into question the assumption that crypsis-driven foraging variations are driving the evolution of sexual dichromatism in titipounamu.

2.2. Introduction

Sexual selection has often been considered the primary explanation for sexually dimorphic traits (Hedrick & Temeles, 1989; Li et al., 2021; Shine, 1989). Darwin's sexual selection theory suggested that female mate choice can drive ornamentation of males and may explain the presence of exaggerated traits in males of some species (Darwin, 1871). There is considerable support for sexual dichromatism being driven by sexual selection (Bell & Zamudio, 2012; Kimball & Ligon, 1999), with countless examples of species where one sex has extravagant colouration and ornamentation linked to mate choice, such as the diverse colours exhibited by birds of paradise (Paradisaeidae) (Irestedt et al., 2009). However, other studies emphasise the influence of natural selection (Badyaev & Hill, 2003). Wallace (1891) proposed that sexual dichromatism can be driven by natural selection acting on females to become more cryptic; increased cryptic colouration could reduce the predation risk for females during incubation and chick rearing. For example, breeding female chaffinches (*Fringilla coelebs*) spend more time provisioning their offspring than males, resulting in a higher risk of predation and selection for cryptic colouration (Götmark et al., 1997). There is considerable support for both hypotheses across different species (Drury & Burroughs, 2016; Matysioková et al., 2017; Shultz & Burns, 2017; Simpson et al., 2020). Often both mechanisms can occur in the same species or same sex at once (Delhey et al., 2017; Selander, 1972), with cryptic colouration being selected for by predation pressures, with patches of more conspicuous colouration being driven by sexual selection (Gomez & Théry, 2007; Simpson et al., 2020). For example, in ground-nesting North American wood warblers (Parulidae) males have conspicuously coloured under-bodies that may be sexually selected, but cryptic dorsal colour to conceal them from predators above (Simpson et al., 2020)

Selection for crypsis can act solely upon the female to reduce risk of predation at the nest, driving sexual dichromatism (Wallace, 1891). In species where females do most of the nest care, natural selection can act on females to increase their camouflage (Götmark et al., 1997; Soler & Moreno, 2012). This is not, however, the only way that crypsis or natural

selection can drive sexual dichromatism. In species where the males and females use different habitats, natural selection for crypsis may drive divergence between the sexes based on the need to match their respective backgrounds. This explanation for sexual dichromatism has yet to be explored in birds but has been found in other taxonomic groups such as lizards (Medina et al., 2017; Orton & McBrayer, 2018), snakes (Forsman, 1995), and insects (Forsman & Appelqvist, 1999; Ramírez-Delgado & Cueva del Castillo, 2020). Each sex of a species may also display different types of cryptic colouration. Male and female *Sphenarium* grasshoppers appear to utilise different cryptic strategies; females display high background colour matching, while males show more disruptive colouration but less background matching (Ramírez-Delgado & Cueva del Castillo, 2020). This sexual dichromatism is likely driven by differing natural selection pressures in the different microhabitat each sex utilises. The male grasshoppers also range widely in their search for females to mate with (Thornhill & Alcock, 1983), resulting in selection for a camouflage that is effective across a wider range of environments than females (Stevens & Cuthill, 2006; Stevens et al., 2006). Therefore, both the environment and behaviours of each sex can influence the selective forces acting upon colouration, and thus drive sexual dichromatism.

A more subtle sexual dichromatism can occur in primarily 'forest' green birds, such as titipounamu (*Acanthisitta chloris*), a small forest bird endemic to New Zealand. Males and females have distinct differences between their dorsal plumage; males are solid green while females display a mottled yellow-brown pattern (Hunt & McLean, 1993), and these subtle differences make them an interesting model for exploring crypsis as a driver of sexual dichromatism. Green and brown colour as seen in titipounamu is often assumed to be cryptic but can depend what environments the subject is using; in a forest, for example, the background colour is a complex mosaic and will change depending on where the bird is foraging (Gomez & Théry, 2007). Thus, exploring crypsis in a green and brown forest bird may reveal the relative influences impacting the evolution of more subtle forms of sexual dichromatism. Titipounamu are a monogamous species who are also facultative cooperative

breeders, with biparental care and no extra pair paternity (Preston et al., 2013). Males do most of the nest building, but both sexes invest in raising chicks and incubating, although males often incubate for longer and feed chicks more frequently (Sherley, 1990; Sherley, 1994). They also use cavity nests, reducing their visibility to predators while on the nest. Thus, Wallace's "female nest crypsis" hypothesis does not seem a suitable explanation for the sexual dichromatism of titipounamu (Wallace, 1891). While sexual selection does occur in monogamous species, it occurs less often and typically results in less pronounced traits than in other breeding systems (Dunn et al., 2001; Kirkpatrick et al., 1990). Therefore, the evolutionary drivers of titipounamu sexual dichromatism are not clear.

Despite the interesting conundrum this species poses, titipounamu colour has been the subject of very little research. Hunt and McLean (1993) found evidence of foraging niche divergence between male and female titipounamu, which they suggested was linked to their sexual dimorphism. Females, who have larger hind claws and body size, and more decurved beaks than males, were found to mostly forage on trunks, whereas males spent more time higher up in the canopy on small branches, probing at leaves. Plumage comparisons between leaves and bark using Munsell Chroma measures suggested that males were a closer colour match to the leaves within this particular forest type, and females a closer match to bark (Hunt & McLean 1993). These results could imply that the sexual dichromatism seen in titipounamu is potentially driven by their need to be camouflaged against different backgrounds while foraging. The green plumage of males may help them be cryptic against the canopy they spend the most time foraging in, while the mottled yellow-brown of the females may increase their camouflage against the brown trunks they forage upon. However, some of the methodologies Hunt and McLean (1993) used and certain aspects of titipounamu life history challenge this idea of crypsis driving titipounamu dichromatism. The study site used by Hunt & McLean (1993), a primary successional kānuka (*Kunzea* spp. complex) stand, is not representative of the complex, heterogenous

forests titipounamu populations are typically found in across both the North and South Islands of New Zealand. Likewise, the study focused on birds breeding in nest boxes, thus the birds' behaviours may not reflect typical populations breeding in natural nests. The difference in foraging was also only found in the breeding season, which would suggest that outside of the breeding season birds are not closely matching their backgrounds; permanent plumage differences may not be selected for if only needed for part of the year. Additionally, the high level of male parental care would lead to the green males being seen often against the brown substrates that they use to nest in, such as trunks, branches and tree fern skirts; this would be counterintuitive if male colour is selected to be cryptic, as increased visibility at the nest may increase nest predation.

The aim of this chapter is to build on previous research by investigating whether foraging niche divergence occurs in titipounamu in a wild, native population in a complex forest environment. If crypsis is driving sexual dichromatism in titipounamu, I expect to find differences in habitat use between males and females. Birds should also be foraging more often against background substrates that match their plumage colours: males primarily against green backgrounds such as leaves and moss, and females against brown backgrounds, such as tree trunks, branches and leaf litter. Furthermore, I investigated whether these differences persisted across the breeding and non-breeding seasons. Previous work suggested that titipounamu may only display foraging differences while breeding to reflect the need for increased caloric influx during this season; outside the breeding season, birds may have more time to be alert and also spend more time foraging in pairs, thus increasing the chance of predator detection and reducing the need for crypsis (Hunt & McLean, 1993). However, I predict that given their plumage colouration is consistent throughout the year, we should also expect to see foraging differences persisting across seasons.

2.3. Methods

2.3.1. Study species

Titipounamu are a small (5.5-7g), insectivorous wren species endemic to New Zealand with two subspecies, the North Island titipounamu (*A. c. granti*) and the South Island titipounamu (*A. c. chloris*) (Sherley, 1993). Males and females are sexually dimorphic, having different morphological and chromatic features. Females are slightly larger than males, have larger hind claws and a more decurved beak (Hunt & McLean, 1993). Males and females are easily distinguished by their distinct dorsal plumages (Figure 1). Males have solid, bright green dorsal plumage across the crown, mantle and extending onto the upper wing and tail coverts. Females have a dark brown dorsal plumage, with each feather being tipped with yellow-green colour, creating a mottled or striped effect. This distinct plumage also extends across the crown, mantle and upper wing and tail coverts.

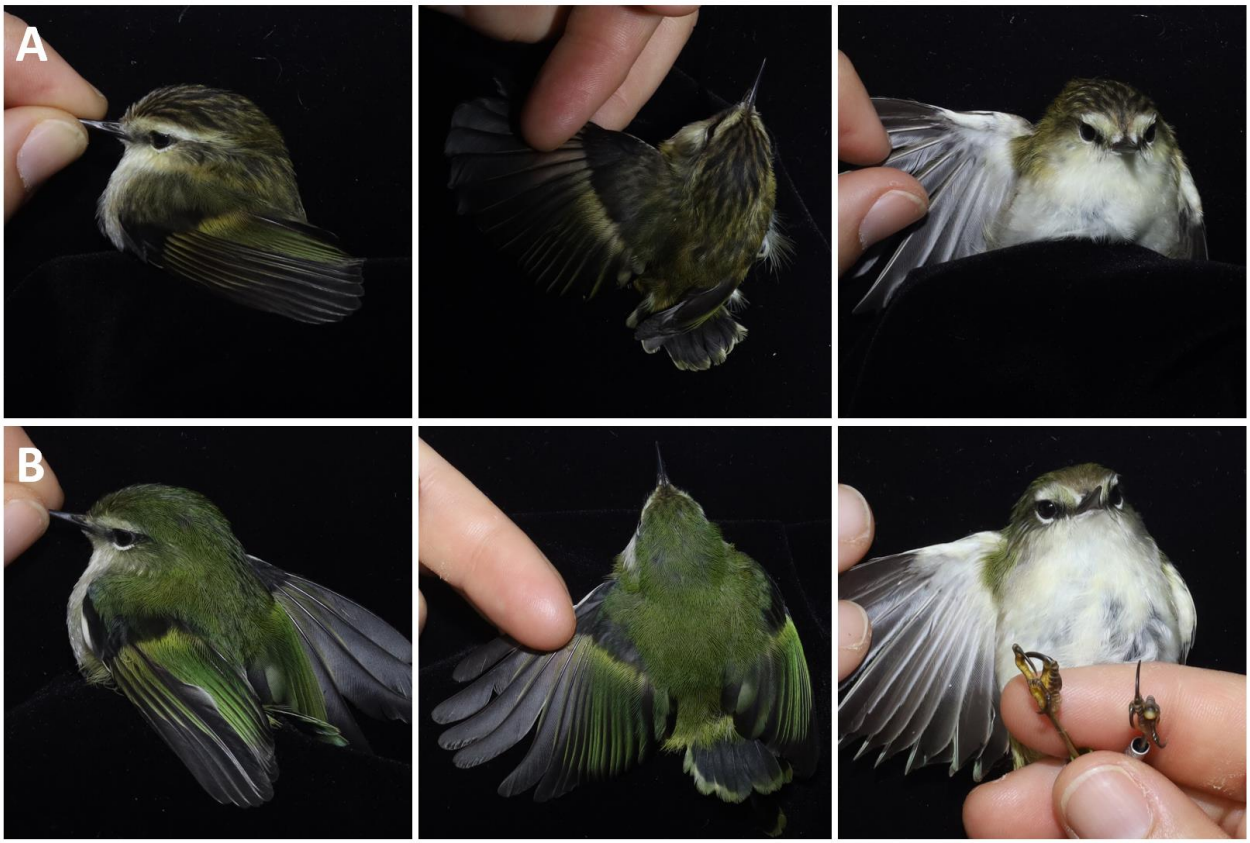


Figure 1: Lateral, dorsal, and ventral views of North Island titipounamu or rifleman (*Acanthisitta chloris granti*). A) female colouration, distinguished by the yellow-green dorsal plumage mottled with brown. B) male colouration, distinguished by the solid green dorsal plumage.

Titipounamu are found in a range of forest habitat types including coastal broadleaf forests, high altitude podocarp forest, mature complex inland forests and regenerating native bush (Higgins et al., 2001). Titipounamu form monogamous pair bonds and spend most of their time foraging in close proximity to their partner within small, exclusive home ranges (Cameron, 1990). They hunt a variety of small invertebrates, particularly beetles (Coleoptera) and moths (Lepidoptera) in both larval and adult stages, as well as spiders (Araneae) (Higgins et al., 2001). They hunt mostly by gleaning from or probing into substrates, but occasionally on the wing. While foraging, titipounamu often adopt a 'spiral' behaviour, where they will start at the base of a trunk or branch, and slowly spiral up and across the limb probing and gleaning insects from the surface or under the bark (Hunt & McLean, 1993). They will also forage in leaf litter or coarse woody debris on the ground, as well as in amongst leaves and mossy surfaces (Higgins et al., 2001). Females typically spend more time foraging on trunks than males, while males spend more time on small branches and leaves (Hunt & McLean, 1993). Titipounamu are also often identified and located by a constant wing-flicking motion they perform while foraging.

Titipounamu have a variety of potential native and introduced predators. Native avian raptors such as moreporks/ruru (*Ninox novaeseelandiae*), New Zealand falcon/kārearea (*Falco novaeseelandiae*), Australasian swamp harriers/kāhu (*Circus approximans*) as well as sacred kingfishers/kōtare (*Todiramphus sanctus*) are all likely to be current predators of titipounamu (Higgins et al., 2001). Likewise, long-tailed cuckoo/koekoeā (*Urodynamis taitensis*) have been found to predate chicks at titipounamu nests (Moran et al., 2019). Other extinct native predators could include the New Zealand crow (*Corvus antipodum*), the laughing owl (*Sceloglaux albifacies*) and potentially some reptile species, particularly at the nest. Alongside native predators, a range of introduced mammalian species likely also

predate titipounamu, such as cats (*Felis catus*), mice (*Mus musculus)*, rats (*Rattus* spp.), stoats (*Mustela erminea*), ferrets (*Mustela furo*), and possums (*Trichosurus vulpecula*).

Titipounamu are small and relatively poor fliers, resulting in limited dispersal ability. Previous work on the North Island subspecies has found that they have significant genetic differences across populations, with evidence of gene flow restrictions between geographic regions linking to both geological and climate events (Withers et al., 2021). Population differences in characteristics such as size, vocalisations and plumage colour have also been identified in the North Island subspecies (Withers, 2013).

2.3.2. Study site

All field work was conducted on a wild titipounamu population at Boundary Stream Mainland Island (Figure 2) in the Maungaharuru Ranges, North Island, New Zealand (Department of Conservation, 2021). The Boundary Stream Mainland Island reserve was established in 1996, with extensive ongoing pest management alongside efforts to promote improvement of native flora and fauna populations (Department of Conservation, 2021). The reserve covers around 800 ha, ranging from 300m to 950m a.s.l. Vegetation varies throughout the reserve, moving through mature red (*Nothofagus fusca*) and black beech forest (*Fuscospora solandri*), dense mixed broadleaf-podocarp habitat to large stands of kāmahi (*Weinmannia racemosa*) and rewarewa (*Knightia excelsa*). Densities of introduced mammalian predators are low at this field site, but include cats, mice, rats, stoats, ferrets and possums. Native

avian predators are also present at the site such as ruru, kārearea, kāhu and koekoeā (personal observation). Public walking tracks and trapping/bait lines throughout the forest allowed easy access through vegetation to search for and catch birds. Field work was focused around 4 accessible tracks where titipounamu were most abundant – Bell Rock track, Tumanako Loop track, Kamahi Loop track and the Bellbird Bush track.

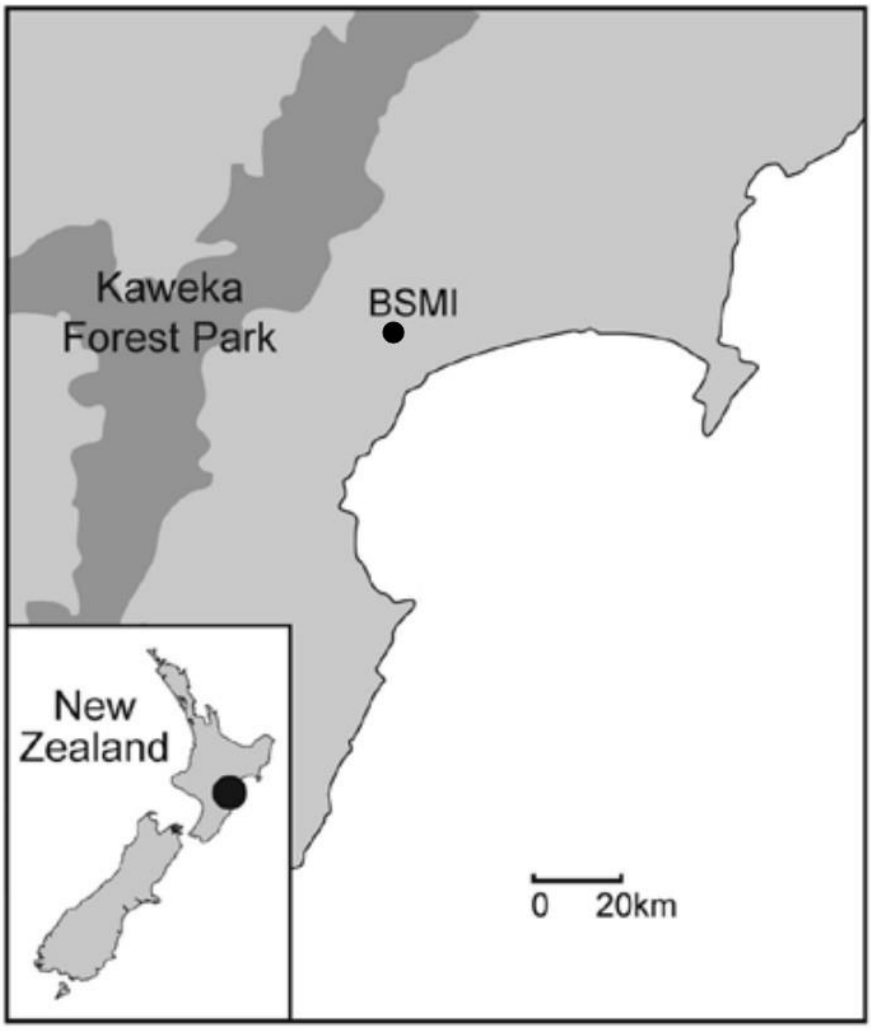


Figure 2: A map depicting the location of the study site, Boundary Stream Mainland Island (BSMI) in New Zealand. Adapted from Withers (2013) thesis.

2.3.3. Foraging observations

Birds were observed foraging at Boundary Stream Mainland Island, New Zealand in a mature and diverse native forest during the breeding season (November 2020 to January 2021) and outside of the breeding season (April 2021 to June 2021). Breeding season observations were focused on 28 individual birds (12 females, 16 males) involved with parental care at 12 nests. At least 10 observations for each parent and helper that visited the nest were recorded. Birds were located when they approached the nest to feed and identified as male or female using their plumage colouration, and their unique colour band combination was noted if they had been banded by previous researchers at the study site. At nests that had unbanded birds where I could not confirm individual identification, I treated the nest as a unit and grouped all bird visits into either male or female. However, nests were used as a focal starting point to locate birds which ensured each nest unit was independent. Once the bird had fed the chicks, I followed the individual (focal animal sampling) and recorded foraging observations. The first perch they used after leaving the nest was always excluded, and specific behaviours that suggested foraging, such as spiralling, gleaning and probing (Higgins et al., 2001; Hunt & McLean, 1993) were necessary to consider the bird to be foraging. Birds were followed and observed until they moved out of sight. No further observations were made for at least 1 minute after recording an observation of an individual to ensure samples were independent. This period of time is sufficient to enable independence of observations due to the rapid nature with which titipounamu move through the forest while foraging.

Outside of the breeding season, individuals were located and followed to obtain at least 5 foraging observations. I found focal individuals by visiting known territories and listening for calls. This resulted in a sample size of 47 birds, consisting of 22 females and 25 males. Individual birds were identified by their unique band combinations and their sex. However, many pairs were not banded, so I considered pairs that were observed at least 100m away from each other as different individuals, as titipounamu typically have small and consistent

territories (Withers, 2013), which are maintained during the non-breeding season. An offline mapping app, Maps.me, was used to record and measure distances between locations of observations. In the case of observations of groups with numerous unbanded birds, I grouped all foraging observations into either male or female as focal individual observations were not possible in such fast-moving groups. Thus, for both breeding season and outside of breeding season data, I have a minimum number of individuals, not a definitive number of individuals. Only adult birds were used during the breeding season for foraging observations, however during the non-breeding season sub-adult birds, born during the 2020/2021 breeding season, were also recorded if they had fully adult plumage. Titipounamu juveniles often pair and establish territories immediately upon independence and so the inclusion of these sub-adults was deemed a reasonable representation of adult titipounamu behaviour.

I recorded a total of 852 observations, including 372 during the breeding season and 480 outside of the breeding season. For each observation, I identified the sex of the bird as well as any band combination. I gave individual identification (ID) codes to unbanded birds. A nest ID code was given to each nest to record which individual birds were associated with each nest (recorded for observations in the breeding season only). The type of perch that the bird was standing on during the observation was recorded, alongside the background substrate, which was the type of surface that the bird was visible against during the observation (see Table 1 for details). Perch and substrate were defined differently so I could differentiate between what the bird was standing on, compared to the background it was seen against. I visually estimated the height of the perch (m) for each observation. The season, either breeding or non-breeding, was recorded. During the breeding season, the status of the birds' nest was recorded as either early chicks or late chicks. As titipounamu nestlings remain in the nest for approximately 20 days (Sherley, 1985), nests were classed as early if parents were still partly incubating, chicks were not making multi-note calls (which begin between days 9-13 after hatching; Y. Loo, personal communication, December 8th, 2020) or if it was less than 10 days after hatching.

For analysis, I tested for sex differences in the use of perch types and substrate types individually and then background substrates were then grouped into generalised colours. Bark, leaf litter and skirt observations were classified as “brown” backgrounds, and moss and leaves were classified as “green”. Dead leaves or moss were also classified into the brown category. Lichen colour was too variable to fit into either category, so I excluded the observations on lichen substrates from analyses involving the colour variable.

Table 1: Description of the categories used during titipounamu foraging observations for the variables perch type and background substrate.

Variable	Variable categories	Description
Perch type	Ground	The soil, leaf litter or woody debris on the ground.
	Small branch	A branch smaller than or equal to the bird in width.
	Large branch	A branch larger than the bird in width.
	Trunk	The main upright stem of a tree or tree fern.
Background substrate	Bark	The plain bark of a trunk or branch, including woody debris.
	Moss	Any collection of bryophytes growing on the surface of a trunk, branch or ground.
	Lichen	Any lichen growing on the surface of a trunk, branch or ground.
	Leaves	Any arrangement of living leaves or fronds.
	Leaf litter	The collection of dead leaves on the ground of the forest.
	Tree fern skirt	The arrangement of dead fronds around the growing crown of a tree fern.

2.3.4. Analysis

All analyses were performed using R version 4.1.2, (R Core Team, 2021). I used binomial generalised linear mixed effects models (GLMMs) to compare the response variable background colour with the fixed effects of sex, breeding season and nest status using the 'lmer' function of 'lme4' package ver. 1.1-27.1; (Bates et al., 2015). A second model was run with only the breeding season data to test nest ID as a random effect as well as individual ID. To identify the model that best explained the data, I used a step-wise elimination process through likelihood ratio tests (LRTs) for significance testing. Each model started by comparing the response variable and interaction term, which was then compared to a model with the same variables but no interaction term, using the base ANOVA function with test set to "LRT". A non-significant *p*-value ($p > 0.05$) result suggested that the interaction term did not add any predictive power to the model and could therefore be removed. This process was then repeated, removing one variable at a time to simplify the model, until a significant LRT result was acquired to signify the most accurate model. The interaction term between sex and status, and status as a fixed effect were not significant, so were removed from the final GLMM. A linear model was used to compare sex and perch height. I built two multinomial logistic regressions, with individual ID included as a random effect, to test whether (1) substrate type varied with sex, status or season and whether (2) perch type varied with sex, status or season. These models were built using the 'nnet' package (Venables & Ripley, 2003). Variables were selected in a step-wise fashion, also using LRTs to determine whether adding variables improved the fit of the models. Where adding variables did not improve the fit, I opted for the simplest model. Goodness-of-fit of the model was assessed using the Hosmer-Lemeshow Test for multinomial logistic regression with the 'generalhoslem' package (Jay, 2019). The model was considered a good fit if p-values for this test were > 0.05. Pairwise contrasts were calculated between the variables, using Tukey adjustment. Contrasts that were deemed relevant to the aims of this study were included in the results section, but a full table of contrasts can be found in Appendices I and II.

2.4. Results

2.4.1. Sex differences in foraging behaviour

Perch type

To explore whether there were differences in where male and female titipounamu forage, I recorded the types of perches that birds used while foraging. Females were 1.17 times more likely to be observed foraging on trunks than males (Table 2; $p = 0.004$). In contrast, males were 1.15 times more likely to be observed foraging on small branches than females ($p = 0.017$). Males were significantly more likely to be observed on small branches than any of the other perch types (all $p < 0.001$), whereas females were significantly more likely to be observed on trunks than the ground ($p < 0.001$) or large branches ($p < 0.001$), but there was no significant difference between how likely females were to be observed on trunks and small branches ($p = 0.219$). On average, both sexes spent the greatest proportion of observations on small branches (Figure 3), with females averaging 53% (SE = ± 3.2%) of observations on small branches and males averaging 68.7% (SE = ± 3.5%). Females averaged 35.3 (SE = ± 3.3%) of observations on trunks, while males averaged 23.9% (SE = ± 2.4%) of observations on trunks. Differences in trunk use remained consistent between the breeding season and non-breeding season, with females still significantly more likely to be found on trunks than males during both the breeding and non-breeding season (Table 2). However, despite males being significantly more likely to be found on small branches during the breeding season (Table 2; $p = 0.039$), there was no significant difference in how likely each sex was to be found on small branches during the non-breeding season ($p = 0.160$).

Table 2: Multinomial logistic regression results comparing sex, perch type and status. Pairwise contrasts were calculated using Tukey adjustment. Significant results at $p < 0.05$ are presented in bold, with asterisks placed according to $^{*}p < 0.05$; $^{**}p < 0.01$ and $p < 0.001$***. For a full list of contrasts, see Appendix I.

Contrast	Estimate	Standard error	df	t ratio	p value
F ground - F trunk	-0.339	0.028	12	-12.286	< **0.001*** **
M ground - M small branch	-0.600	0.029	12	-20.761	< **0.001*** **
F large branch - F trunk	-0.252	0.034	12	-7.400	< **0.001*** **
M large branch - F small branch	-0.385	0.031	12	-12.405	< **0.001*** **
M large branch - M small branch	-0.530	0.034	12	-15.431	< **0.001*** **
F small branch - M small branch	-0.145	0.034	12	-4.279	**0.017***
F small branch - M trunk	0.293	0.036	12	8.149	< **0.001*** **
M small branch - F trunk	0.277	0.038	12	7.360	< **0.001*** **
M small branch - M trunk	0.438	0.043	12	10.218	< **0.001*** **
F small branch – F trunk	0.132	0.049	12	2.672	0.219
F trunk - M trunk	0.161	0.031	12	5.158	**0.004****
F small branch breeding - M small branch breeding	-0.171	0.036	12	-4.696	**0.039***
F small branch nonbreeding – M small branch nonbreeding	-0.125	0.033	12	-3.729	0.160
F trunk breeding - M trunk breeding	0.186	0.036	12	5.151	**0.020***
F trunk nonbreeding - M trunk nonbreeding	0.151	0.029	12	5.208	**0.019***

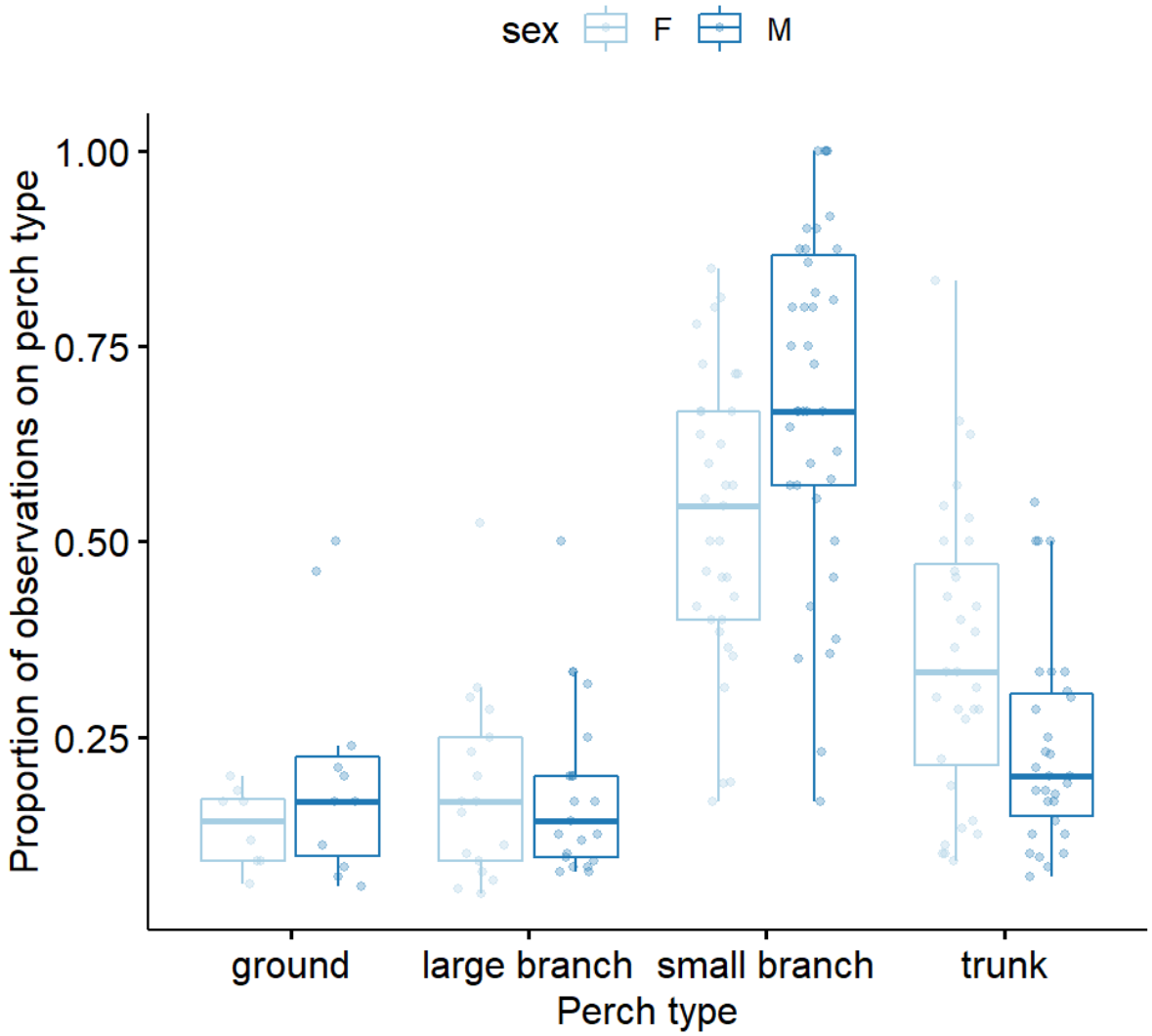


Figure 3: The proportion of observations (frequency) in which individual titipounamu (*Acanthisitta chloris)* were observed using different perch types while foraging, compared across sexes. Each sex is represented as a separate boxplot, with light blue (left) as female and dark blue (right) as male. Sample size includes 40 males and 33 females across both breeding and non-breeding seasons. Boxplots show the median values (bold middle line), the interquartile range (box), and the range values (whiskers) including some outliers. Each dot represents the proportion of observations in which an individual bird was observed using a specific perch type while foraging with the minimum number of observations being 10.

Perch height

I also recorded the height that the bird was foraging at for each observation (Figure 4). I found no significant difference in the height at which birds foraged between males and females (*N* = 852, t = -1.206, *p* = 0.228). The average perch height for females was 8m (SE = ± 0.28) and 7.6m for males (SE = ± 0.261), with both sexes being recorded at all heights between 0 and 22m. Birds were likely foraging above these heights but were too challenging to observe and get an accurate identification of sex.

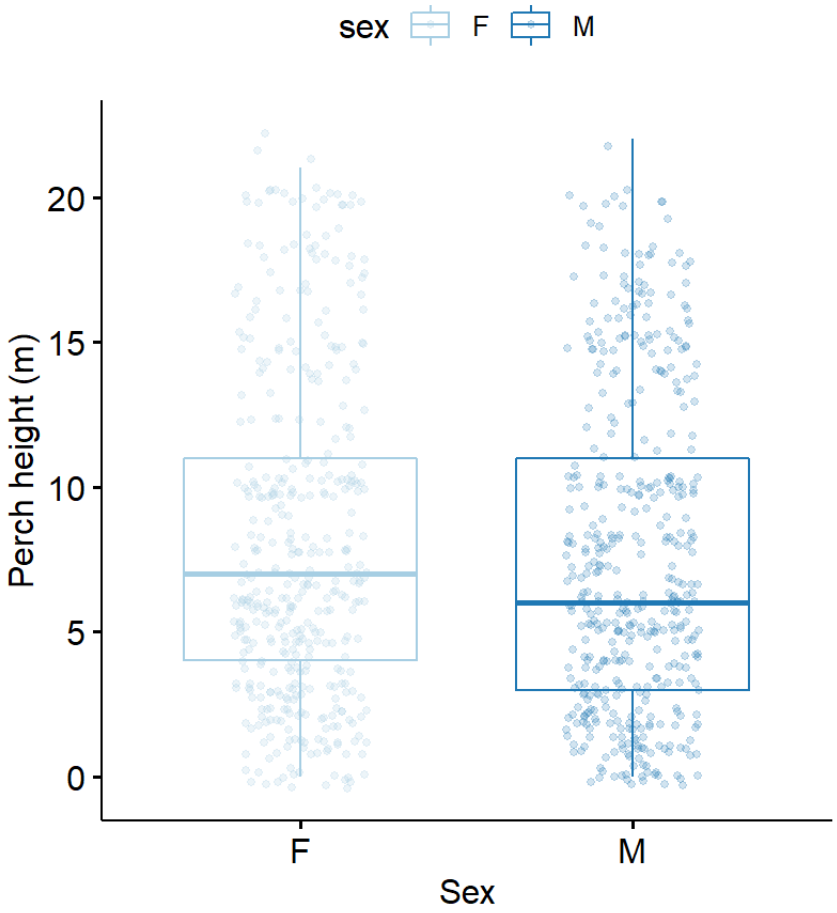


Figure 4: The height of the perch (m) that titipounamu (*Acanthisitta chloris*) used while foraging compared between sexes. Each sex is represented as a separate boxplot, with light blue (left) as female (F) and dark blue (right) as male (M). Sample size includes 40 males and 33 females across both breeding and non-breeding seasons. Boxplots show the median values (bold middle line), the interquartile range (box), and the range values (whiskers) including some outliers (unattached dots). Each dot represents an observation of a bird foraging.

Background substrate

To investigate whether there were differences in the type of backgrounds that each sex was seen against while foraging, I recorded the type of background substrate that the bird was seen against for each observation. When comparing sex and background substrate, I found that there were no significant differences between how often each sex was observed against each substrate type (Table 3; all $p > 0.05$). On average, both sexes spent the greatest proportion of observations against leafy backgrounds (Figure 5; females at 50.2% ± 3.1%) and males at 63.4% ± 3.5%) and were significantly most likely to be seen against leaves than the other substrates (Table 3; all $p < 0.05$). Except for leaves, both sexes were more likely to seen against bark backgrounds than the other background substrate types (leaf litter, lichen, moss and tree fern skirts all with $p < 0.001$), with females averaging 35.2% (SE = ± 2.8%) of observations against bark and males averaging 32.1% ± 3.1% (Figure 5). There was also no difference in how likely birds (both sexes combined or each sex) were to be observed against different substrate types across the breeding and non-breeding season, except for a very small but significant difference in leaf litter, in which birds (both sexes combined) were 1.05 times more likely to be seen against leaf litter in the non-breeding season compared to the breeding season (Table 3; $p = 0.036$).

Table 3: Multinomial logistic regression results comparing sex, substrate type and season. Pairwise contrasts were calculated using Tukey adjustment. Significant results at $p < 0.05$ are presented in bold, with asterisks placed according to $^{*}p < 0.05$; $^{**}p < 0.01$ and $p < 0.001$***. For a full list of contrasts, see Appendix II.

Contrast	Estimate	Standard error	df	t ratio	p value
F bark - F leaf litter	0.298	0.025	15	11.908	< **0.001*****
F bark - F leaves	-0.179	0.044	15	-4.069	**0.032***
F bark - F lichen	0.320	0.024	15	13.601	< **0.001*****
F bark - F moss	0.190	0.032	15	5.887	**0.001****
F bark - F skirt	0.319	0.024	15	13.580	< **0.001*****
M bark - M leaf litter	0.228	0.024	15	9.470	< **0.001*****
M bark - M leaves	-0.328	0.041	15	-7.926	< **0.001*****
M bark - M lichen	0.259	0.022	15	11.779	< **0.001*****
M bark - M moss	0.203	0.026	15	7.861	< **0.001*****
M bark - M skirt	0.261	0.022	15	11.966	< **0.001*****
F leaf litter - F leaves	-0.478	0.027	15	-17.690	< **0.001*****
M leaf litter - M leaves	-0.556	0.027	15	-20.574	< **0.001*****
F leaves - F lichen	0.499	0.025	15	19.677	< **0.001*****
F leaves - F moss	0.369	0.036	15	10.361	< **0.001*****
F leaves - F skirt	0.499	0.025	15	19.643	< **0.001*****
M leaves - M lichen	0.587	0.025	15	23.935	< **0.001*****
M leaves - M moss	0.531	0.030	15	17.925	< **0.001*****
M leaves - M skirt	0.589	0.024	15	24.224	< **0.001*****
F bark - M bark	0.054	0.031	15	1.738	0.826
F leaf litter - M leaf litter	-0.016	0.011	15	-1.364	0.954
F leaves - M leaves	-0.094	0.033	15	-2.790	0.273
F lichen - M lichen	-0.006	0.006	15	-1.038	0.993
F moss - M moss	0.067	0.020	15	3.219	0.140
Leaf litter breeding - Leaf litter nonbreeding	-0.048	0.012	15	-4.011	**0.036***

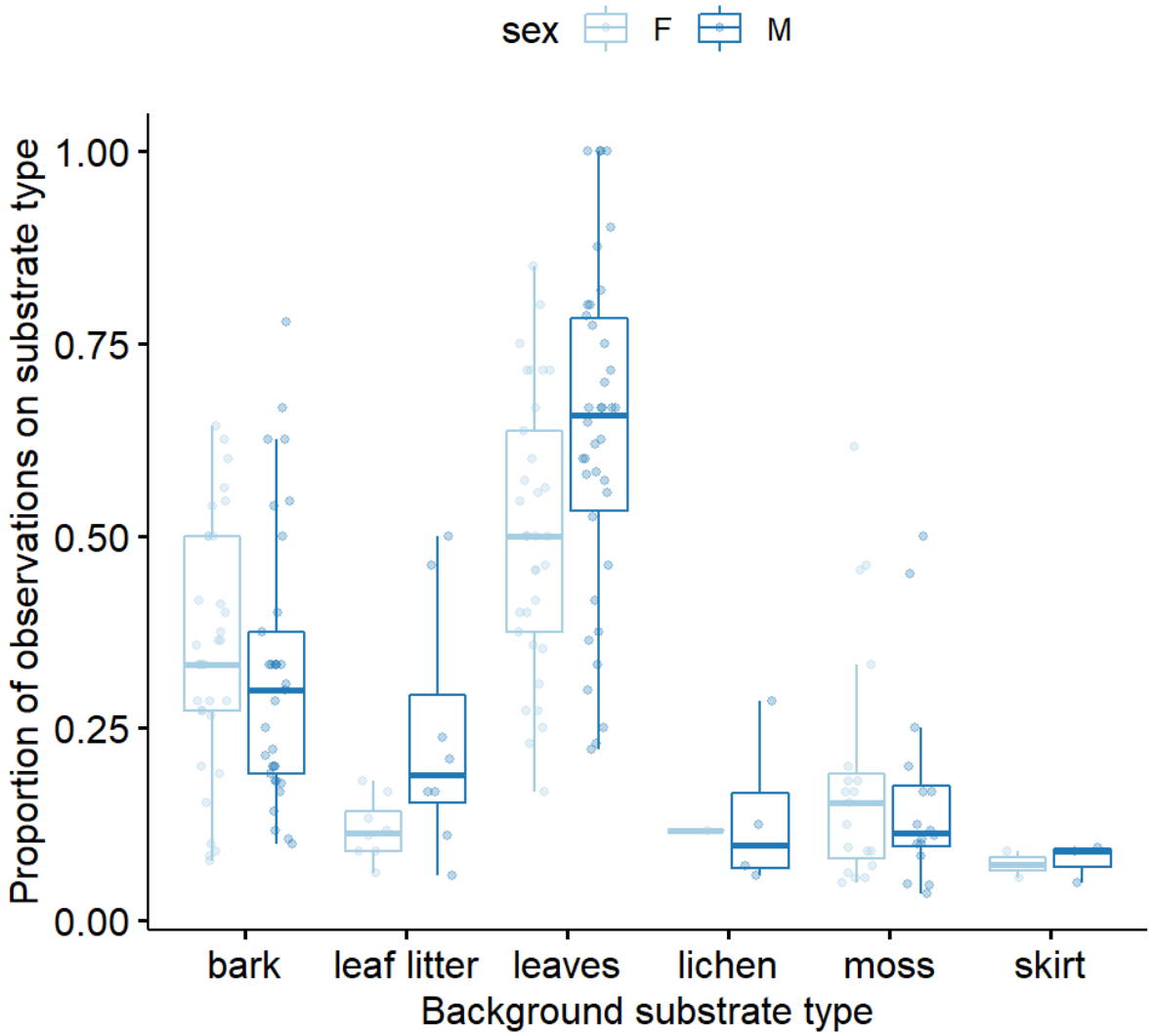


Figure 5: The proportion of observations (frequency) in which individual titipounamu (*Acanthisitta chloris)* were observed using different background substrate types while foraging, compared across sexes. 'Skirt' refers to the ring of dead fronds around the base of a tree fern crown. Each sex is represented as a separate boxplot, with light blue (left) as female and dark blue (right) as male. Sample size includes 40 males and 33 females across both breeding and non-breeding seasons. Boxplots show the median values (bold middle line), the interquartile range (box), and the range values (whiskers) including some outliers. Each dot represents the proportion of observations in which an individual was observed against a specific substrate type with the minimum number of observations being 10.

2.4.2. Sex differences in background colour

To see if males and females forage against different coloured backgrounds, I classified the substrates birds used in each observation into either green or brown. Overall, I did not find any significant sex differences in the background colour birds were observed against (Table 4; $X^2 = 0.5$, $p = 0.4795$; $N = 845$). Males and females both spent similar proportions of observations against either brown or green background substrates (Figure 6), spending a combined average of 36.5% (SE = ± 2.1%) of observations against brown backgrounds and 63.8% (SE = ± 2.4%) of observations against green backgrounds. When I incorporated random effects such as nest and individual ID into generalised linear mixed effects models, there was still no significant difference between the background colours each sex was seen against (Table 4). I also found no significant differences across different breeding stages or nesting status (Table 4), suggesting that the background colours each sex is observed against stays constant throughout the year, even across different nest stages.

Table 4: Generalised linear mixed effects model results comparing background colour, sex, nest status and season. Individual ID was included as a random factor for all models, and nest ID was also included as a random factor in model 2. Model 1 includes the interaction term between sex * season, which was removed from analyses, to demonstrate the insignificant effects. Model 2, which only includes data from during the breeding season, includes the interaction term between sex * nest status, which was removed from analyses, to demonstrate the insignificant effects. Model 3 was used for analysis as it represents the model that predicts the data most accurately as determined through likelihood ratio tests. The values represent the estimate and standard error (in brackets) for each variable.

	Dependent variable: Background colour		
	(Model 1)	(Model 2)	(Model 3)
Sex	-0.132	0.025	-0.209
	(0.321)	(0.508)	(0.210)
Season	0.443		
	(0.293)		
Sex: Season	-0.086		
	(0.403)		
Nest status		-0.267	
		(0.491)	
Sex: Status		-0.350	
		(0.615)	
Constant	-0.781***	-0.577	-0.499***
	(0.236)	(0.444)	(0.151)
Observations	845	368	845
Log Likelihood	-536.894	-211.354	-538.823
Akaike Inf. Crit.	1,083.789	434.707	1,083.646
Bayesian Inf. Crit.	1,107.485	458.156	1,097.864
Note:			**p<0.05; ***p<0.01

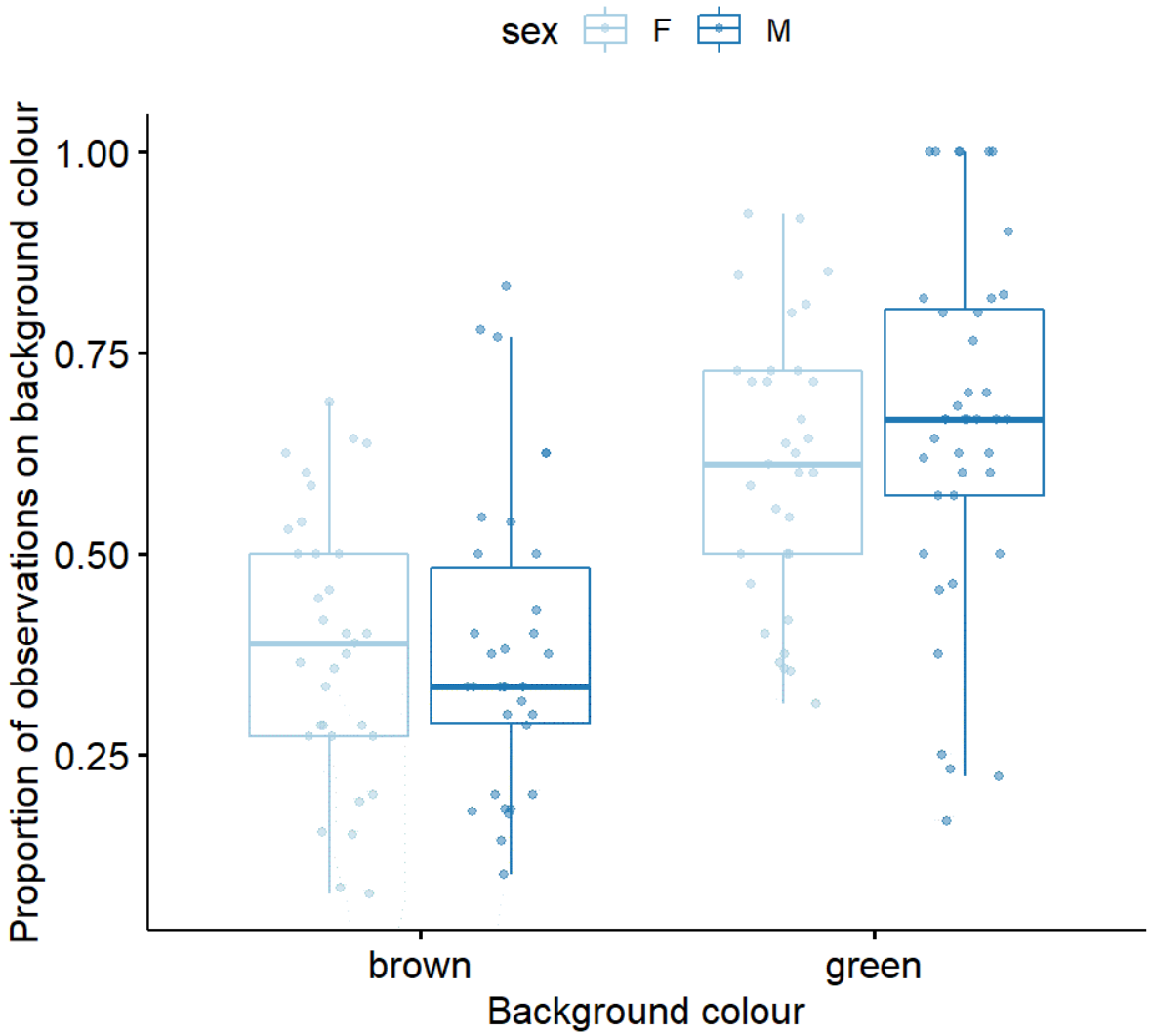


Figure 6: The proportion of observations (frequency) that individual titipounamu (*Acanthisitta chloris)* were observed against different background colours while foraging, compared across sexes. Each sex is represented as a separate boxplot, with light blue (left) as female and dark blue (right) as male. Sample size includes 40 males and 33 females across both breeding and non-breeding seasons. Boxplots show the median values (bold middle line), the interquartile range (box), and the range values (whiskers) including some outliers. Each dot represents the proportion of observations in which an individual was observed with a certain colour as their background with the minimum number of observations being 10.

2.5. Discussion

Previous research focussed on titipounamu sexual dichromatism has suggested that titipounamu may be sexually dichromatic as a result of selection for crypsis against sexually divergent foraging backgrounds (Hunt & McLean, 1993). The dorsal colouration of each sex correlated to the colour of their foraging substrate; brown females spend more time on trunks, and green males spent more time foraging amongst leaves on small branches (Hunt & McLean, 1993). Some of my findings corroborate this previous work; females were found to forage on trunks more than males, and males were observed foraging on small branches more frequently than females. However, when I separated out background substrate type and colour, I found that males and females were not more likely to be seen against any substrate or colour. There were no significant differences in how often males or females were seen against brown nor green background colours. Males were also not more likely to be seen against leaves than females, nor any other substrate type. I also found no difference in background substrate nor colour across breeding stage nor season. There were also no significant differences in perch use across season, except that males were only more likely to use small branches than females in the breeding season.

2.5.1. Sexual dichromatism driven by crypsis

Selection for cryptic colouration can drive sexual dichromatism when the need for camouflage is different for each sex (Forsman, 1995; Orton & McBrayer, 2018). Species where each sex uses different microhabitats may benefit from sexual dichromatism to better match their respective backgrounds (Medina et al., 2017; Orton & McBrayer, 2018; Ramírez-Delgado & Cueva del Castillo, 2020). Sexual dichromatism may therefore be advantageous for species with niche divergence to increase crypsis. For example, dorsal patterning in Greater Antillean *Anolis* lizards is often sexually dimorphic, with sex differences

in perch height, mobility and habitat use likely driving the differences in colour (Medina et al., 2017).

I found differences in perch type use between male and female titipounamu, suggesting some niche divergence in this species. Females were more likely to be found foraging on trunks than males, while males were more likely to be observed on small branches, although females were also more likely to be found foraging on small branches than other perch types. These differences correlate with the sex differences in claw and beak morphology; larger females with larger hind claws and more decurved beaks may be more suited to foraging on trunks, whereas the smaller males may be better adapted to forage amongst small branches and leaves (Hunt and McLean, 1993). Although my results indicate that each sex uses habitat differently, there was still substantial overlap between many aspects of habitat use, including perch height. Both sexes were observed using small branches the most frequently, and both sexes used trunks as well other perch types. If the need to be cryptic against different backgrounds was acting as a selection pressure strong enough to drive sexual dichromatism in titipounamu, we might expect to see less overlap in these behaviours (Forsman & Appelqvist, 1999; Medina et al., 2017; Ramírez-Delgado & Cueva del Castillo, 2020).

Additionally, despite sexual differences in perch use, when I grouped observations into the background colour each sex foraged upon, I did not find any significant differences between males and females; both sexes were observed using both green and brown substrates in similar proportions. If titipounamu sexual dichromatism was being driven by crypsis, the generalised background colour should match the colour of each sex's dorsal plumage (Price et al., 2019; Ramírez-Delgado & Cueva del Castillo, 2020). Our results suggest that, while titipounamu do display some niche divergence, this is not correlated to differences in the colour background they are seen against. This expands upon findings by Hunt and McLean (1993), suggesting that foraging differences are potentially more driven by perch type rather than substrate colour. The lack of background matching could be because of the

heterogenous nature of titipounamu perch types within a natural, diverse forest (Cuthill et al., 2005; Murali et al., 2021; Schaefer & Stobbe, 2006; Stevens et al., 2006); trunks are often covered in patches of moss and lichen, while the canopy consists of patches of dead leaves and thick branches. Native New Zealand forest is also composed of a wide variety of leaf types and colours. This creates an inconsistent mosaic of colours that titipounamu are foraging against, reducing the efficiency of background colour matching for either sex (Murali et al., 2021). Other cryptic strategies, such as disruptive colouration and patterning, are often more effective in heterogenous environments (Murali et al., 2021; Price et al., 2019). Nightjars (Caprimulgidae) adapt to their heterogenous nesting environment with a combination of behaviour and pattern; birds that are a closer pattern match to their nest environment show shorter escape distances as perceived predators' approach, while poorly matched birds will flee sooner (Wilson-Aggarwal et al., 2016). Likewise, it is the quality of background pattern matching to an incubating bird's plumage that predicts nest survival in ground nesting birds, not colour matching (Troscianko et al., 2016). Future research could explore the potential of these alternative cryptic strategies being utilised by titipounamu (see Chapter 3 for a pattern analysis example).

Potentially, the substrate that the bird was seen against could have been influenced by the angle I viewed the birds at; I was observing the birds from a grounded, human perspective, rather than an aerial perspective that some avian predators may view titipounamu from. Titipounamu predators, such as the kārearea/NZ falcon or ruru/morepork, are likely to be hunting within or under the canopy, rather than from above. The angle that predators view titipounamu from is therefore likely to vary from below, level, or above as I found that titipounamu use all strata of the forest. Thus, if angle does have an effect, this study at least captured part of that variation as birds were viewed from below and level. Substrate was also categorised based on what the birds were closest to or perched on, so it was likely a close representative of their background.

The study in which the crypsis hypothesis was proposed focused on the South Island subspecies of titipounamu, *Acanthisitta chloris chloris* (Hunt & McLean, 1993), while this study focused on a population of the North Island subspecies, *A. c. granti*. This could potentially account for some of the differences found in my results; there could be subspecies level differences, or potentially population level differences in titipounamu behaviour. However, as all *A. chloris* display the sexual dimorphism I am investigating, any hypothesis surrounding its evolution must hold true for both subspecies. Thus, if the crypsis cannot be supported as the driver of sexual dichromatism in this study, it is reasonable to apply the results to *A. c. chloris* as well. This study has also built on Hunt and McLean's (1993) work as I observed titipounamu in a much more complex environment that is more representative of their typical habitat. The more heterogenous habitat could have also driven the differences in our results (Murali et al., 2021), which would suggest that the environment can influence titipounamu behaviour – a potentially interesting avenue for future study.

2.5.2. Sexual dimorphism driven by ecomorphology

Although sexual dimorphism is often attributed to sexual selection, it can also be driven by different ecological selection pressures acting on each sex (Selander, 1966; Slatkin, 1984). As the environment strongly influences selection for morphological characteristics, diverging characteristics can evolve in each sex if males and females are found in different habitats or interact with their habitat differently. Differences in trophic structures such as bills are often selected for, as if each sex is using a different habitat, they will likely also be accessing different food resources (Aplin & Cockburn, 2012; Pasinelli, 2000; Radford & Du Plessis, 2003; Vergara et al., 2016). This is an example of feeding ecomorphology, in which the foraging ecology of a species impacts its morphological characteristics. A classic New Zealand bird example is the now extinct huia (*Heteralocha acutirostris*), which displayed extreme bill dimorphism. Males are hypothesised to have used their short, chisel-like bills to

dig at rotting wood, whereas females used long slender curved bills to probe and reach insects deeper within (Frith, 1997; Moorhouse, 1996; Selander, 1966; Tomotani et al., 2021).

I propose that the differences in perch use observed in this study could be better explained by the morphological differences in beak and hind claws between the sexes as opposed to choices related to background colour matching. Titipounamu display clear sexual dimorphism in their eco-morphology (Hunt & McLean, 1993); alongside their colour differences, females are larger, have more decurved bills and larger hind claws than males. Hunt and McLean (1993) suggested that these morphological differences were driven by the differing foraging niches of the sexes. The larger hind claws and decurved bills of the females likely make it easier to hold onto and probe under the bark of tree trunks. Females are thought to be larger than males because of constraints on their minimum size due to egg laying (Lill, 1991; Sherley, 1993); titipounamu eggs are large comparative to female body size, weighing up to 1.5g each, with 5 eggs laid per clutch. Females may be adapted to foraging on trunks to meet their high nutritional needs, as trunks could provide an easier and higher density source of insect prey than other areas of their habitat (Jackson, 1979). The smaller males potentially represent a more ideal body size for titipounamu when the constraint of egg laying is removed. Their small size may also make it easier to navigate through small branches and leaves to forage, or alternatively, they may use this habitat to reduce resource competition with their female partner (Chaves et al., 2017; Freeman, 2014a; Morrison & With, 1987). Particularly in monogamous species, males can benefit from selecting alternative food resources to reduce competition with their partners; increased female fitness will likely result in increased reproductive success for the male as well (Li et al., 2021). This phenomenon has been observed in other cooperatively breeding and biparental bird species as well (Aplin & Cockburn, 2012). Male green woodhoopoes (*Phoeniculus purpureus*) have 36% longer bills than females and use larger branches while foraging, spending more time scaling and probing bark than females who spent more time pecking (Radford & Du Plessis, 2003). Overall, sexual dimorphism driven by intersexual

resource competition and ecomorphology is a feasible explanation for the morphological and foraging differences observed in titipounamu.

Sex differences in foraging height have been observed in many species, often in response to factors such as reproductive strategy and need for territory defence (Chaves et al., 2017; Duron et al., 2018; Freeman, 2014; Medina et al., 2017). For example, in restinga antwrens (*Formicivora littoralis*), the highly territorial males tend to forage higher than females in the canopy, providing them with a better vantage point to invigilate their territories and mate guard (Chaves et al., 2017). However, I found no significant differences in foraging height between male and female titipounamu. Despite differences in perch use, neither sex was more likely to be in the canopy nor close to the ground. As trunks and leaves are found at all strata of their habitat, titipounamu foraging at all heights aligns with their ecomorphology. Their monogamous breeding system and low territoriality also reduce the need for males to use higher perches for reproductive reasons, such as displays (Cameron, 1990). However, this result contradicts previous titipounamu research that noted females foraging lower than males (Hunt & McLean, 1993). However, my observations were made in a complex, mature forest with varying canopy heights, while Hunt and McLean (1993) focused on a primary successional kānuka (*Kunzea* spp. complex) stand with an average canopy height of only 6m, and a lack of complex understory, reducing the range in heights that birds could forage at. Potential sex differences in foraging height could also have been masked by observer bias; birds are less likely to be detected while foraging at height. I also only estimated perch height, which could obscure small differences in foraging height. Despite these limitations, the results make it feasible to conclude that there is substantial overlap in foraging height between males and females. The large variation in foraging heights also reinforces that both sexes are foraging at all heights of their environment.

2.5.3. Breeding season differences

Intersexual differences in foraging niches are often only seen at certain times as the requirements of birds can change across different reproductive stages and times of year (Fogg et al., 2013; Paiva et al., 2018). The breeding season is often the most energy demanding time of the year, requiring birds to obtain more resources to maintain themselves and to produce their offspring (Franzreb, 1983; Petit et al., 1990; Pinet et al., 2012). Thus, resource competition between male and females, as well as between other pairs, can be exacerbated during reproductive stages (Radford & Du Plessis, 2003). However, selection for different behaviours during winter can also be exacerbated by the scarcity of resources increasing competition (Duron et al., 2018). Thus, selection for adaptations and flexible behaviours that allow each sex to use different food resources during these times can be beneficial to reducing intersexual competition, particularly for monogamous species.

Previous research on titipounamu indicated that the intersexual foraging differences were only present during the breeding season when energy demands were increased (Hunt & McLean, 1993). They suggested that outside of the breeding season the benefits of background matching were decreased, as birds consistently forage in pairs and have more time to scan for predators. This increased predator vigilance reduces the need for crypsis, allowing each sex to exploit a wider foraging niche (Powell, 1974; Watson et al., 2007). However, my results found that the sex differences in trunk use persisted across the breeding and non-breeding seasons, although the sex differences in small branch use did not. If the differences in claw and beak morphology between the sexes are linked to their foraging niche, the sex difference in foraging behaviour should persist outside of the breeding season. As my results suggest that the titipounamu foraging differences are not linked to background colour matching, the main benefit for each sex to use a specific perch type is likely their morphological advantage. The male's incentive to forage on small branches should continue even outside of the breeding season as his morphological adaptations that make him less suited to foraging on trunks are static. This finding aligns

with other species with ecomorphological adaptations, in which niche partitioning is persistent across seasons (Aplin & Cockburn, 2012; Medina et al., 2017; Orton & McBrayer, 2018). Interestingly, while females were significantly less likely to use small branches than males during the breeding season, there was no significant sex difference in small branch use during the non-breeding season. This suggests that while females may be more adapted to use trunks than males, their morphology allows them to use small branches as well, explaining why small branches were their most frequently used perch type. The separation in foraging niche may be more pronounced in the breeding season to reduce intersexual niche competition while both sexes are foraging to provision chicks. Once this period of increased caloric demand has ended, females may start to diversify where they forage as competition for food resources with her partner is diminished.

2.5.4. Evolutionary significance

This research contributes an example to the relatively small body of work on how ecomorphology and potentially intersexual niche partitioning can drive sexual dimorphism (De Lisle, 2019; Li et al., 2021). The analyses used in this study have provided a deeper understanding that builds on previous research and has helped to tease out the various influences of feeding related ecomorphology as well as crypsis via colour matching. My approach of isolating the data in terms of perch types and substrate colour allowed me to provide a more accurate test of whether titipounamu foraging behaviour is linked to their foraging behaviours. These results indicate that previous assumptions that titipounamu sexual dichromatism is driven by selection for crypsis may be incorrect, as green male titipounamu were observed just as often as brown females against both green and brown backgrounds. If titipounamu colour is not driven by a need for crypsis, it implies that there is a different selection pressure driving their differences in colouration, or perhaps it could be non-adaptive and simply a ‘hangover’ trait retained from an ancestral species. Future

research could explore potential correlates of green colouration to investigate alternative functions for titipounamu colour, such as signalling to partners or between sexes.

2.5.5. Conclusions

Following the work by Hunt and McLean (1993) it has been suggested that titipounamu dichromatism is driven by crypsis due to different foraging niches - the different use of habitat is suggested to drive different needs for camouflage from each sex. I tested this hypothesis with a population that occupies a natural, complex forest and found that males and females do vary in where they forage, with females more likely to be found on trunks than males, and males more likely to be found on small branches than females. These results support previous findings by Hunt and McLean (1993) and suggest that titipounamu do vary in their foraging niches. However, the additional analyses performed here challenge the idea that crypsis is driving titipounamu sexual dichromatism. My analyses separated the foraging location choices made by titipounamu into perch type and background colour and found that neither sex was more likely to be seen foraging against green nor brown background substrates, despite sex differences in perch use. This suggests that while titipounamu are under selection to utilise different perch types, they are not necessarily under selection for background colour matching nor crypsis. Key findings of previous research were also not replicated in this study; I did not find sex differences in foraging height and some foraging differences persisted throughout the breeding and non-breeding seasons. Overall, these results suggest that crypsis may not be a complete explanation for titipounamu sexual dichromatism and I suggest that niche divergence in titipounamu may be driven by ecomorphological variations as opposed to colour adaptations.

Chapter 3

Do titipounamu demonstrate sex-specific crypsis in their natural environment?

3.1. Abstract

Bird colour is influenced by a trade-off between using colour to increase camouflage to reduce predation risk and using conspicuous colour for communication. As more conspicuous birds may be at greater risk of predation, many strategies have evolved to use both cryptic and conspicuous colour, such as adopting localised and concealed patches of bright colour, adopting conspicuous colour only during the breeding season and displaying sexual dichromatism. Whether colour is cryptic also depends on the visual system of the receiver; plumage that appears cryptic to humans may not be cryptic to birds or their predators. This may be especially important in green plumage, which is often assumed to be cryptic but can also provide honest signals of quality, including within the ultraviolet spectrum. Titipounamu (*Acanthisitta chloris*) are an interesting species in which to study crypsis as they have sexually dichromatic green plumage which is thought to be cryptic; previous work implied that their sexual dichromatism was driven by each sex needing to be cryptic against different foraging environments. However, no studies have explored titipounamu colour using avian visual models. To investigate whether titipounamu dichromatism may be driven by sex-specific crypsis, I assessed whether titipounamu were cryptic in their native environment, and if this varied between sex or background environment type using relevant avian visual models. Using calibrated digital imaging, I found that titipounamu dorsal plumage was chromatically and achromatically distinguishable against the tested background types in both an ultraviolet sensitive passerine and violet

sensitive bird of prey visual model. Female colour was more contrasted against the background types than males. Males were a closer chromatic match than females to green backgrounds (leaves and moss) but were still detectable to both visual models. In contrast, both sexes were a close pattern energy match to all the different background types. Thus, titipounamu dorsal plumage does not appear to be strongly cryptically coloured, but further research is necessary to ascertain whether they may be cryptically patterned.

3.2. Introduction

In highly visual species, a trade-off exists between using colour to signal conspecifics and needing colour to camouflage oneself from predators or prey (Gomez & Théry, 2007). While bright colours and ornamentation may help signal individual quality and attract a mate, they can also increase the risk of predation. Some species that experience high predation risk evolve highly cryptic colouration and instead use other sensory mechanisms for communication, such as vocalisations or scent (Barreira & García, 2019; Hagelin & Jones, 2007). Others run the risk of being brightly coloured by balancing it with behaviours that reduce predation risk, such as increased vigilance, spending time under cover and fleeing more often in response to alarm calls (Fowler-Finn & Hebets, 2011; McQueen et al., 2017; Møller et al., 2016; Silva et al., 2008). However, some species balance this trade-off by maintaining a mixture of both cryptic and conspicuous plumage. Some species have highly localised colourful patches only on parts of the body that are viewed during interactions with conspecifics, such as around the head, while displaying cryptic colouration on areas that are commonly observed by predators (Delhey, 2020; Gomez & Théry, 2007; Gruson et al., 2021). For example, a study of North American wood warblers (Parulidae) found that males of ground nesting species had conspicuously coloured under-bodies but cryptic dorsal colour to conceal them from aerial predators, while canopy nesting species had conspicuous colour on their dorsal plumage but cryptically coloured undersides to conceal them from predators

below (Simpson et al., 2020). Other species only adopt conspicuous plumage during the breeding season (McQueen et al., 2019), such as male red fodies (*Foudia madagascariensis*), who develop striking red plumage during the breeding season, which may act as an honest signal of male quality (Estep et al., 2006). Behavioural adaptations to reduce visibility can also contribute; more conspicuous male red-capped plovers (*Charadrius ruficapillus*) incubate nests at night when predator visibility is reduced, while the more cryptic females incubate during the day (Ekanayake et al., 2015). Note that all these examples show this partly conspicuous colouration in just one sex, highlighting the role of sexual dichromatism in balancing the trade-off between bright and cryptic plumage. It may be beneficial for one sex to be completely cryptically coloured if they are providing most of the nest care to avoid drawing attention of predators to the nest, especially at nests that are exposed (Gömark et al., 1997; Soler & Moreno, 2012; Wallace, 1868).

The extent of natural selection for cryptic strategies is influenced by a species' predators and their visual capabilities (Bennett & Cuthill, 1994; Osorio & Vorobyev, 2008). It is, therefore, important to study cryptic colouration through the perspective of the relevant predators, rather than making judgements based on human vision. Species that appear highly conspicuous to us may be cryptic through the eyes of their predators; for example, a recent study showed that the colouration of the giant panda (*Ailuropoda melanoleuca*) provides camouflage in its natural environment, despite seeming highly conspicuous to humans (Nokelainen et al., 2021). Many animals, including birds, can see in the ultraviolet (UV) spectrum, resulting in potentially colourful signals that are hidden from human view (Håstad et al., 2005). For example, multiple bird species previously thought to be sexually monochromatic have been found to have sex differences in UV colour (Eaton, 2005). In birds, the extent of this UV vision depends on the avian group, as it is mediated by a fourth type of short wave sensitive single cone that is classed into either ultraviolet sensitive (UVS) or violet sensitive (VS) (Ödeen et al., 2011; Ödeen & Håstad, 2013). Species with UVS vision can see further into the ultraviolet spectrum than most birds of prey, which tend to

have VS vision (Carvalho et al., 2011; Lind et al., 2014; Potier, 2020). While many mammalian predators likely have some capability for UV vision, this also tends to only extend into the longer wavelengths of the UV spectrum (Douglas & Jeffery, 2014; Marcos Gorresen et al., 2015). UV colour can therefore be used by UVS bird species to have bright, conspicuous colour that conspecifics can see, but their predators cannot (Bennett & Cuthill, 1994; Håstad et al., 2005). For example, a study of 18 songbirds found that colourful plumage patches were much more conspicuous to other songbirds with UVS vision than they were to VS avian predators (Håstad et al., 2005).

Green colour is often associated with cryptic colouration against vegetated backgrounds. However, although birds with green plumage may appear to be cryptic in these environments to humans and predators, they may not be cryptic to their conspecifics (Håstad et al., 2005). The green plumage of male *Eclectus* parrots appears cryptic to their predators with limited UV vision, but the UV reflectance of their green plumage increases their conspicuousness to conspecific females (Heinsohn, 2008). This example, along with a growing body of work (Andersson, 1999; Bajer et al., 2011; Griggio et al., 2009; Hausmann et al., 2003; Siefferman & Hill, 2005), shows that green colour often has an ultraviolet component that can have a role in conspecific signalling (Hausmann et al., 2003; Heinsohn et al., 2005), leading us to challenge the common assumption that the role of green colouration is only to increase crypsis. As green colour in birds is often produced through carotenoids that are only obtained through diet, it can also act as a signal of quality (Blount & McGraw, 2008; Pike et al., 2009; Saks et al., 2003). Thus, it is apparent that the appropriate species visual system must be used when analysing colour, as it is easy to make erroneous assumptions about the function of colours based on human perception.

Titipounamu (*Acanthisitta chloris*) are a particularly interesting species in which to explore crypsis. They are sexually dichromatic, with males having green dorsal plumage, while the larger females display brown plumage mottled with yellow-green stripes. Titipounamu are monogamous with both parents contributing to incubating and feeding chicks in cavity nests

mostly constructed by the male (Sherley, 1994). They are also cooperative breeders, with both related and unrelated individuals of both sexes contributing to feeding chicks (Sherley, 1990). Previous work by Hunt and McLean (1993) found that titipounamu use different foraging substrates, with the females spending more time against trunks and males foraging more in the leaves and canopy. Their results implied that the need for each sex to be cryptic against their different coloured backgrounds may be driving the sex differences in colour; the green males are a closer colour match to their leafy backgrounds, whereas browner females are a closer match to the bark backgrounds against which they forage (Hunt & McLean, 1993). However, the colour measurements made by Hunt & McLean (1993) used only Munsell colour charts, a visual assessment that relies solely on human perception. Thus, further colour assessments from the perspective of titipounamu's predators are required to understand whether titipounamu are cryptic. Additionally, this work was carried out in a forest type that is not representative of their usual natural habitats, potentially biasing results toward an unusual vegetation type. Previous research using spectrophotometry, an unbiased measurement method (Tella et al., 1998), has indicated that male and female colour both contains a peak in the UV spectrum (Withers, 2013) and that carotenoids are likely to play a part in the colour mechanisms for this species (Thomas et al., 2014). Given the extensive literature linking carotenoid colouration to honest signalling, the green colour found in titipounamu may provide more signalling content than previously considered. The biparental nest care and cavity nesting behaviours also make hypotheses about the need for crypsis while incubating an unlikely explanation, and their monogamous breeding system and lack of a clearly more ornamented sex also cast doubt on sexual selection as a driving factor (Hunt & McLean, 1993). Overall, these factors make titipounamu a fascinating species to study the selective pressures that drive crypsis and sexual dichromatism.

In this chapter, I test whether titipounamu dorsal plumage is in fact cryptic against their native environment using relevant avian perception models for the first time. If males and females are selected for crypsis, I would expect that male dorsal colour and pattern is more

similar to green backgrounds present in their environment and female dorsal colour and pattern are more similar to brown backgrounds. I chose to use calibrated digital imaging as a methodology as although titipounamu colour has already been described using spectrophotometry (Withers, 2013), photography allows for broad and specific colour and pattern measurements as opposed to only intricate point measurements. Additionally, photography allowed for a less invasive way to measure colour that could be done in the field.

3.3. Methods

3.3.1. Study species

Titipounamu are a small (5.5-7g), insectivorous wren species endemic to New Zealand with two subspecies, the North Island titipounamu (*A. c. granti*) and the South Island titipounamu (*A. c. chloris*) (Sherley, 1993). Males and females are sexually dimorphic, having different morphological and chromatic features. Females are slightly larger than males, have larger hind claws and a more decurved beak (Hunt & McLean, 1993). Males and females are easily distinguished by their distinct dorsal plumages (Figure 1). Males have solid, bright olive-green dorsal plumage across the crown, mantle and extending onto the upper wing and tail coverts. Females have a dark brown dorsal plumage, with each feather being tipped with yellow-green colour, creating a mottled or striped effect. This distinct plumage also extends across the crown, mantle and upper wing and tail coverts. Other less noticeable differences include a coloured patch on each wing as well as a thin line of colour along each wing primary, both of which are bright green in males (similar to their dorsal plumage), but more yellow in females. Both sexes have short, dark tail feathers tipped with light green-yellow colour, and dark wing primaries, as well as some dark patches on the wings. Both sexes also have white ventral plumage along their chest and a white supercilium and bright white partial eye ring under the eye. Males can have darker plumage around the top and either

side of the eye. Detailed work describing the physiological mechanisms responsible for titipounamu plumage colouration has not been carried out to date, however previous research has found that their plumage did reflect in the ultraviolet spectrum in both sexes (Withers, 2013) and that their plumage contains carotenoids (Thomas et al., 2014). Subtle population differences in colour have been found in terms of chroma and brightness, but all populations are sexually dimorphic with similar colourations (Withers, 2013).

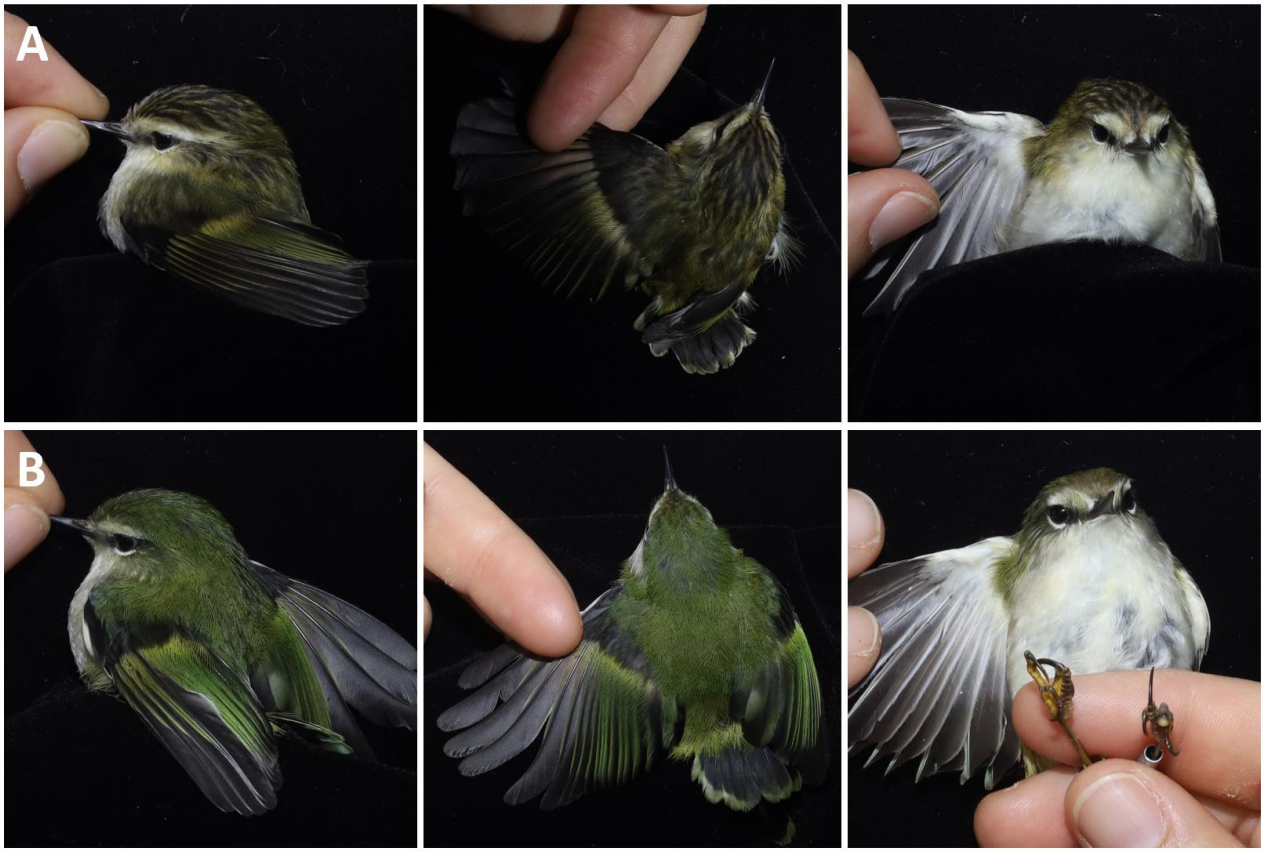


Figure 1: Lateral, dorsal, and ventral views of titipounamu (*Acanthisitta chloris*). A) female colouration, distinguished by the yellow-green dorsal plumage mottled with brown. B) male colouration, distinguished by the solid green dorsal plumage.

Titipounamu are found in a range of forest habitat types including coastal broadleaf forests, high altitude podocarp forest, mature complex inland forests and regenerating native bush (Higgins et al., 2001). Titipounamu hunt a variety of insects mostly by gleaning from or probing into substrates, but occasionally on the wing (Higgins et al., 2001). While foraging,

titipounamu often adopt a ‘spiral’ behaviour, where they start at the base of a trunk or branch, and slowly spiral up and across the limb probing and gleaning insects from the surface or under the bark (Hunt & McLean, 1993). They also forage in leaf litter or coarse woody debris on the ground, and in amongst leaves and mossy surfaces. Females typically spend more time foraging on trunks than males, while males spend more time on small branches and leaves (Hunt & McLean, 1993). Titipounamu are also often located and identified by a constant wing-flicking motion they perform while foraging. They form monogamous pair bonds and spend most of their time foraging in close proximity to their partner within small, exclusive home ranges (Cameron, 1990). Males do most of the work towards nest building, but both sexes contribute to incubation and feeding chicks, although often the male contributes more than the female, spending longer incubating and visiting more frequently (Sherley, 1994). Titipounamu display cooperative breeding at some nests (Sherley, 1990). Titipounamu typically nest in enclosed cavities in trunks and branches of trees, but have relatively flexible nesting patterns, often choosing to nest in other enclosed areas such as nest boxes, holes in the ground and tree fern skirts (Higgins et al., 2001; Moran et al., 2019).

Titipounamu have a variety of potential native and introduced predators. Native avian raptors such as moreporks/ruru (*Ninox novaeseelandiae*), New Zealand falcon/kārearea (*Falco novaeseelandiae*), Australasian swamp harriers/kāhu (*Circus approximans*) as well as sacred kingfishers/kōtare (*Todiramphus sanctus*) are all likely current predators of titipounamu (Higgins et al., 2001). Likewise, long-tailed cuckoo/koekoeā (*Urodynamis taitensis*) have been found to predate chicks at titipounamu nests (Moran et al., 2019). Other historic, but now extinct, native predators could include the New Zealand crow (*Corvus antipodum*), the laughing owl (*Sceloglaux albifacies*) and potentially some reptile species, particularly at the nest. Alongside native predators, a range of introduced mammalian species likely also predate titipounamu, such as cats (*Felis catus*), mice (*Mus musculus)*,

rats (*Rattus* spp.), stoats (*Mustela erminea*), ferrets (*Mustela furo*), and possums (*Trichosurus vulpecula*).

3.3.2. Study site

All field work was conducted on a wild titipounamu population at Boundary Stream Mainland Island (Figure 2) in the Maungaharuru Ranges, North Island, New Zealand (Department of Conservation, 2021). The Boundary Stream Mainland Island reserve was established in 1996, with extensive ongoing pest management alongside efforts to promote improvement of native flora and fauna populations (Department of Conservation, 2021). The reserve covers around 800 ha, ranging from 300m to 950m a.s.l. Vegetation varies throughout the reserve, moving through red (*Nothofagus fusca*) and black beech forest (*Fuscospora solandri*), dense mixed broadleaf-podocarp habitat to large stands of kāmahi (*Weinmannia racemosa*) and rewarewa (*Knightia excelsa*). Titipounamu territories are found throughout these varied forest types. Densities of introduced mammalian predators are low at this field site, but include cats, mice, rats, stoats, ferrets and possums. Native avian predators are also present at the site such as ruru, kārearea, kāhu and koekoeā (pers. obs.). Public walking tracks and trapping/bait lines throughout the forest allowed easy access through vegetation to search and catch birds. Field work was focused around 4 accessible tracks where titipounamu were most abundant – Bell Rock track, Tumanako Loop track, Kamahi Loop track and the Bellbird Bush track.

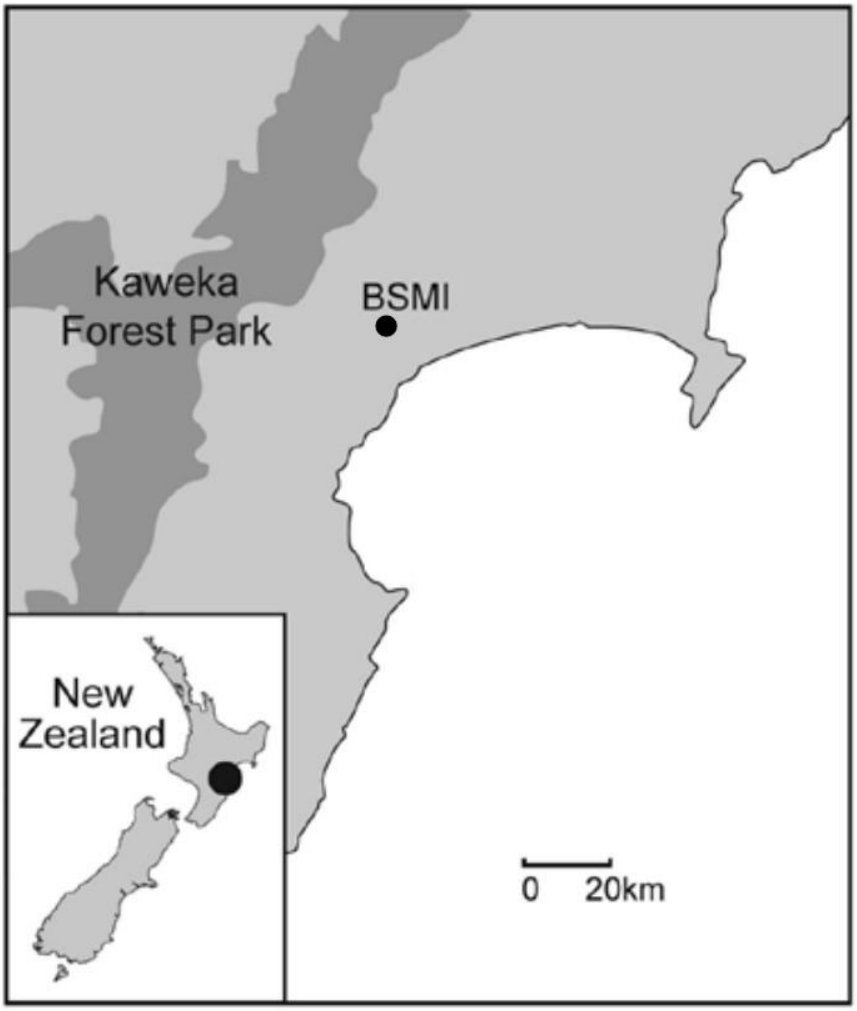


Figure 2: A map depicting the location of the study site, Boundary Stream Mainland Island (BSMI), New Zealand, with a black dot. Adapted from Withers (2013) thesis.

3.3.3. Bird photography

Birds were mist netted at Boundary Stream Mainland Island along the Tumanako, Kamahi Loop and Bellbird Bush tracks in April 2021. Seven males and five females were caught, although one female escaped part way through photographing. Two individuals, one male and one female were clearly sub-adults based on the speckling on their chest – the last remnants of their juvenile plumage. Another female was confirmed as a sub-adult as she was caught in the previous breeding season (December 2020) for banding, although she appeared to have mature plumage. Given I aim to provide a general understanding of

titipounamu colour, rather than explore individual or population variation, this sample size is sufficient as an indicative measure of a typical male or female titipounamu within their natural habitat.

I used calibrated digital imaging to sample colouration of titipounamu plumage and their background environments. I followed the photography protocols outlined by Troscianko and Stevens (2015). I took images of birds with a Canon EOS RP and a Canon EF 50mm f/1.8 II lens. To allow for UV photography, the camera was modified through quartz conversion to enable full-spectrum sensitivity. I used a Kolari Vision KV-FL1 Multispectral IR UV Flash to illuminate the images. Separate photos were taken for both the human-visible light spectrum (400-700nm) and the UV range (300-400nm range). The lens was fitted with a UV and infrared blocking filter for photographs in the human-visible spectrum (Kolari Vision UV/IR Cut Color Correcting Hot Mirror Filter) and swapped with a Kolari Vision UV bandpass filter for UV photographs. Camera calibration was performed according to Troscianko & Stevens (2015) and the micaToolbox user guide (Troscianko, 2019) using their chart-based method (See Appendix III for details). Human visible and UV photos were taken in quick succession to minimise movement of the subject between images. Photographs were taken with a shutter speed of 180s, ISO1600 for all photos. The fastest shutter speed available was used to minimise effects of the subject moving and variable light conditions. To achieve correct exposure, I performed exposure bracketing by varying the aperture between images, using between f/4-7 for UV images and f/11-14 for visible spectrum images. Each image had included a Spectralon™ 99% reflectance standard (Labsphere, Congleton, UK) and an X-Rite ColorChecker Passport for image standardisation. The X-Rite ColorChecker Passport includes a 5cm scale bar.

Live birds were held against a black, non-reflective velvet bean bag to reduce their movement during photography. The camera was positioned 30cm directly above the bird on a tripod. All subjects were positioned at the same orientation (0 ° of the vertical plane) and level with the scale bar and standards. Birds were positioned in a pose that allowed for a

clear view of their dorsal plumage (see Figure 1). I gently extended one wing for the dorsal view images. Birds were banded with unique colour combinations before release to avoid pseudoreplication.

3.3.4. Environment photography

Environment images (backgrounds against which titipounamu forage) were also taken at Boundary Stream Mainland Island along the Tumanako, Kamahi Loop, Bell Rock and Bellbird Bush tracks in June 2021. Substrates and species were selected based on foraging observations recorded throughout the 2020/2021 breeding season (see Chapter 3). The 10 most frequently visited plant species during foraging observations were selected within each of the following substrate types: bark of trunks, mossy trunks, branches and leaves (Table 1). Only 4 species of tree with lichen were visited, as well as five types of leaf litter. *In situ* photographs were taken of trunk bark, mossy trunks, branches, leaves and leaf litter. Trunks and branches were photographed with the same photography method outlined above for the bird imaging, except the lens was aimed horizontally with the focal plant species situated directly in front of and 1m away from the camera. Images of leaf litter and leaves were taken from directly above but still maintaining a 1m distance.

Table 1: Plant species used for colour analysis of each background substrate type. Each species reflects the most frequently recorded species that titipounamu perched on during foraging observations in Chapter 3, arranged in alphabetical order. Leaf litter is named after the most dominant plant species observed in the sample.

Background substrate type					
Trunk bark	Moss	Leaves	Leaf litter	Lichen	Branch bark
Fuscospora solandri	*Fuscospora solandri*	*Fuscospora solandri*	*Dacrycarpus dacrydioides*	*Weinmannia racemosa*	*Fuscospora solandri*
Coprosma spp.	*Fuchsia excorticata*	*Coprosma* spp.	*Olearia* sp.	*Melicytus ramiflorus*	*Coprosma* spp.
Griselinia lucida	*Griselinia lucida*	*Griselinia lucida*	*Fuscospora fusca*	*Fuscospora fusca*	*Griselinia lucida*
Pseudowintera colorata	*Pseudowintera colorata*	*Pseudowintera colorata*	*Elaeocarpus dentatus*	*Beilschmiedia tawa*	*Pseudowintera colorata*
Weinmannia racemosa	*Weinmannia racemosa*	*Weinmannia racemosa*	*Dicksonia* and *Cyathea* spp.		*Weinmannia racemosa*
Melicytus ramiflorus	*Melicytus ramiflorus*	*Melicytus ramiflorus*			*Melicytus ramiflorus*
Fuscospora fusca	*Fuscospora fusca*	*Fuscospora fusca*			*Fuscospora fusca*
Knightia excelsa	*Knightia excelsa*	*Knightia excelsa*			*Knightia excelsa*
Beilschmiedia tawa	*Beilschmiedia tawa*	*Beilschmiedia tawa*			*Beilschmiedia tawa*
Elaeocarpus dentatus	*Elaeocarpus dentatus*	*Dicksonia* and *Cyathea* spp.			*Elaeocarpus dentatus*

3.3.5. Image analysis and visual modelling

To analyse images and perform visual modelling, I used the Multispectral Image Calibration and Analysis (MICA) toolbox version 2.2.2 (Troscianko & Stevens, 2015) and the integrated Quantitative Colour Pattern Analysis (QCPA) Framework (van den Berg et al., 2020) for ImageJ version 1.5.3 (Schneider et al., 2012). RAW images were used for all analyses. Overexposed images were identified using the micaToolbox's photo screening function and then discarded from analysis. The pair of images most closely aligned in terms of body position for each subject were then selected to be used for further image analysis

(determined subjectively by sight). I converted each set of photographs into a calibrated multi-spectral image, which consists of a stack of photographs taken at different wavelengths, calibrated by the toolbox using the Spectralon™ 99% reflectance standard present across each image. For this study, the stack included the three human visible channels (vR, vG, vB) alongside the two UV channels (uR and uB). These corresponded to the bird's long wavelength (LW), medium wavelength (MW), short wavelength (SW) and ultraviolet (VS/UVS) photoreceptors respectively. Regions of interest (ROIs) were selected on each multi-spectral image using the polygon tool. To provide a comparative model for titipounamu colour, I randomly selected one adult male image and one adult female image to use as a representative for all modelling comparisons. Because these crypsis analyses are concerned with the dorsal colouration, I selected the dorsal view images and created ROIs around the crest and mantle of each bird using the polygon tool. For the environment images, a rectangular ROI of roughly 10x10cm was selected where possible, and a polygon ROI was used to outline smaller objects such as branches, leaves or moss patches. The environmental substrates I sampled often had uneven surfaces and were sometimes shiny, meaning that the angle they were photographed at could influence colour measurements as a result of specular reflection (Norman et al., 2004). Only areas with no specular reflection were selected in regions of interest to avoid any misrepresentation of colour.

To make assessments about the crypticity of titipounamu against their backgrounds, their colours must be analysed from the perspective of their potential predators and conspecifics. Thus, each multi-spectral image was transformed to animal-vision cone-catch quanta in the micaToolbox. This conversion produces images that are calibrated to the visual sensitivities of a particular species. To investigate whether titipounamu are cryptic, I chose to model titipounamu background matching using two perception systems to represent the visual system of their most likely predators and of conspecifics. As titipounamu reflect in the UV spectrum and some of their avian predators may also see in this spectrum, it is necessary to model a receiver that has similar spectral sensitivities. However, there are few species with

complete visual models and no information on spectral sensitivities are available for titipounamu avian predators. To overcome this issue, it is standard practice to use a closely related or ecologically similar species as a proxy. In this study, I used the common buzzard (*Buteo buteo*) spectral sensitivities from Lind et al. (2013) as a representative for native avian predators. Common buzzards have similar foraging behaviours and habitats to the New Zealand diurnal raptors that are predators of titipounamu (Clements, 2002) and provide an example of a species with VS vision (Lind et al., 2013). While a complete visual model for a *Falco* species is not available, the ocular media transmittance of common buzzards is also comparable to that of species in the *Falco* genus, which includes the New Zealand falcon or *kārearea* (Potier et al., 2020). As there was no visual model available for titipounamu nor for any closely related species, I used the blue tit (*Cyanistes caeruleus*) as a representative of the passerine order and a species with UVS vision (Hart, Partridge, Cuthill, & Bennett, 2000). The R^2 values for each model with the camera calibration were between 0.89-0.91 for the common buzzard photoreceptors, and 0.88-0.92 for the blue tit photoreceptors. These values are below what is recommended (> 0.97 R^2; Troscianko, 2019), but I could not access the equipment to redo the camera calibration due to a COVID-19 lockdown.

3.3.6. Colour and luminance measurements

I used the receptor noise-based visual discrimination (RNL) model to measure the level of chromatic and achromatic differences between the titipounamu dorsal plumage and their various background types (Vorobyev & Osorio, 1998). This analysis produces 'just noticeable difference' (JND) values that can be used to determine the distance in colour space between the bird dorsal plumage and the different background types. JND values that are less than one suggest that the visual system being modelled would not be able to distinguish between the two colours, whereas values greater than three suggest that the spectra being compared are clearly distinguishable and increasingly easier to discriminate

between as the value increases. Thus, higher JND values indicate reduced levels of chromatic or achromatic background matching between titipounamu and their background. (Siddiqi et al., 2004; Troscianko et al., 2015)

Cone catch images were first run through Gaussian Acuity Control and rescaled to 5 px per minimum resolvable angle. Acuity control adjusts the spatial resolution of the image to remove any information that the receiver being modelled would not be able to see at the set distance. This was done for the whole image for a viewing distance of 5000mm, using the scale bar as reference. The blue tit model used a spatial acuity value of six cycles per degree. Unfortunately, the spatial acuity for the common buzzard nor any of titipounamu's native predators are not known. Thus, I used the mean spatial acuity for the Harris's hawk (*Parabuteo unicinctus)* found in (Potier et al., 2016) which was 37.3 cycles per degree. Mitkus et al., (2018a) found that visual acuity in diurnal raptors was correlated to prey size, the distance they viewed their prey from and raptor body size. I chose Harris's hawks as they predate on small birds, can be found in wooded habitats and are in a similar size class to titipounamu's avian predators (Bednarz, 1988).

Colour and luminance measurements were then taken from the ROIs on each acuity-controlled cone catch image using the toolbox's Image Analysis function. The bird's double cone was set as the luminance channel for analyses and weber fractions were set to 0.05 for both model species. Colour and luminance JNDs were then calculated between bird and environment ROIs across images for each model.

3.3.7. Pattern measurements

Cone-catch images were processed the same as above using Gaussian Acuity control, but an additional granularity analysis was performed alongside using Fast Fourier Transform (FFT) bandpass filtering. This analysis filters the ROIs at multiple spatial frequency scales, measuring pattern "energy" at each scale as the standard deviation of each pixel. Pattern

processing is thought to be mediated by the double cones in birds, so I used this channel for pattern analysis (Osorio & Vorobyev, 2005). I used a step multiplier of two, beginning with two pixels and ending at 1200 pixels as a measurement scale. The results from this analysis can be directly compared across ROIs using the toolbox's pattern and luminance difference distribution calculator to measure the differences between pattern energy results across each spatial scale. This gives a pattern energy difference (PED) value, which represents the absolute difference in pattern spectra between samples across different spatial scales (Troscianko & Stevens, 2015). Lower PED values arise from patterns that display similar energy at each spatial scale, which signifies a closer level of background pattern matching. A PED value for each titipounamu sex was calculated for each background sample.

3.3.8. Statistical analyses

All image analysis results were analysed using R version 4.1.2, (R Core Team, 2021). I used linear mixed effects models to compare colour JND, luminance JND and PED values for each visual model (common buzzard and blue tit) using the 'lmer' function of 'lme4' package ver. 1.1-27.1; (Bates, Mächler, Bolker, Walker, 2015). This model could account for the random effect of plant species in background substrate type (trunks, moss, leaves, leaf litter, branches, and lichen), while comparing sex and background substrate type as fixed effects. For each of the response variables (colour JNDs, luminance JNDs and PED values) the model that best explained the data was selected using a step-wise elimination process through likelihood ratio tests (LRTs) for significance testing. Each model started by comparing sex and background as an interaction term, which was then compared to a model with the same variables but no interaction term using the base ANOVA function with test set to "LRT". A non-significant *p*-value result suggested that the interaction term did not add any predictive power to the model and could therefore be removed. This process was then repeated, removing one variable at a time to simplify the model, until a significant LRT result was acquired to signify the most accurate model. Once the final model had been decided,

post-hoc tests of multiple comparisons were conducted for significant interactions ($p < 0.05$) using the 'emmeans' function of the emmeans package ver. 1.7.1-1 (Lenth, 2021). This function performs pairwise comparisons between fixed effects using a Tukey *p*-value adjustment. A background colour variable was created by grouping together generally brown substrates (leaf litter, trunk, and bark samples) and green substrates (leaves and moss). Lichen colour was not consistently green nor brown, so I excluded these samples from the background colour variable. I then ran a separate model using the same step-wise process as above with colour JND as the response variable, comparing background colour (green or brown) and sex as interaction terms, with plant species as a random effect.

3.4. Results

3.4.1. Chromatic matching

There were no significant interactions between sex and background type using either the VS bird of prey (common buzzard) or the UVS passerine (blue tit) visual system (Table 2), suggesting that neither sex is significantly more chromatically contrasted than the other against any background type. However, males do appear to have lower chromatic discrimination values (JND) than females against moss, leaves and leaf litter (Figure 3), suggesting that they may be slightly less discriminable than females against these background types, although the difference is not statistically significant (Table 2). There were also no significant differences in colour and luminance values between the background types for either visual model (Table 2), indicating that titipounamu have a similar level of chromatic matching across each type of background.

Although there were no significant interactions between sex and background type (Table 2), the linear mixed effects models found a significant difference between the chromatic matching across sex for both visual systems (VS bird of prey model: $p < 0.001$; UVS passerine model: $p < 0.001$). Overall females were more discriminable using the VS bird of

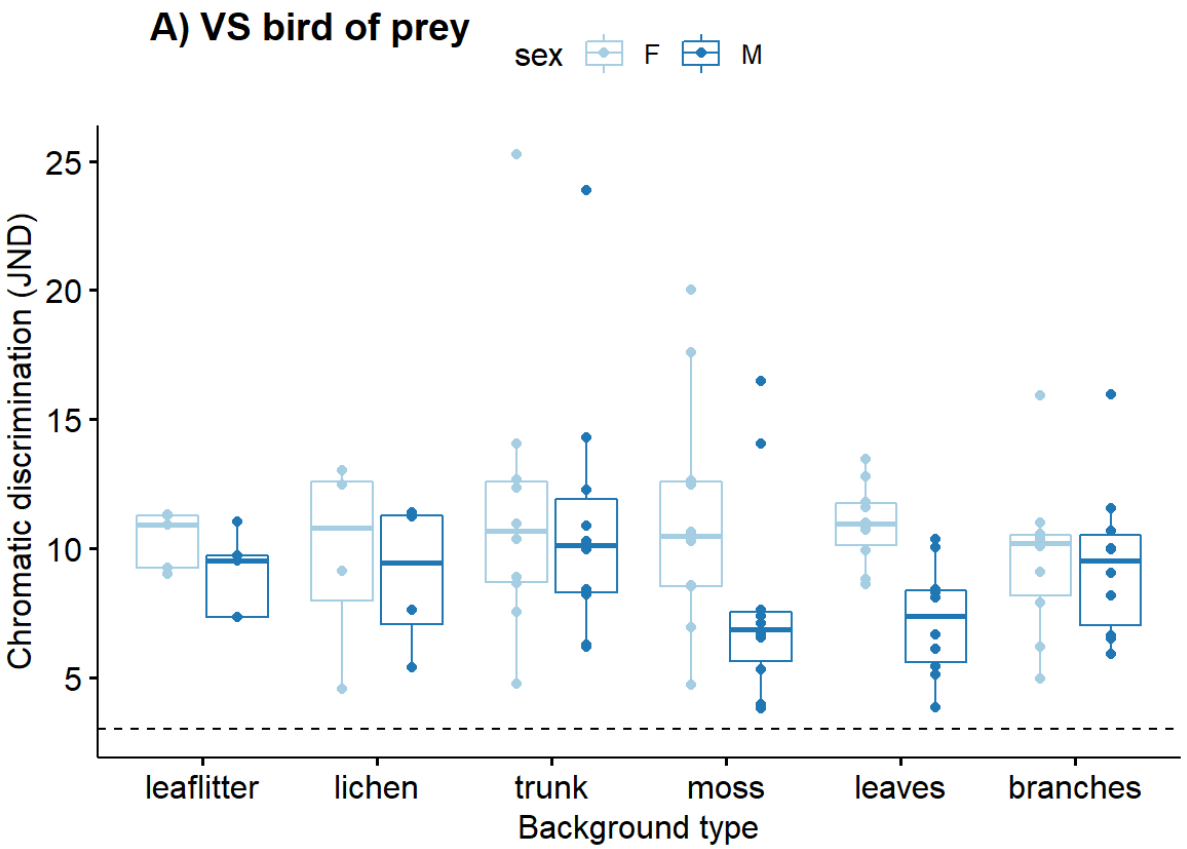
prey model than males (p = 0.004), with females having a mean JND value of 10.7 (SE = ± 0.526) and males having a mean JND value of 8.92 (SE = ± 0.522). Females were also more discriminable using the UVS model than males (p = 0.0014), with females having a mean JND of 8.90 (SE = ± 0.601) and males having a mean JND value of 6.62 (SE = ± 0.439). This suggests that male dorsal colour overall is a closer match to the environment backgrounds than females. However, the mean values for both sexes are still well above a JND value of 3, indicating that both sexes are discriminable against their backgrounds to both VS avian predators and UVS passerine receivers.

Table 2: Linear mixed effects model results for violet sensitive common buzzard (*Buteo buteo*) and ultraviolet sensitive blue tit (*Cyanistes caeruleus*) visual models across sex and background type. Values represent estimates from each model with standard error (in brackets). Asterisks mark significant results (p < 0.05). Each visual system has 4 models, one for pattern energy differences, luminance JNDs and colour JNDs, and a fourth one for colour JNDs (2) of background colour. The species of plant the background image was sampled from was included as a random factor for all models. Although the interaction term (not significant) between sex * background type was removed from the best model, it is included here as a key term of interest.

	Dependent variable:							
	Common Buzzard visual model				Blue tit visual model			
	Pattern PED	Luminance JND	Colour JND	Colour JND 2	Pattern PED	Luminance JND	Colour JND	Colour JND 2
Leaf litter	0.004	-8.538**	0.162		0.001	-7.276**	1.949	
	(0.005)	(3.379)	(1.790)		(0.003)	(3.223)	(1.936)	
Leaves	-0.012***	-4.604	1.943		-0.005**	-6.242**	-2.215	
	(0.004)	(2.712)	(1.351)		(0.003)	(2.605)	(1.545)	
Lichen	0.003	21.261***	0.888		0.003	19.778***	-1.977	
	(0.006)	(3.611)	(1.812)		(0.003)	(3.461)	(2.060)	
Moss	-0.010**	-9.394***	1.726		-0.006**	-7.396***	1.708	
	(0.004)	(2.712)	(1.355)		(0.003)	(2.605)	(1.545)	

Trunk	-0.001	-1.839	1.907		-0.002	-0.575	-2.417	
	(0.004)	(2.705)	(1.341)		(0.003)	(2.601)	(1.540)	
Background colour				0.998				0.365
				(0.910)				(1.104)
Sex	-0.0003	-4.031	-0.196	-0.545	-0.0005	-1.801	-2.643	-1.788
	(0.004)	(2.705)	(1.341)	(0.847)	(0.003)	(2.601)	(1.540)	(1.036)
Leaflitter:Sex	-0.001	2.579	-1.169		-0.0002	-1.005	-0.823	
	(0.008)	(4.686)	(2.323)		(0.004)	(4.506)	(2.668)	
Leaves:Sex	0.001	0.930	-3.521		0.00003	0.442	0.422	
	(0.006)	(3.826)	(1.897)		(0.004)	(3.679)	(2.178)	
Lichen:Sex	0.0001	-3.786	-0.680		-0.0003	-3.627	1.872	
	(0.008)	(5.061)	(2.510)		(0.005)	(4.867)	(2.881)	
Moss:Sex	-0.0004	5.817	-3.152		0.001	2.257	-1.558	
	(0.006)	(3.826)	(1.897)		(0.004)	(3.679)	(2.178)	
Trunk:Sex	-0.0002	0.709	-0.286		0.001	-0.769	2.551	
	(0.006)	(3.826)	(1.897)		(0.004)	(3.679)	(2.178)	
Background colour:Sex				-2.989**				-1.424
				(1.270)				(1.554)
Constant	0.015***	13.766***	9.438***	10.171***	0.008***	12.627***	9.403***	8.847***
	(0.003)	(1.971)	(1.142)	(0.834)	(0.002)	(1.870)	(1.134)	(0.784)
Observations	98	98	98	90	98	98	98	90
Log Likelihood	261.127	-291.255	-237.820	-231.307	308.031	-286.974	-243.467	-242.245
Akaike Inf. Crit.	-494.253	610.509	503.641	474.613	-588.061	601.948	514.934	496.489
Bayesian Inf. Crit.	-458.064	646.699	539.831	489.612	-551.872	638.137	551.124	511.488

Note: **p<0.05; ***p<0.01


A) VS bird of prey
sex
F
M
Chromatic discrimination (JND)
25
20
15
10
5
leaflitter
lichen
trunk
moss
leaves
branches
Background type

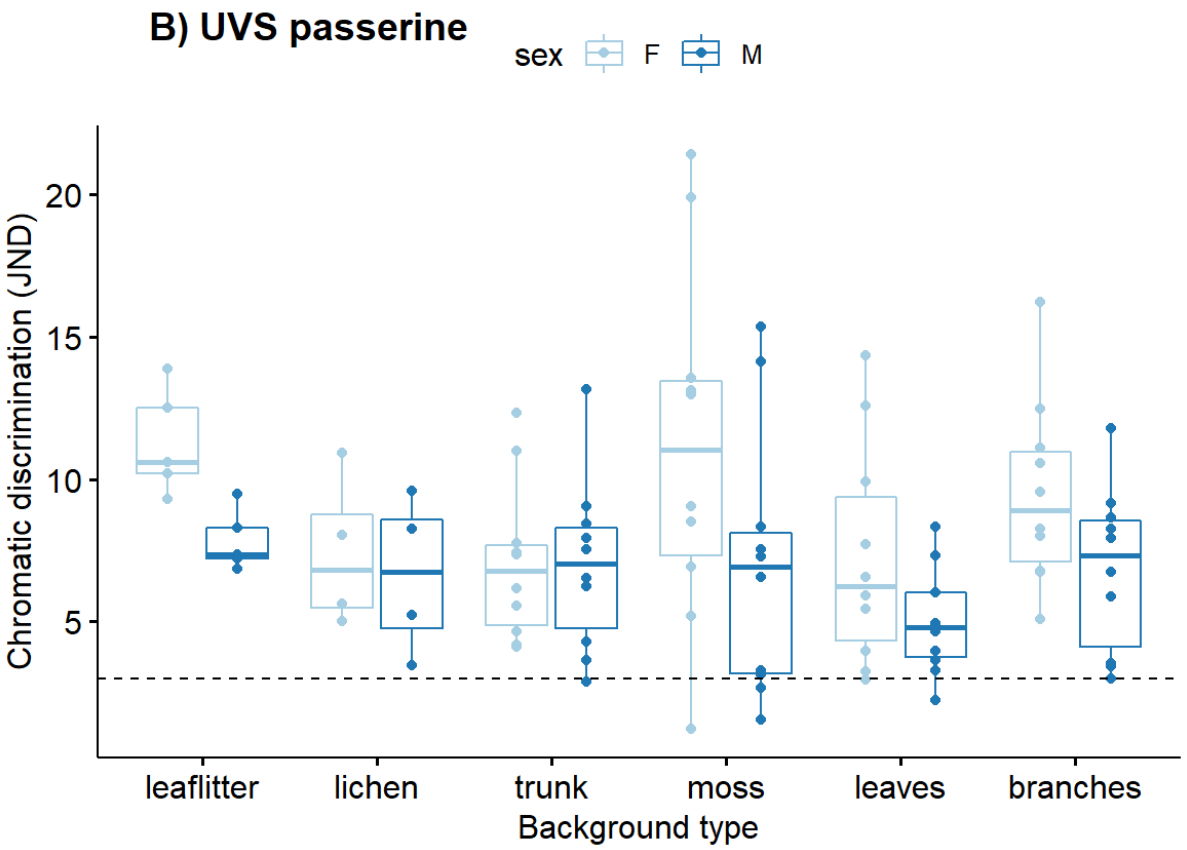
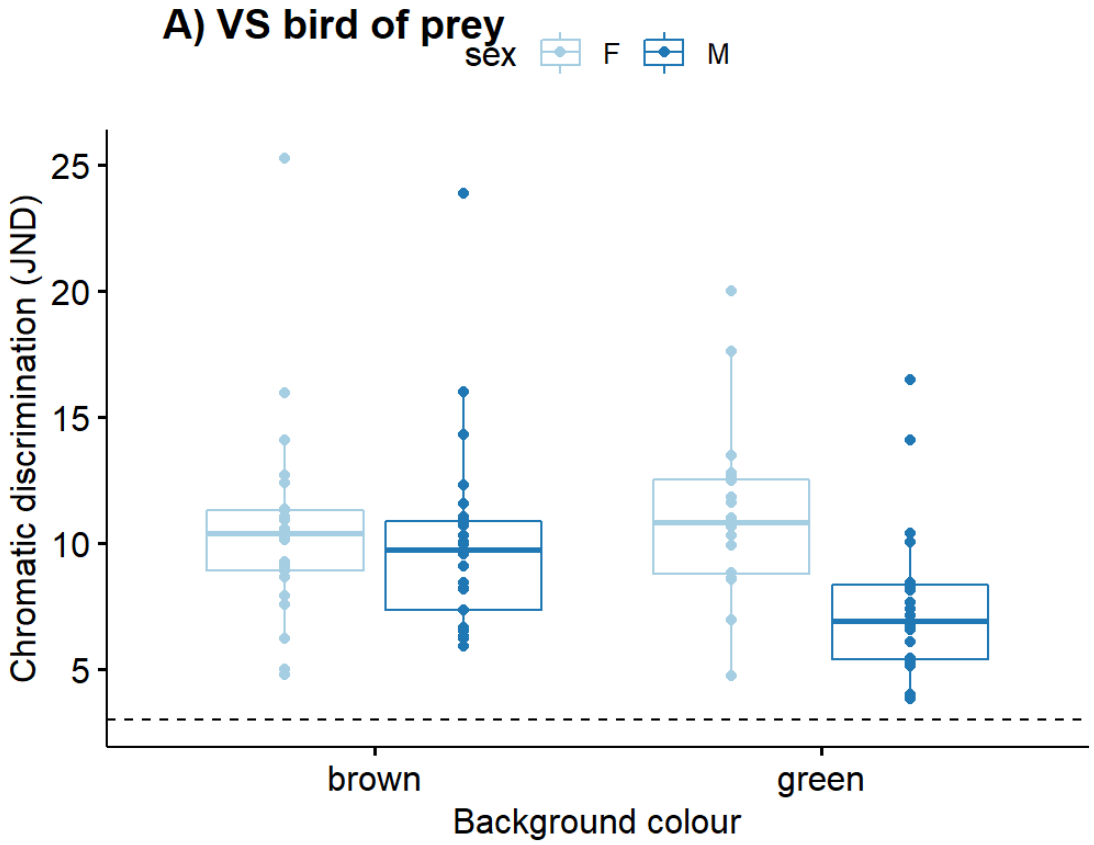

B) UVS passerine
sex
F
M
Chromatic discrimination (JND)
20
15
10
5
leaflitter
lichen
trunk
moss
leaves
branches
Background type

Figure 3: Chromatic (colour) discrimination values or 'just noticeable differences' (JNDs) for titipounamu dorsal plumage compared to different background types as modelled under A) violet sensitive (VS) common buzzard (*Buteo buteo*) and B) ultraviolet sensitive (UVS) bluetit (*Cyanistes caeruleus*) vision. Each sex is represented as a separate boxplot, with light blue (left) as female and dark blue (right) as male. Boxplots show the median values (bold middle line), the interquartile range (box), and the range values (whiskers) including some outliers (unattached dots). Each data point is represented with a dot. The dashed black line intersects at a JND value of 3, indicating the range above which colours are increasingly discriminable to the visual system being modelled.

I then re-ran the analyses but with the background types grouped into either green (moss and leaves) or brown (leaf litter, trunk and branches) to see whether an effect was present across different background colours. Using the VS bird of prey model, females were significantly more distinguishable against green backgrounds than males ($p = 0.002$), suggesting males are a closer colour match to green backgrounds, such as leaves and moss. As above, the values for both sexes are still clearly distinguishable to a buzzard receiver (Figure 4), with females having a mean JND value of 11.10 (SE = ± 0.760) against green backgrounds, and males having a mean JND value of 7.57 (SE = ± 0.722). There was no significant difference in how distinguishable either sex was against brown backgrounds ($p = 0.917$). Under the blue tit model, there was no significant interaction between background colour and sex (Table 2). Once again, to UVS passerine receivers, females were more chromatically contrasted against the background colours than males ($p = 0.002$), with females having a mean JND of 9.04 (SE = ± 0.643) and males having a mean JND value of 6.62 (SE = ± 0.466). The mean values for both sexes are still well above a JND value of 3, indicating that both sexes are discriminable against their backgrounds to both VS avian predators and UVS passerine receivers. However, overall, the JND values are low in the UVS model, with some samples less than 3, therefore UVS receivers may find titipounamu challenging to see against some background colours, especially green ones (Figure 4).


A) VS bird of prey
sex
F
M
Chromatic discrimination (JND)
25
20
15
10
5
brown
green
Background colour

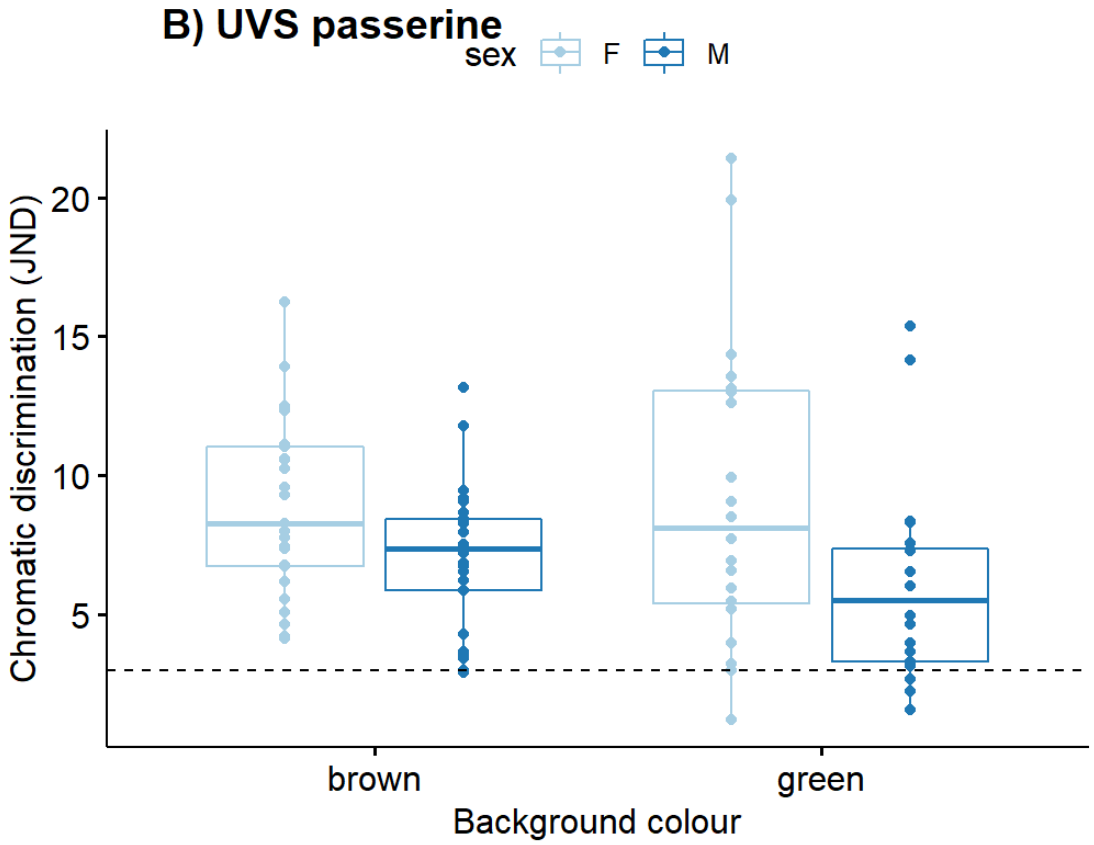

B) UVS passerine
sex
F
M
Chromatic discrimination (JND)
20
15
10
5
brown
green
Background colour

Figure 4: Chromatic (colour) discrimination values or 'just noticeable differences' (JNDs) for titipounamu dorsal plumage compared to different background colours grouped in either brown or green, as modelled under A) violet sensitive (VS) common buzzard (*Buteo buteo*) and B) ultraviolet sensitive (UVS) bluetit (*Cyanistes caeruleus*) vision. Each sex is represented as a separate boxplot, with light blue (left) as female and dark blue (right) as male. Boxplots show the median values (bold middle line), the interquartile range (box), and the range values (whiskers) including some outliers (unattached dots). Each data point is represented with a dot. The dashed black line intersects at a JND value of 3, indicating the range above which colours are increasingly discriminable to the visual system being modelled.

3.4.2. Achromatic matching

There were no significant interactions between sex and background type for the VS bird of prey nor the UVS passerine visual system for luminance JNDs (Table 2), suggesting that neither sex was significantly more achromatically contrasted than the other against any background type. There were, however, multiple significant differences in JND values between the background types for both visual models (Table 2), indicating that the level of achromatic matching varies depending on what type of background titipounamu are compared with (Figure 5).

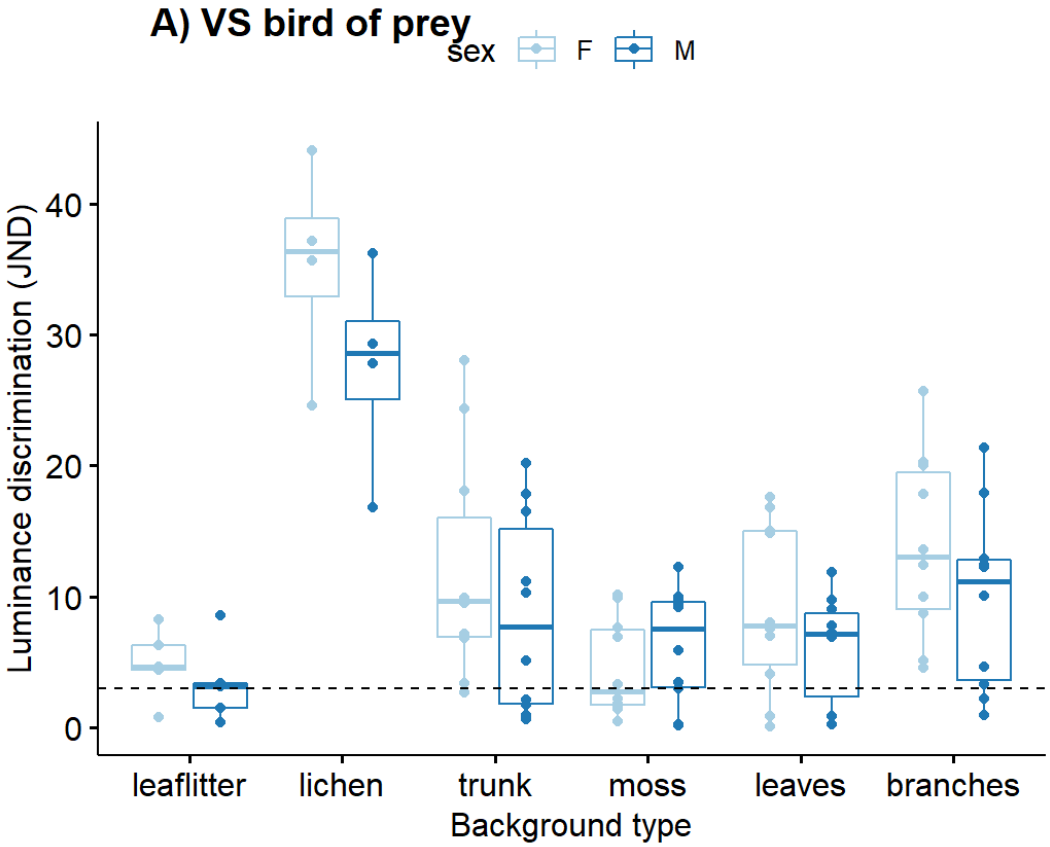
Under the VS bird of prey visual system, lichen backgrounds (mean JND ± SE = 31.11 ± 2.29) had significantly higher JND values compared to every other background type (all *p*-values < 0.001), suggesting that lichen has the lowest achromatic match to titipounamu plumage. Branch backgrounds had the second highest mean JND value (mean JND ± SE = 11.75 ± 1.44) and were significantly higher than both moss ($p = 0.014$; mean JND ± SE = 5.26 ± 1.44) and leaf litter backgrounds ($p = 0.047$; mean JND ± SE = 4.51 ± 2.04), which had the two lowest luminance JND values. Moss and leaf litter are therefore a closer achromatic match to titipounamu dorsal plumage than branches, although they are still above the discrimination threshold of 3 JND for the VS visual model. There were no other significant differences in luminance JND values across the background types for the VS visual model (Table 2), suggesting that the level of achromatic matching to titipounamu

dorsal plumage is similar across these backgrounds. While the linear mixed effects model reported a significant result for the leaves background (p = 0.034, Table 2; mean JND ± SE = 7.61 ± 1.44), the post hoc Tukey test found no significant difference between leaves and the other background types (all p-values > 0.05), except for lichen (p < 0.001).

Under the UVS passerine visual system, lichen backgrounds (mean JND ± SE = 29.68 ± 2.13) also had significantly higher JND values compared to every other background type (all p-values < 0.001), suggesting that lichen has the lowest achromatic match to titipounamu plumage for UVS receivers and well as VS bird of prey receivers. The branch background once again had the second highest mean luminance JND value (mean JND ± SE =) and was significantly higher than moss (p = 0.011; mean JND ± SE = 5.46 ± 1.33), leaves (p = 0.016; mean JND ± SE = 5.70 ± 1.33) and leaf litter (p = 0.014; mean JND ± SE = 3.98 ± 1.89) background types. The trunk background (mean JND ± SE = 10.76 ± 1.33) also had significantly higher JND values compared to moss (p = 0.049) and leaf litter (p = 0.045). Moss and leaf litter, therefore, provide closer achromatic matches for titipounamu dorsal plumage than lichen, branch and trunk backgrounds. There were no other significant differences in luminance JND values across the background types for the UVS visual model (Table 2), suggesting that the level of achromatic matching to titipounamu dorsal plumage is similar across these backgrounds.

As with the chromatic analysis, despite there being no significant interactions between sex and background type for luminance JNDs (Table 2), the linear mixed effects models found evidence for a difference between the achromatic matching across sex for the VS bird of prey visual system (p = 0.039) but not the UVS passerine visual system (p = 0.121). Females were more discriminable to a VS species against the background types than males (p = 0.0393), with females having a mean JND value of 13 (SE = ± 1.01) and males having a mean JND value of 10.5 (SE = ± 1.01). While under the UVS visual system females did still have a higher mean JND (mean JND ± SE = 12.1 ± 0.917) than males (mean JND ± SE = 10.3 ± 0.917), this difference was not found to be statistically significant (p = 0.121). This

suggests that male dorsal colour is a closer achromatic match across the different background types than females for the VS bird of prey model, but there is only weak evidence of this for the UVS passerine model. However, as with the chromatic values, the mean achromatic values for both sexes are still above a JND value of 3, indicating that both sexes are discriminable against their backgrounds for both VS and UVS receivers. This is true across all background types except when male plumage luminance is compared to leaf litter luminance (Figure 5). For the UVS model, the mean luminance JND for male plumage compared to leaf litter is 2.27 (SE = ± 1.141), below the JND discrimination threshold of 3. This suggests that a UVS receiver may not be able to clearly discriminate between the achromatic colour values of leaf litter and male titipounamu dorsal plumage. Under the VS model, the mean luminance JND is just greater than 3 (mean JND ± SE = 3.420 ± 1.407) for male plumage compared to moss but the standard error still brings some values under 3 JNDs. This suggests that a VS avian predator may be able to discriminate between the achromatic colours of male titipounamu and leaf litter more easily than an UVS passerine but could still find it challenging (JND values below 1 are not distinguishable, while values over 3 are clearly distinguishable). Overall, males on leaf litter present the closest achromatic matching of any of the background and sex combinations, with other backgrounds exhibiting levels of achromatic contrast that would make the birds distinguishable under both the UVS passerine and VS bird of prey model.


A) VS bird of prey
sex
F
M
Luminance discrimination (JND)
0
10
20
30
40
leaflitter
lichen
trunk
moss
leaves
branches
Background type

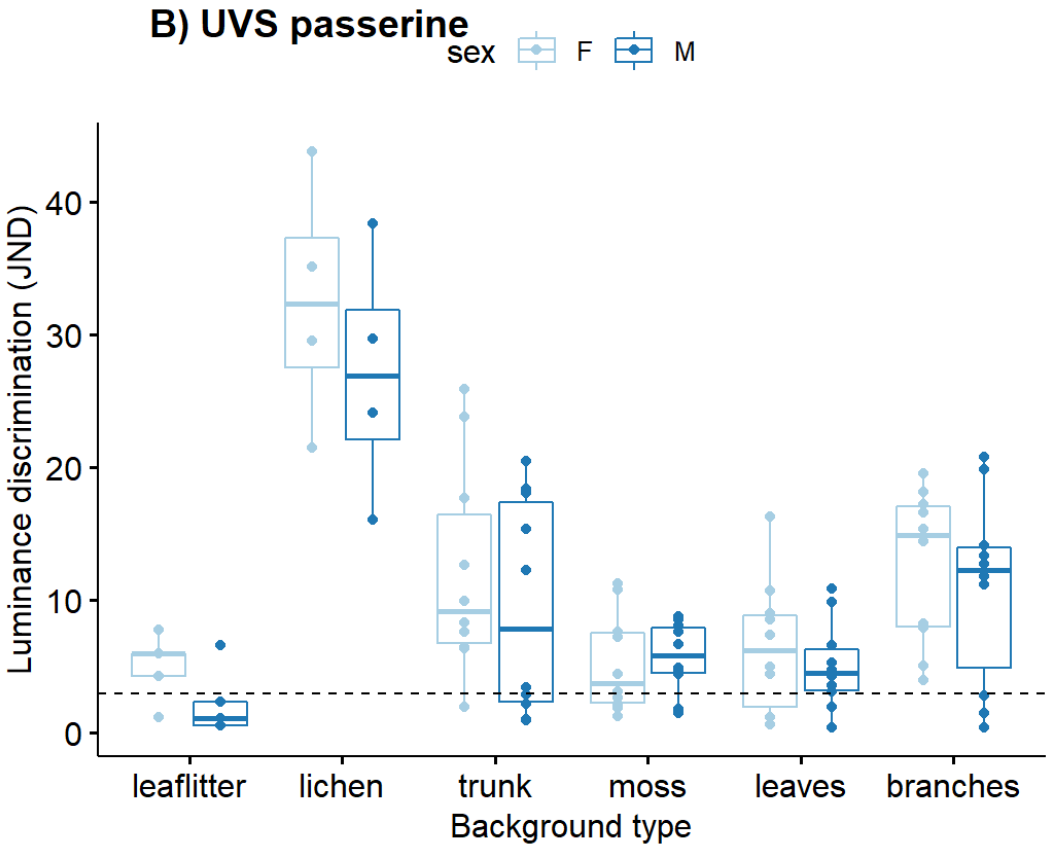

B) UVS passerine
sex
F
M
Luminance discrimination (JND)
0
10
20
30
40
leaflitter
lichen
trunk
moss
leaves
branches
Background type

Figure 5: Achromatic (luminance) discrimination values or 'just noticeable differences' (JNDs) for titipounamu dorsal plumage compared to different background types as modelled under A) violet sensitive (VS) common buzzard (*Buteo buteo*) and B) ultraviolet sensitive (UVS) bluetit (*Cyanistes caeruleus*) vision. Each sex is represented as a separate boxplot, with light blue (left) as female and dark blue (right) as male. Boxplots show the median values (bold middle line), the interquartile range (box), and the range values (whiskers) including outliers (unattached dots). Each data point is represented with a dot. The dashed black line intersects at a JND value of 3, indicating the range above which colours are increasingly discriminable to the visual system being modelled.

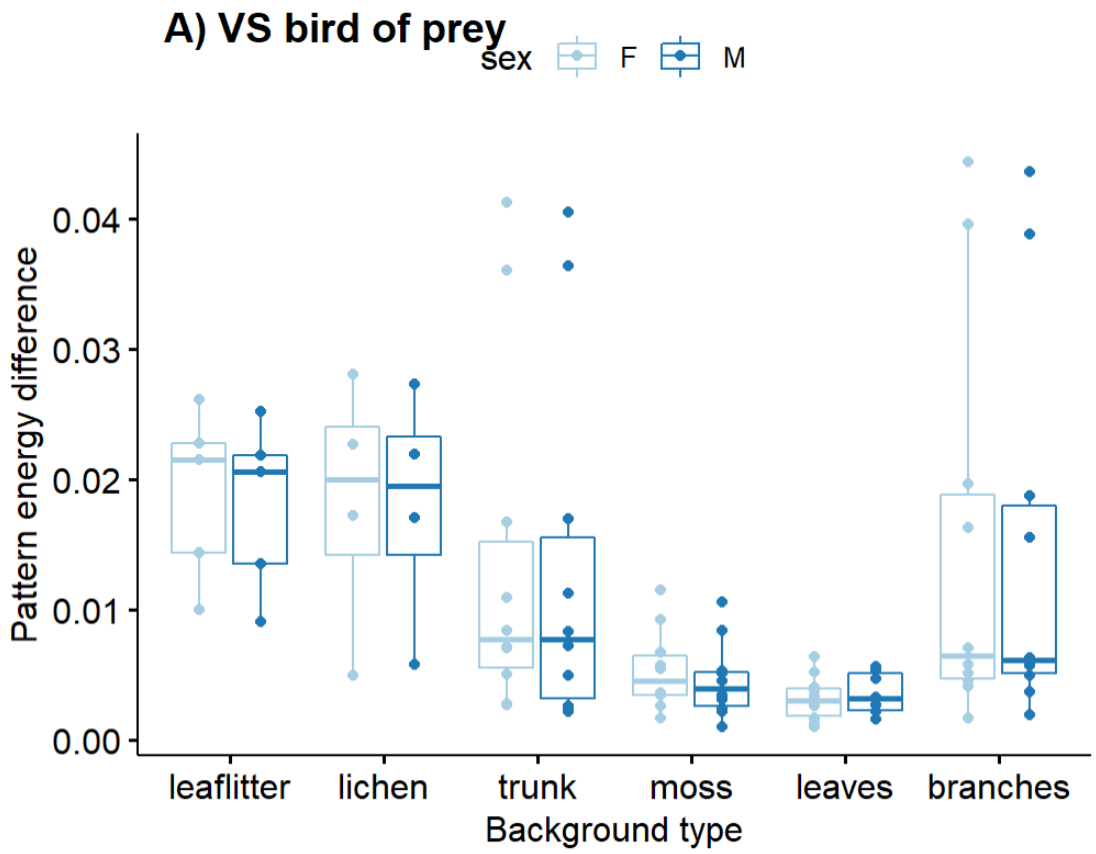
3.4.3. Pattern matching

From the granularity analysis, I calculated pattern energy difference (PED) values as a camouflage metric; these measure the degree of background pattern matching between titipounamu and the different background types using the VS bird of prey and UVS passerine visual systems. The PED values are a way to evaluate the absolute difference in pattern spectra between samples across different spatial scales (Troscianko & Stevens, 2015). Lower PED values arise from patterns that display similar energy at each spatial scale, which signifies a closer level of background pattern matching.

There were no significant interactions between sex and background type for the VS bird of prey nor the UVS passerine visual system for pattern energy difference values (Table 2), suggesting that neither sex was significantly more contrasted in terms of pattern than the other against any background type (Figure 6). The linear mixed effects models also provided no evidence of a difference between the levels of pattern matching between either sex (buzzard model: $p = 0.860$; blue tit model: $p = 0.764$), with both sexes having similar mean PED values in the VS model (female: mean PED ± SE = 0.0122 ± 0.00157; male: mean PED ± SE = 0.0119 ± 0.00157) and the UVS model (female: mean PED ± SE = 0.0122 ± 0.00157; male: mean PED ± SE = 0.0119 ± 0.00157). The low values for both sexes suggest that both male and female dorsal plumage is a close pattern match for their backgrounds. There were, however, some significant differences in PED values between the background

types for both visual models (Table 2), indicating that the level of pattern matching varies depending on what type of background titipounamu are compared with.

Leaf and moss background types had the lowest PED values under the VS bird of prey model (leaves: mean PED ± SE = 0.00327 ± 0.00226; moss: mean PED ± SE = 0.00483 ± 0.00226) and the UVS passerine model (leaves: mean PED ± SE = 0.00301 ± 0.00130; moss mean PED ± SE = 0.00304 ± 0.00130), suggesting that these backgrounds have the closest pattern matching with titipounamu plumage. For the VS bird of prey model, I found evidence that both leaves and moss had lower PED values than branches (leaves: p = 0.0045; moss: p = 0.022; branches: mean PED ± SE = 0.01467 ± 0.00226), leaf litter (leaves: p = 0.003; moss: p = 0.01; leaf litter: mean PED ± SE = 0.01828 ± 0.00322) and lichen backgrounds (leaves: p = 0.01; moss: p = 0.03; lichen: mean PED ± SE = 0.01769 ± 0.00361), with leaves also having significantly lower PED values than trunks (p = 0.014; trunks: mean PED ± SE = 0.01353 ± 0.00226). This suggests that a VS avian predator would find it harder to distinguish between the patterns of a titipounamu and its background if it was against leaves or moss compared to these other background types. Under the UVS model, leaves and moss were only significantly different from the lichen background type (leaves: p = 0.013; moss: p = 0.014; lichen: mean PED ± SE = 0.01114 ± 0.00209), which had the highest mean PED value. There were no other significant differences in PED values across the background types for either visual model (Table 2), suggesting that the level of pattern matching to titipounamu dorsal plumage is similar across these backgrounds.


A) VS bird of prey
sex
F
M
Pattern energy difference
0.04
0.03
0.02
0.01
0.00
leaflitter
lichen
trunk
moss
leaves
branches
Background type

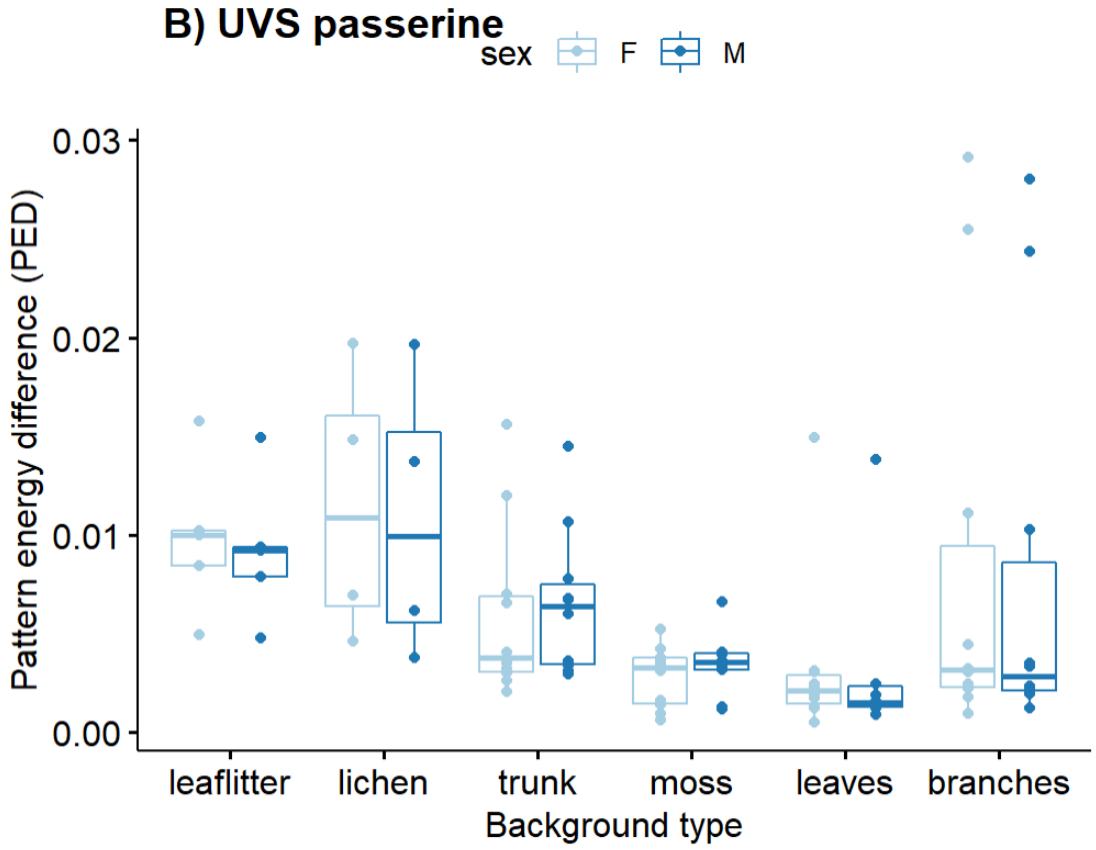

B) UVS passerine
sex
F
M
Pattern energy difference (PED)
0.03
0.02
0.01
0.00
leaflitter
lichen
trunk
moss
leaves
branches
Background type

Figure 6: Pattern energy difference (PED) values for titipounamu compared to the different background types as modelled under A) violet sensitive (VS) common buzzard (*Buteo buteo*) and B) ultraviolet sensitive (UVS) bluetit (*Cyanistes caeruleus*) visual models. Lower values indicate a closer match between titipounamu dorsal plumage and the background. Each sex is represented as a separate boxplot, with light blue (left) as female and dark blue (right) as male. Boxplots show the median values (bold middle line), the interquartile range (box), and the range values (whiskers) including outliers (unattached dots). Each data point is represented with a dot.

3.5. Discussion

In this chapter I investigated whether titipounamu dorsal plumage is cryptic against the background colours of their native environment. I found that titipounamu were chromatically and achromatically distinguishable against their environmental backgrounds to both a UVS passerine (blue tit) and a VS raptor (common buzzard) receiver. I did find, however, that they may have close pattern background matching, although this did not vary between males and females. While both sexes were distinguishable against their backgrounds, males were a closer chromatic and achromatic match to the background substrates, particularly against green backgrounds. Females were more chromatically and achromatically contrasting than males against most backgrounds. These results challenge previous work that implied that titipounamu sexual dichromatism may be driven by a need for crypsis against their respective foraging backgrounds. It also does not support my prediction that females may be under selection for increased crypsis due to their foraging behaviours.

3.5.1. Chromatic colour differences

Interestingly, there were no significant differences in chromatic contrast between any of the backgrounds for either sex, suggesting that titipounamu colour is just as distinguishable against all backgrounds. However, when background substrates were grouped in terms of colour, male plumage was a significantly closer match to green backgrounds than female

plumage. This is partly aligned with findings from previous work (Hunt and McLean, 1993), which found that the colour of each sex matched more closely to their most frequently used background types. I found that males were less contrasted against green backgrounds such as leaves and moss, but both sexes were similarly contrasted against brown backgrounds like bark and trunks. The difference in conspicuousness against green backgrounds between males and females may suggest that there is selection for males specifically to be more cryptic, although they are still distinguishable to the predator visual model. As neither sex was particularly well matched to the background substrates, overall, the results cast doubt on whether crypsis could be driving the sexual dichromatism seen in titipounamu. However, it does not necessarily mean titipounamu are not cryptic at all; they could have evolved a 'compromise' strategy, where they do not match any background perfectly, but do match all potential backgrounds to a certain degree (Merilaita et al., 1999; Stevens & Ruxton, 2019). Models have found that this camouflage strategy can be selected for in species that live in a heterogenous environment where predation occurs equally across all background types (Houston et al., 2007; Merilaita et al., 1999). Titipounamu are found in a range of forest habitat types including coastal broadleaf forest, high altitude podocarp forest, mature complex forest and regenerating native bush and use all strata of the forest environment (Higgins et al., 2001). They are, therefore, found in a wide range of vegetation, with a high diversity of colours and textures. Additionally, titipounamu do appear to display countershading, a common crypsis strategy in habitats where light is coming from above, such as in forests (Gomez & Théry, 2007). Light ventral colouration matches the lighter canopy environment to reduce detectability by predators below, while darker dorsal colouration blends in with the lower light levels and darker colours of the forest floor to conceal the bird from predators viewing from above. The white ventral plumage of titipounamu may, therefore, be acting as a form of cryptic colour, although countershading does not always reduce predation risk (Ruxton et al., 2004; Speed et al., 2005).

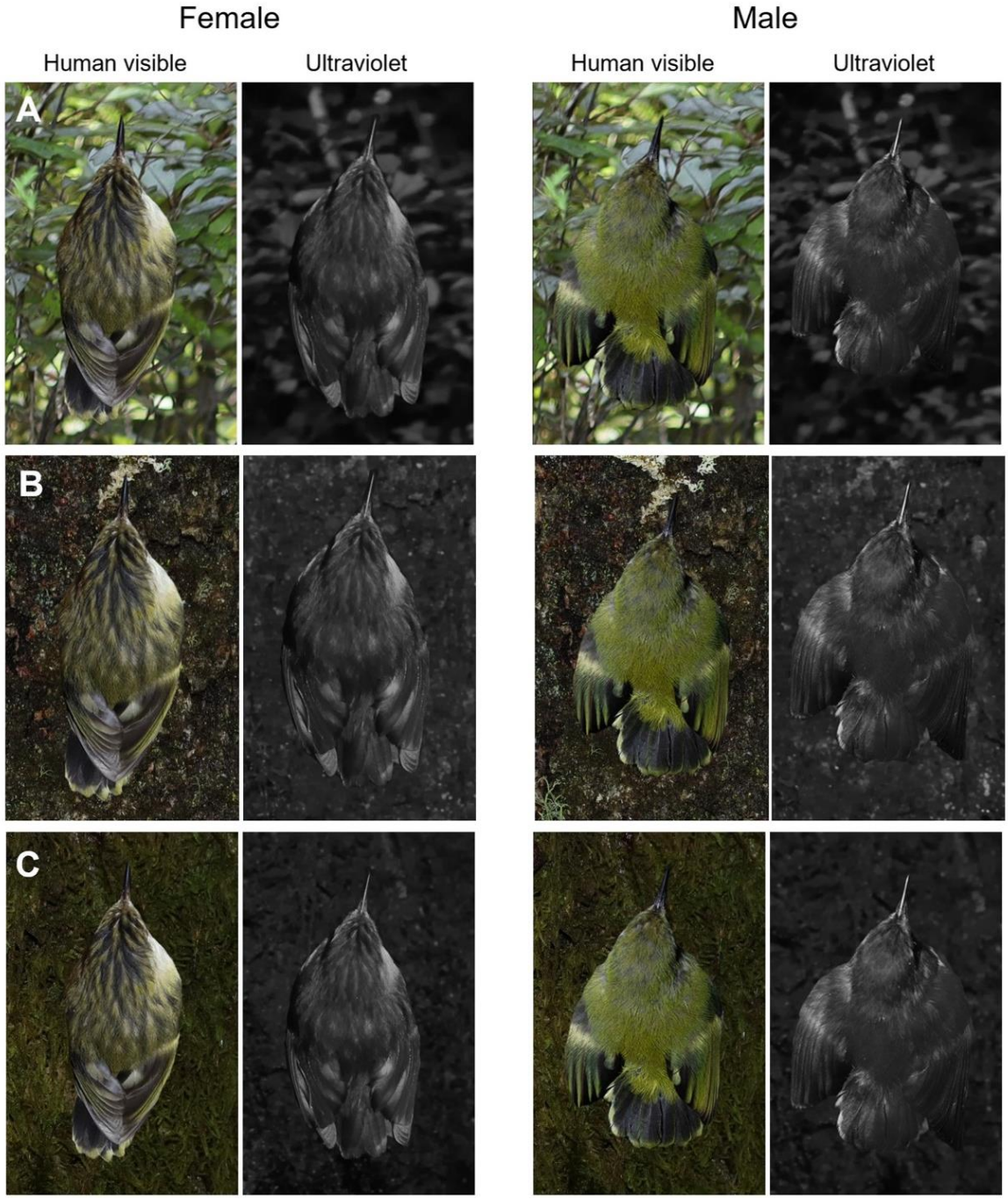
While the dorsal plumage of both sexes was discriminable against all background types for both avian visual models, females were more contrasted than males overall, particularly against green backgrounds. This result challenges my prediction that the sexual dichromatism in titipounamu is driven by the female's need to be cryptic while foraging, rather than the need for each sex to be cryptic against different backgrounds. Instead, it suggests that males are potentially more cryptic than females but only when on green backgrounds, although both sexes were clearly distinguishable for both the VS bird of prey and UVS passerine models. This finding also contradicts other hypotheses for sexual dichromatism. Wallace (1891) hypothesised that sexual dichromatism could be driven by natural selection acting on females to become more cryptic; he suggested that increased cryptic colouration would reduce predation risk for females during incubation and chick rearing. While this theory does not align with titipounamu life history as both sexes contribute to nest care (Sherley, 1990; Sherley, 1994), the finding that females are slightly more conspicuous than males makes it more unlikely as an explanation for titipounamu sexual dichromatism.

It is important to note that the visual models used for this study are only proxies for the visual systems of titipounamu predators and the birds around them (Hart, Partridge, Cuthill, & Bennett, 2000; Lind et al., 2013). The vision of New Zealand birds has not been well studied, and thus we cannot be sure that the models used are representative of titipounamu predators. This may be particularly important to consider while interpretating small differences in colour, and these may not persist if a different visual model was used. Likewise, neither of these visual models can be used to represent titipounamu vision, so future research is needed before I can definitively assess how cryptic or conspicuous their colour is to conspecifics. Titipounamu have an unusual opsin gene sequence that controls the class of UV cone in birds (Ödeen & Håstad, 2013), so we cannot be sure of the extent of UV vision in titipounamu. There are also no closely related species with visual models to use as a proxy for titipounamu spectral sensitivities. Thus, care needs to be taken before making

conclusions about how titipounamu individuals see conspecifics' colouration based on the UVS passerine model.

This finding also contributes to the growing body of research challenging the idea that green plumage is always cryptic (Bajer et al., 2011; Blount & McGraw, 2008; Griggio et al., 2009; Saks et al., 2003); in this study, neither the male (green) nor the female (yellow-green stripes) were found to be close chromatic matches with their background environments. Although green colour often does contribute to crypsis, it can also signal information about the health and quality of the animal (Blount & McGraw, 2008). Green colouration can be produced through structural blue colour combined with carotenoids or melanin (Shawkey & D'Alba, 2017). Previous research has indicated that titipounamu feathers contain carotenoids and so this system is a likely mechanism for the green colour found in titipounamu plumage (Thomas et al., 2014). Carotenoid-based plumage colouration is often dependent on the foraging success and physical condition of birds (Blount & McGraw, 2008; Pike et al., 2009), and thus can provide honest signals about the quality of a potential mate or rival. Green colour also often has an ultraviolet component which can provide additional signalling that is not visible to us nor predators with limited UV visual capabilities and can inform receivers on signaller quality and health (Andersson, 1999; Doucet & Montgomerie, 2003; Griggio et al., 2009; Håstad et al., 2005; Siefferman & Hill, 2005). Both sexes of titipounamu show UV reflectance of their green or yellow-green plumage (Figure 7), which may not be visible to their avian predators, which likely have limited UV vision (Lind et al., 2013; Potier, 2020). How well titipounamu can see into the UV spectrum is speculative (Ödeen & Håstad, 2013), but if they do have UVS vision their UV colouration could have a signalling function. This is the case for *Eclectus* parrots, in which the green males appear cryptic to their predators, but their UV reflectance allows them to be conspicuous to conspecific females (Heinsohn, 2008). As my results indicate that the green colouration in titipounamu may not be driven by a need for crypsis, future research could explore whether

titipounamu green is important for mate selection or competitive interactions with other individuals.



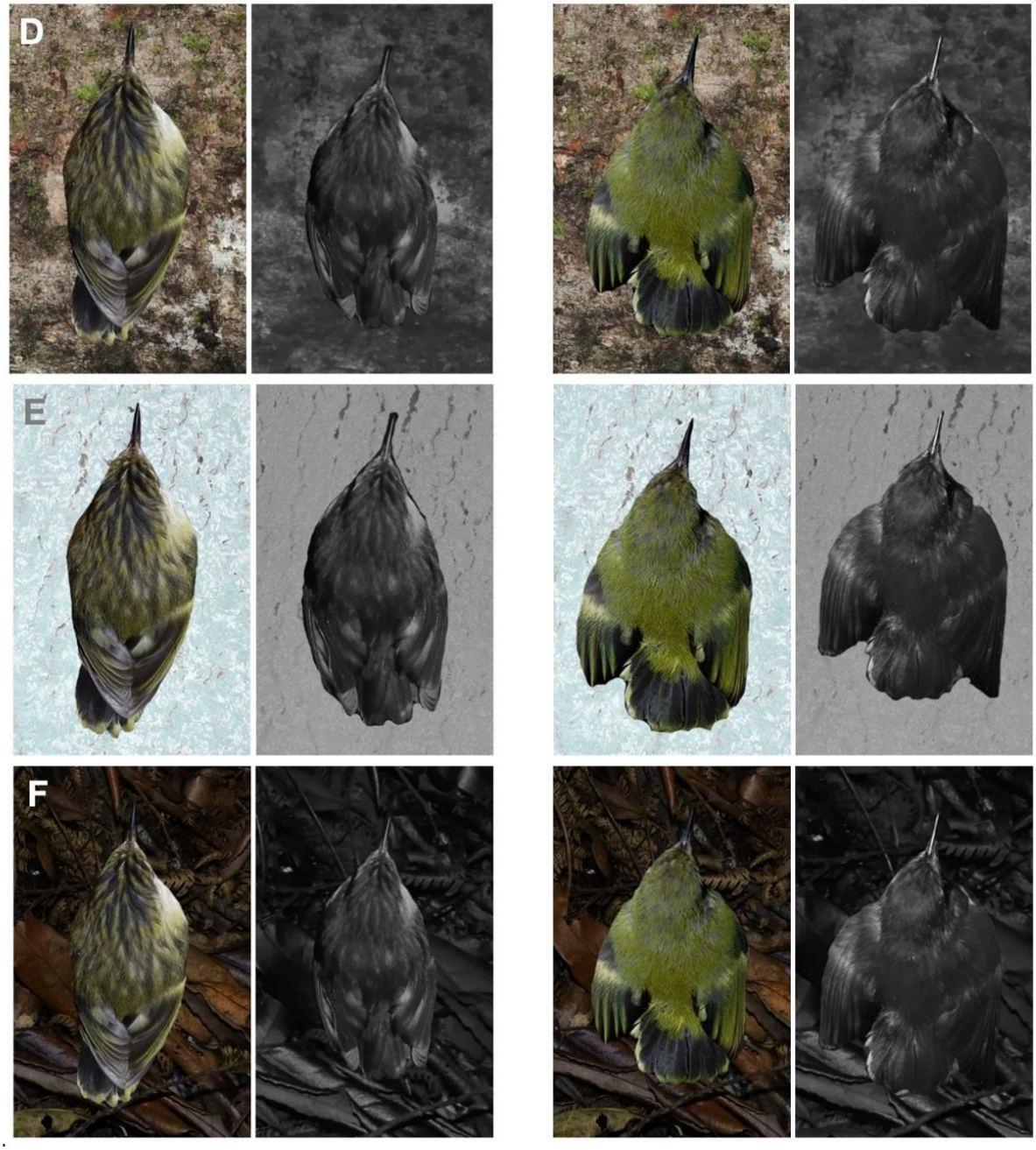


Figure 7: Dorsal views of titipounamu (*Acanthisitta chloris*) edited to appear against different background substrates in human visible and ultraviolet images. Note that this figure is only for demonstrative purposes, and the colour of the birds and background in these images have not been calibrated and may not be to scale. A) leafy background of horopito (*Pseudowintera colorata)*; B) bark on the trunk of a red beech (*Fuscospora fusca*); C) moss on the trunk of a red beech; D) bark of a red beech branch; E) White crustose lichen on the trunk of a kamahi (*Weinmannia racemosa*); F) mixed leaf litter.

3.5.2. Luminance and achromatic colour differences

Achromatic background matching is another important but less represented aspect of camouflage. Often thought of as brightness, high achromatic differences can increase how easy it is to distinguish between two subjects, even if chromatic differences are very low (van den Berg et al., 2020). Thus, when exploring background matching and crypsis, considering both chromatic and achromatic colour is vital (Hiramatsu et al., 2008; Isaac & Gregory, 2013). I found that achromatic contrasts, like the chromatic values, were mostly above the JND discrimination threshold, suggesting that titipounamu are clearly distinguishable to blue tits and common buzzards across multiple background types. Surprisingly, females were significantly more contrasted in achromatic colour than males, but only in the VS bird of prey model. This means that females were both chromatically and achromatically more distinguishable overall than males, especially to the predator model, further emphasising the points discussed above.

High achromatic differences between lichen and titipounamu plumage colour may be why I rarely observed titipounamu against lichen backgrounds (see Chapter 2). There are many examples of species that are aware of how contrasted they against their background and change their behaviour accordingly (Stevens & Ruxton, 2019). For example, nightjars (*Caprimulgus* spp.) flee their nest sooner in the presence of perceived predators when the incubating adult's plumage is a poorer match to their surrounding environment (Wilson-Aggarwal et al., 2016). Likewise, common potoo (*Nyctibius griseus*) tend to choose perches that increase background matching and masquerade (Cestari et al., 2018), and some ground-nesting birds choose and modify their nest location to increase its camouflage with the surrounding habitat (Gómez et al., 2018; Stevens et al., 2017). Titipounamu, therefore, could be avoiding lichen substrates to reduce their conspicuousness to predators. Alternatively, lichen may just be less common than other background types at our study site, making titipounamu less likely to be seen against it. While lichen had a significantly higher achromatic difference to titipounamu plumage than any other background, titipounamu were

also found to be distinguishable against the other background types as well, so may still be conspicuous even when not against lichen.

3.5.3. The contribution of pattern matching to crypsis

Measures of chroma are often used as the main metric to measure the degree of crypsis or chromatic background matching. However, other factors such as luminance and pattern are increasingly being acknowledged as important contributors to camouflage (Troscianko et al., 2016). The role of egg patterning in clutch survival has been well documented for birds, with eggs with patterns that closely match their nest and environment background having increased chance of survival across multiple species and environments (Gómez et al., 2018; Lee et al., 2010; Westmoreland, 2008). Likewise, having a contrasting plumage pattern that matches the contrast of the background can also improve camouflage; nightjar nests were less likely to be depredated when the incubating adult's plumage pattern was a close contrast match to their background (Troscianko et al., 2016). Selection for cryptic patterning can also vary across sex, driving sexual dichromatism. For example, female *Sphenarium* grasshoppers are closely chromatically matched to their backgrounds, while the highly mobile males exhibit disruptive colouration that camouflages them against their greater variety of background types (Ramírez-Delgado & Cueva del Castillo, 2020).

Titipounamu males and females had similar pattern energy differences across all background types, suggesting that both sexes are similarly contrasted to their backgrounds in terms of their pattern matching for both blue tit and common buzzard visual systems. This result provides further evidence to challenge the idea that titipounamu sexual dichromatism is driven by the need for each sex to be cryptic against different background types. If this hypothesis were the case, we would expect males to be more closely matched to leaves and branches, and less so to substrates found on trunks (such as bark and moss) as males are less likely to forage on trunks than females (see Chapter 2). However, we see both sexes

closely matched to a range of background types, and very little difference between the pattern matching of each sex. While this result challenges the idea that different colour matching needs are driving titipounamu sexual dichromatism, it may still indicate that titipounamu are cryptic in their environment as they display high pattern matching (Cuthill et al., 2005; Gómez et al., 2018; Price et al., 2019; Troscianko et al., 2016).

Disruptive colouration is an important type of pattern that can provide a more generalised camouflage, even independently of colour background matching (Schaefer & Stobbe, 2006). Disruptive colour works by having highly contrasted patterns along the edges of the body that mask the shape's outline, making it harder for a receiver to distinguish between body and background and reducing prey recognition (Price et al., 2019b). Disruptive colouration around the edges of crab shells alongside variation in patterns across the population were also found to hinder search image formation, where predators focus on a certain morph to improve their hunting efficiency (Troscianko et al., 2021). Although I am not aware of any studies of this as of yet, future research could investigate the benefits of pattern variation across a population and how this could potentially be a driver of sexual dichromatism – a greater variation in the population and across sexes could make it more challenging for a predator to select a morph to focus on. For species that spend a lot of time in pairs or groups such as titipounamu (Higgins et al., 2001; Sherley, 1990), it could also reduce the risk of a predator attacking all of the individuals at once if that predator has formed a search image for a particular sex (Pietrewicz & Kamil, 1979; Troscianko et al., 2021). Unfortunately, as I could not photograph the birds while they were on their background environments, I could not evaluate their potential for disruptive colouration. However, both males and females have coloured stripes along their otherwise dark wings (Figure 8) which could potentially play a role in disrupting their edges, alongside the females' brown dorsal mottling (Price et al., 2019; Stevens et al., 2006). The more intricate patterning on female birds could also be compensating for their increased colour contrast against their background compared to males. The potential for disruptive colouration in titipounamu could be an interesting avenue

for future studies to explore the importance of pattern and edge disruption in camouflage of species that is a poor chromatic and achromatic colour match to their background.

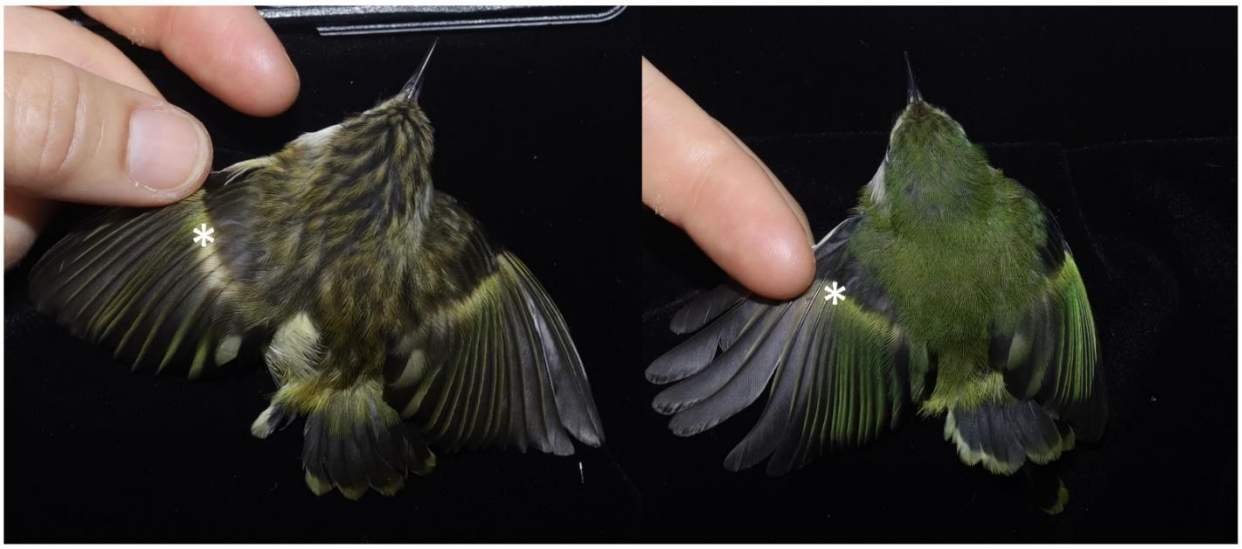


Figure 8: Images of titipounamu (*Acanthisitta chloris*) showing the coloured stripes along the dark wing primaries in each sex (female on the left, male on the right), as well the dark mottling of the female dorsal plumage that could potentially play a role in disruptive colouration. Also note the coloured patch (labelled with a white *) below a dark patch that could act to break up the wing shape, and the coloured edges to the otherwise dark tail feathers.

My results also appear to show greater pattern matching for the UVS passerine model compared to the VS bird of prey. This may be due to the UVS blue tits having a lower visual acuity than that used for the VS common buzzard model, and therefore not being able to see the patterns at high resolution, resulting in some loss of detail (Caves, Brandley et al., 2018; Donner, 1951). This is still an interesting result as it may indicate how passerines see each other in forest environments, including how titipounamu see each other. Visual acuity is influenced by body size, diet, and habitat (Mitkus et al., 2018). Titipounamu likely have comparable acuity to blue tits as both species are small, insectivorous passerines that live in forested areas (Banbura et al., 1999; Higgins et al., 2001). Thus, if it is the acuity influencing the pattern matching, titipounamu may also struggle to differentiate between plumage and

background patterns of their partner while foraging. If this is the case, it may explain why pairs constantly make contact calls to keep track of where each other are (Higgins et al., 2001). They also perform a constant wing flicking motion while foraging (pers. obs.), which could also make it easier for partners to see each other as motion can reduce the effects of camouflage (Hall et al., 2013; Wilson-Aggarwal et al., 2016). Future research could focus on testing how the effectiveness of pattern matching is affected by changes in receiver distance and visual acuity; this would be an interesting way to explore how different types of pattern matching might evolve depending on the specific predator and environment.

3.5.4. Do titipounamu demonstrate sex specific crypsis in their natural environment?

This study suggests that for the avian visual systems modelled, titipounamu chromatic and achromatic colour is clearly distinguishable against most background types, although overall males are less conspicuous than females against green backgrounds and females are more conspicuous overall. Thus, titipounamu do not appear to be cryptically coloured to a diurnal VS raptor nor a general UVS passerine model. They may be using pattern matching to reduce their conspicuousness; however, I found no difference in pattern matching between the two sexes. Further research is required to explore different types of pattern matching before we can conclude whether titipounamu are cryptic or not, but overall, these findings cast doubt on the hypothesis that titipounamu sexual dichromatism is driven by the need to be cryptic against different backgrounds. This study also demonstrates how incorporating ultraviolet reflectance and visual modelling to a study can significantly change how we view a species – this result is the opposite of previous work (Hunt and McLean, 1993), which implied that titipounamu were cryptic in their respective environments when viewing them solely from a human perspective.

Chapter 4

Are there sex differences in titipounamu nesting behaviour to compensate for conspicuousness?

4.1. Abstract

More conspicuously coloured birds are often at a greater risk of being detected by predators. In sexually dichromatic species, if one sex is more conspicuous than the other, they may have an increased risk of attracting predators to the nest. Thus, increased anti-predation behaviours to compensate for a higher nest predation risk may be selected for in the more conspicuous sex. Titipounamu (*Acanthisitta chloris*) are an interesting species to explore this idea in as males and females contribute evenly to parental care and both sexes display sexually dichromatic plumage that could be conspicuous against their nest background. Thus, I aimed to determine whether there were sex differences in anti-predation behaviours at the nest in titipounamu that could be linked to one sex being more conspicuous than the other. I found no evidence of sex differences in anti-predation behaviours such as vigilance and time spent visible at the nest. This suggests that either titipounamu do not vary in how conspicuously coloured each is sex at the nest, or that the differences in conspicuousness are not large enough for behavioural differences to be selected for. I also found that females were more vigilant after feeding at exposed nests, implying that the location of the nest can influence anti-predation behaviours. This study provides an interesting example of where sexual dichromatism has not led to selection for different anti-predation behaviours at the nest. More exaggerated sex differences in conspicuousness may be needed to drive selection for different nest behaviours.

4.2. Introduction

In birds, being brightly coloured often leads to increased reproductive success, as high-quality individuals can signal their quality to potential mates (Andersson & Simmons, 2006; Tobias et al., 2012). However, being conspicuously coloured also has a cost; it can make an individual more visible to their predators (McQueen et al., 2017; Ruiz-Rodríguez et al., 2013). In sexually dichromatic species, this can result in one sex being more conspicuous than the other, and thus at higher risk of being detected by predators. Attracting the attention of predators may be particularly problematic during the breeding season, as nesting marks a vulnerable stage for birds (Ricklefs, 1969). Nesting requires high parental investment costs in time and energy (Bjerke et al., 1985). Nests are also often vulnerable to predation and adults are at risk of being depredated while incubating or feeding (Cresswell, 1997). Thus, adaptations that can reduce the risk of nest predation are strongly selected for (Matysioková & Remeš, 2018), and may be particularly important compensatory strategies for species that are highly conspicuous around the nest (Colombelli-Négrel & Kleindorfer, 2009; de Moraes et al., 2020). One strategy to reduce nest predation and parasitism is to implement anti-predation behaviours. These behaviours act to avoid predation by reducing how visible the parents are around the nest, given greater activity levels near nests can increase the risk of attracting predators (Matysiokova & Remes, 2018; Remes, 2005; Skutch, 1949). In some sexually dichromatic species, the conspicuous sex reduces their visitation rates or how much time they spend visible at the nest as demonstrated by the conspicuous males in superb fairy wrens, *Malurus cyaneus* (Colombelli-Négrel & Kleindorfer, 2009). Conspicuous birds can reduce their nest visitation rates, while still maintaining the necessary caloric influx for their chicks, by bringing larger or higher quality food items per visit (Colombelli-Négrel & Kleindorfer, 2009; Grieco, 2002). Alternatively, some species, such as the blue-black grassquit (*Volatinia jacarina*), only reduce their visitation rates when a predator has been detected (de Moraes et al., 2020). Being vigilant around the nest can also increase the chance of detecting nearby predators, reducing the risk of leading a predator to the nest or

being trapped in the nest while feeding (Artiss & Martin, 1995; Matysiokova & Remes, 2018; Remes, 2005; Skutch, 1949; Watson et al., 2007; Yasukawa et al., 1992; Yasukawa & Cockburn, 2009). Vigilance behaviours can include increasing the time spent before entering and leaving the nest, alert calls and having sentinels that keep watch around the nest. For example, when perceived predation risk increased, lined seed eaters produced more alarm calls, particularly the more conspicuous males (van den Bemt et al., 2021). American gold finches also alarm call in the presence of predators, and as nestling respond to the calls by crouching and freezing to reduce conspicuousness, finches with higher call rates have greater nest success (Knight & Temple, 1986).

The location of a nest may increase its risk of predation and therefore influence the behaviours of the birds interacting with that nest, especially for more conspicuous birds. More exposed nests may be more easily detectable by predators, putting them at greater risk of failure (Götmark et al., 1995). However, more concealed nests may put the adult birds at greater risk, as it reduces the range at which parents can detect incoming predators, giving them less time to escape (Gómez-Serrano & López-López, 2014a). As a way to balance this trade-off between nest and parental survival, anti-predation behaviours could be selected for (Weidinger, 2002). For example, in blackcaps (*Sylvia atricapilla*) degree of nest concealment did not influence nest survival, likely because parents were compensating for greater exposure with anti-predation behaviours such as increased vigilance (Remes, 2005).

Green colouration in birds is often assumed to be selected for to increase crypsis (Gomez & Théry, 2007; Marshall et al., 2016; Ramírez-Delgado & Cueva del Castillo, 2020). However, as green colour in birds is often produced through carotenoid pigments that are only obtainable through diet, green colour can function as a signal of mate or rival quality (Blount & McGraw, 2008; McGraw & Nogare, 2004; Pike et al., 2009; Saks et al., 2003). Green colour also often has ultraviolet reflectance produced through the pigments and structural blue colour underlying them, that could reduce how camouflaged they appear to species that can see within the UV spectrum (Andersson, 1999; Doucet & Montgomerie, 2003; Griggio et

al., 2009; Hausmann et al., 2003; Shawkey & D'Alba, 2017; Siefferman & Hill, 2005). Thus, in sexually dichromatic species where one sex has green plumage, this green sex may be more conspicuous than the other, although these differences may be more subtle than previously discussed examples with more exaggerated dichromatism. It could be interesting to study whether anti-predation behaviours vary across sex in a green sexually dichromatic species given the potentially less exaggerated differences in conspicuousness. Titipounamu (*Acanthisitta chloris*) are green sexually dichromatic forest birds (Hunt & McLean, 1993), and an interesting species in which to study anti-predation behaviours across sexes of varying conspicuousness. Titipounamu build nests in enclosed cavities and exhibit biparental care shared evenly between parents (Sherley, 1994). Male birds have green dorsal plumage, while the larger females have brown dorsal plumage mottled with yellow-green stripes. While previous work implied that their plumage was cryptically coloured, my results from Chapter 3 suggest that both sexes are distinguishable to predators against different backgrounds. Their sexual dichromatism means that there is potential for one sex to be more conspicuous than the other at the nest. A green bird potentially being the more conspicuous sex also contributes to the growing body of work challenging the assumption that green colouration is only used for crypsis (Bajer et al., 2011; Berg & Bennett, 2016; Burtt et al., 2011; Griggio et al., 2009; Kopena et al., 2020; Saks et al., 2003). The potential native predators of titipounamu are all avian, such as the long-tailed cuckoo (*Eudynamys taitensis*), morepork owl/ruru (*Ninox novaeseelandiae*), New Zealand falcon/kārearea (*Falco novaeseelandiae*), sacred kingfisher/kōtare (*Todiramphus sanctus*), and Australasian swamp harrier/kāhu (*Circus approximans*), meaning that the predators they evolved with locate prey mostly visually (Higgins et al., 2001; Moran et al., 2019). Therefore, compensating for conspicuous colouration may be particularly important for titipounamu to reduce being visually detected by their predators. If one sex is more conspicuous than the other, they may compensate for their increased visibility to predators by performing more anti-predation behaviours at the nest.

In this chapter, I aim to determine whether there are sex differences in anti-predation behaviours at the nest in titipounamu, a sexually dichromatic green forest species in which both sexes may be conspicuous at the nest due to their biparental care and lack of cryptic colouration. I compared male and female behaviour at natural nests for a titipounamu population in the North Island of New Zealand. I predict that due to their differences in colour, one sex will be more conspicuous at the nest than the other and may display more anti-predation behaviours to compensate for their increased predation risk. These anti-predation behaviours could include spending less time visible at the nest (to observers) but spending more time displaying vigilance behaviours. Interestingly, titipounamu also nest concealed in cavities (Higgins et al., 2001; Sherley, 1985), which may reduce the need for anti-predation behaviours as birds are not visible while on the nest (Martin & Li, 1992). However, nests vary in the degree to which the adults are visible while feeding chicks, providing an interesting opportunity to explore how nest exposure influences anti-predation behaviours. I predict that birds, particularly the more conspicuous sex, will display increased vigilance and reduce their time spent visible at more open nests relative to cavity nests, to compensate for increased visibility to predators. The presence or absence of sex differences in anti-predation nesting behaviours will give insights into how conspicuous colour can influence the behaviours of a sexually dichromatic, cavity nesting, biparental green bird.

4.3. Methods

4.3.1. Finding nests and birds

Nests were located by observing behavioural cues from titipounamu across the austral summer breeding seasons (November - January) during 2019-2021 at Boundary Stream Mainland Island (see Chapter 2 for more detail on study species and site). This mature, native forest presents a complex and diverse habitat for titipounamu to nest. Birds were located by listening for their vocalisations and then followed to find natural nests. The titipounamu population is partially banded due to previous research at this study site (for example, see Moran, Loo, & Cain, 2019).

Titipounamu are classified as secondary cavity nesters, but they use a wide variety of nests including in holes in the ground, hollow branches, and tree fern skirts (Higgins et al., 2001). For this study, nests were classified into two types based on how exposed adults are while feeding chicks: open nests, where the adult is visible throughout the entire visit, and closed nests, where the adult fully enters the nest during a visit and is not visible while feeding (Figure 1). Nests were also grouped by the developmental stage the chicks were at during data collection. As titipounamu nestlings remain in the nest for approximately 20 days, nests were classed as ‘early’ stage if parents were still partly incubating, chicks were not making multi-note calls (which begin between days 9-13 after hatching; Loo, personal communication, December 8th, 2020) or if it was less than 10 days after hatching. If the nest and chicks had passed these dates or milestones, nests were classed as ‘late’ stage.

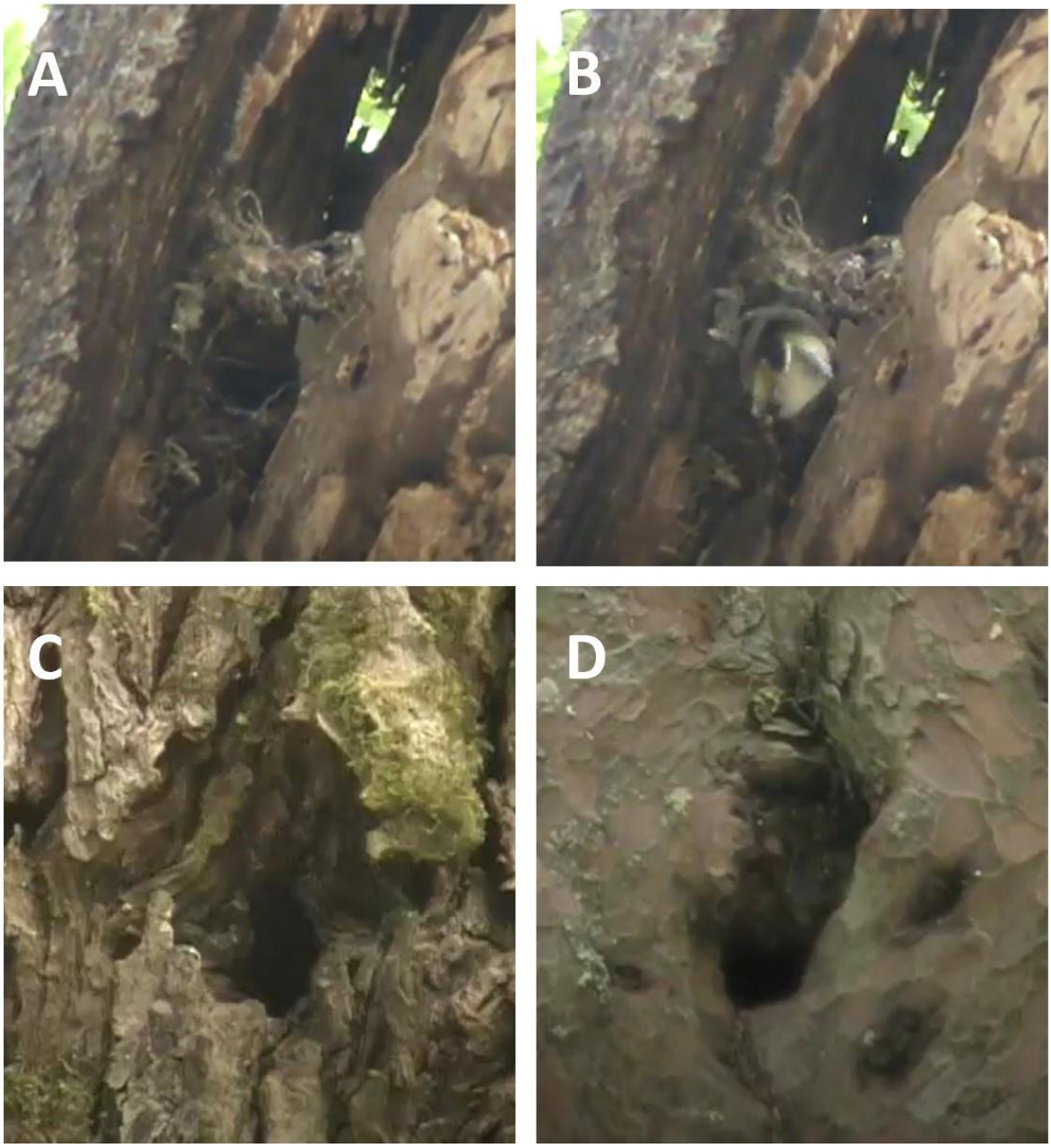


Figure 1: Images of different titipounamu (*Acanthisitta chloris*) nests to demonstrate the difference between open and closed nests. A) An open nest built into a partly hollow, decaying branch, with the circular nest hole clearly visible as well as part of the woven nest structure. B) The same nest as in image A, but with a male titipounamu leaning in to feed the chicks – as he is clearly visible while feeding, this nest is classed as open. C) A closed nest built into a cavity in the trunk of a tree – the nest itself is completely obscured and birds must enter the trunk to feed chicks, completely hiding them from view. D) Another closed nest in a trunk cavity.

4.3.2. Recording behaviour at nests

Videos were taken of nests to record parental feeding activity using JVC GZ-MG330 Everio Hybrid HD camcorders. The video camera was placed on a tripod as close to the nest as possible without disturbing the birds (3-10m) and from an angle that gave an unobscured view of the nest entrance. The camera was zoomed in to give a clear view of the nest entrance and visiting birds, while leaving at least an approximately 50cm radius around the nest hole to observe the behaviour of birds in the vicinity of the nest entrance. This radius was deemed as the “nest area”. When placing cameras, we waited for each parent to visit to ensure they would still enter the nest and were not making alarm calls at the presence of the camera, then left the camera in place for 1-hour periods, with up to 4 hours of footage obtained at each nest, depending on weather and nest stage. In total, 20 nests had video quality that enabled accurate sexing of adults and analysis of 10 visits per sex.

I scored videos using Behavioral Observation Research Interactive Software (BORIS) version 7.9.7 (Friard et al., 2016). Visitation events were initiated at the first frame that a bird made physical contact with the nest area and ended at the first frame after the bird was no longer making physical contact with the nest area. Behavioural events were scored using the ethogram in Table 1. The duration (seconds) of each event was recorded by using the frame-by-frame analysis tool in BORIS. Sex and individual identification were identified by plumage colouration and band colour combination. For each nest, the first 10 male visits and 10 female visits were scored. At nests where birds were unbanded and not individually identifiable, I treated the nest as a unit and grouped all bird visits into either male or female. For nests with early chicks only the first 5 male and 5 female visits were logged, as visitations occurred less frequently. Non-feeding visits were excluded from analysis. These included visits where the bird arrived with no food in its beak, entered an early nest for an extended period of time (more than 5 minutes) presumably to incubate, or arrived with food but left before feeding.

Table 1: Ethogram for scoring titipounamu nest video using BORIS. Behaviours are classified into visible or hidden depending on whether they can be seen from outside of the nest. Behaviours are also classified as open, closed or both, which refers to the type of nest the behaviour can be performed at. Open nests did not require the parents to enter to feed, closed nests required birds to enter and be fully hidden from view during feeding. Durations (s) were taken of state events. Modified from Bidmead, M (unpublished data).

Behaviour	Visible (V) or Hidden (H)	Description	Open (O), Closed (C), or Both (B)	State (S) or Point (P) event
Arrival	V	Parent arrives near nest entrance, more than 5cm away	B	State
Nest entrance	V	Parent arrives at nest entrance, within 5cm	B	State
Enters to feed	H	Parent enters the nest hole, out of sight	C*	State
Feeds	V	Parent remains visible, leans head in to feed chicks	O	State
Exits	V	Parent exits the nest, or removes head from nest	B	State
Leaves	V	Parent flies away from nest entrance, leaves camera view	B	Point
Vigilance	V	Parent displayed vigilance or searching behaviours such as standing still in 'heads up' behaviour, flattened head or moving to search nearby environment.	B	State

***** Birds typically only entered nests during feeding of nestlings, however birds with early-stage nests would occasionally enter nests to incubate. These visits were not included in analysis.

Vigilance behaviour was identified if the bird paused in a 'heads-up' posture around the nest, which involved them being alert, staring away from the entrance of the nest, often turning their heads to survey different directions (Figure 2). Birds would also often display a flattened head and lean away from the surface they were perched on.

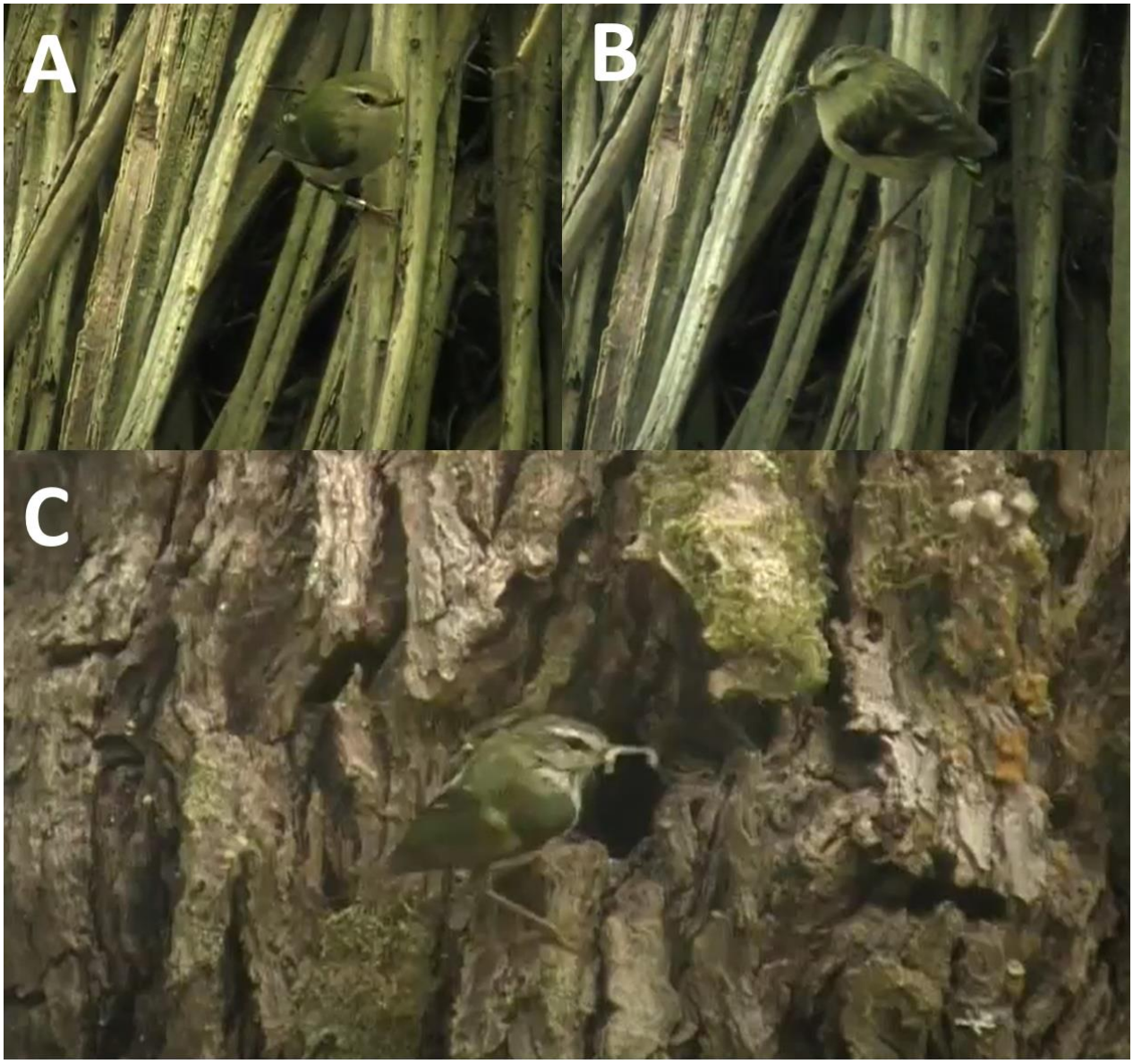


Figure 2: Examples of vigilance behaviour at titipounamu nests. A) Male displaying post-feeding vigilance after feeding at a tree fern nest– note the alert heads-up behaviour, leaning out from the nest and turning head to survey the surroundings. B) Female titipounamu displaying pre-feeding vigilance before feeding with an insect in her beak at a tree fern nest – she is paused to survey the area, keeping body still but head rotating and angled out away from the nest. C) Male fledgling helper bird at trunk cavity nest entrance displaying pre-feeding vigilance with insect in mouth – note the alert, flattened head, leaning away from the nest with head up and moving around to see from multiple directions before entering.

4.3.3. Analysis

The time spent visible per visit (s) was calculated by combining the total time spent at visible locations at the nest (Table 1), including arrival, nest entrance, feeding (only at open nests) and exiting. The time visible prior to feeding events and following feeding events were also analysed as separate nest visitation variables. Vigilance was split into two variables based on the stage of the visit: pre-feeding vigilance (vigilance before entering the nest or feeding) and post-feeding vigilance (vigilance after exiting the nest or finishing feeding) and analysed as a proportion of the time spent during these stages. Total time spent displaying vigilance behaviours at the nest per visit (s) was calculated by combining the total time spent performing vigilance behaviours at the nest both pre and post feeding. These variables were converted to proportions of time spent on each behaviour per visit.

Table 2: Response variables used in generalised linear mixed effect models and their brief description

Response variable	Description
Total duration of visit	How long the visit took to complete in seconds, starting from arrival to when the bird leaves the nest
Time visible before entering nest (pre-entry)	How long birds spent at the nest hole after arriving, but before entering or feeding (s)
Time visible after exiting the nest (post-entry)	How long birds spent at the nest hole after feeding and exiting, but before leaving (s)
Total time spent visible per visit	The combined time that the bird was performing visible actions at the nest (s)
Proportion of time spent vigilant	The proportion of time per visit that the bird was performing vigilance behaviours at the nest
Proportion of time spent vigilant before feeding (pre-feeding vigilance)	The proportion of time per visit that the bird was performing vigilance behaviours before entering the nest or feeding
Proportion of time spent vigilant after feeding (post-feeding vigilance)	The proportion of time per visit that the bird was performing vigilance behaviours after exiting the nest or feeding
Proportion of time spent visible per visit	The proportion of time per visit that the bird spent performing behaviours that were visible at the nest

All statistical analyses were performed in R (ver. 4.1.2; R Core Team, 2021). I used the 'glmer' function in 'lme4' package to create generalised linear mixed-effects models (ver. 1.1-27.1; Bates, Mächler, Bolker, Walker, 2015), accounting for repeated measurements by including individual birds and individual nests as random effects, and including sex, nest type and nest stage as fixed effects. Each model also included an interaction term of sex*nest type and sex*nest stage. A model was performed for each of the response variable in Table 2. Binomial generalised linear models (GLMMs) were used to compare the proportion data, whereas gamma GLMMs were used for the duration variables. To identify the model that best explained the data, I used a step-wise elimination process through likelihood ratio tests

(LRTs) for significance testing. Each model started by comparing the response variable and with fixed effects and interaction terms, which was then compared to a model with the same variables but no interaction term using the base ANOVA function with test set to “LRT”. A non-significant *p*-value ($p > 0.05$) result suggested that the interaction term did not add any predictive power to the model and could therefore be removed. This process was then repeated, removing one variable at a time to simplify the model, until a significant LRT result was acquired to signify the most accurate model. Post-hoc tests of multiple comparisons were conducted for significant interactions ($p < 0.05$) using the ‘emmeans’ function of the emmeans package (ver. 1.7.1-1; Lenth, 2021). This function performs pairwise comparisons between fixed effects using a Tukey *p*-value adjustment.

4.4. Results

4.4.1. Sex differences in nest visitation

The average nest visit by titipounamu adults feeding chicks took 8.34 seconds (SE = ± 1.23), with no difference between the total time males and females spent at the nest per visit (Table 3). Birds spent an average of 4.21 seconds (SE = ± 0.633) visible while at the nest, again, with no difference in time visible between males and females (Table 4). I also found no significant difference between males and females in the amount of time visible at the nest pre-entry ($p = 0.386$) or post-entry ($p = 0.368$). The stage of the nest (whether it had early or late chicks) had no significant effect on pre-entry ($p = 0.585$), post-entry ($p = 0.585$), time spent visible ($p = 0.8874$), or total visit time ($p = 0.460$), and thus was removed from the final models. However, the lack of significance suggests that these behaviours at the nest stay consistent as the chicks age. The type of nest (open or closed) also had no significant effect on pre-entry ($p = 0.748$), post-entry ($p = 0.748$), or total visit time ($p = 0.152$), and thus was removed from these models. However, birds were found to spend significantly more time visible at open nests than closed nests ($p = 0.002$); the average time spent visible at closed

nests was 2.55 seconds (SE = ± 0.147), compared to 8.55 seconds (SE = ± 2.2) at open nests.

Table 3: Summary table with mean values for the duration (seconds) of each titipounamu nest behaviour. Each variable has the mean for each sex and then the combined total dataset. Values represent means ± standard error.

Mean duration (s)	Female		Male	
Time visible before entering nest (pre-entry)	1.4	± 0.118	1.44	± 0.127
Time visible after exiting the nest (post-entry)	1.35	± 0.115	1.27	± 0.122
Time spent vigilant before entering the nest	1.22	± 0.119	1.27	± 0.129
Time spent vigilant after exiting the nest	0.88	± 0.082	0.98	± 0.09
Total time spent vigilant per visit	2.45	± 0.177	2.45	± 0.207
Total time of the visit	8.41	± 1.78	8.26	± 1.69
Total time spent visible per visit	4.55	± 1.09	3.84	± 0.591

Table 4: Gamma generalised linear mixed effects model results for the following variables: the total duration of each visit, the time visible before entering the nest (pre-entry), the time spent visible after exiting the nest (post-entry) and the total time spent visible per visit, all in seconds. The fixed effects include sex and nest type. Values represent estimates from each model with standard error (in brackets). Asterisks mark significant results (see note). Nest and individual identification were included as random factors for all models.

	Dependent variable:			
	Total duration of visit	Time visible before entering nest (pre-entry)	Time visible after exiting the nest (post-entry)	Total time spent visible per visit
	(1)	(2)	(3)	(4)
Sex	0.018	0.064	0.136	0.024
	(0.017)	(0.074)	(0.151)	(0.048)
Nest type				-0.279***
				(0.090)
Constant	0.208***	0.957***	0.862***	0.484***
	(0.024)	(0.127)	(0.120)	(0.058)
Observations	359	342	329	358
Log Likelihood	-971.472	-433.910	-416.879	-755.780
Akaike Inf. Crit.	1,952.943	877.821	843.757	1,523.561
Bayesian Inf. Crit.	1,972.360	896.995	862.738	1,546.844
Note:				**p<0.05; ***p<0.01

4.4.2. Sex differences in vigilance behaviour

I found no significant sex differences in the proportion of each visit spent vigilant (Figure 3), nor the proportion of each visit they spent vigilant before feeding (Table 5). Both males and females appear to spend a similar proportion of each visit being vigilant overall (male mean % ± SE = 46.5 ± 4.4, female mean % ± SE = 44.7 ± 4) as well as being pre-feeding vigilant (male mean % ± SE = 23 ± 1.7, female mean % ± SE = 21.5 ± 1.7). There were also no significant differences in the proportion of each visit that each sex spent visible ($p = 0.342$). Males did have a higher average proportion of each visit vigilant after feeding (Figure 3) than females (male mean % ± SE = 21.1 ± 1.6, female mean % ± SE = 20 ± 1.6), but this effect was small and not statistically significant at $p < 0.05$ ($p = 0.099$).

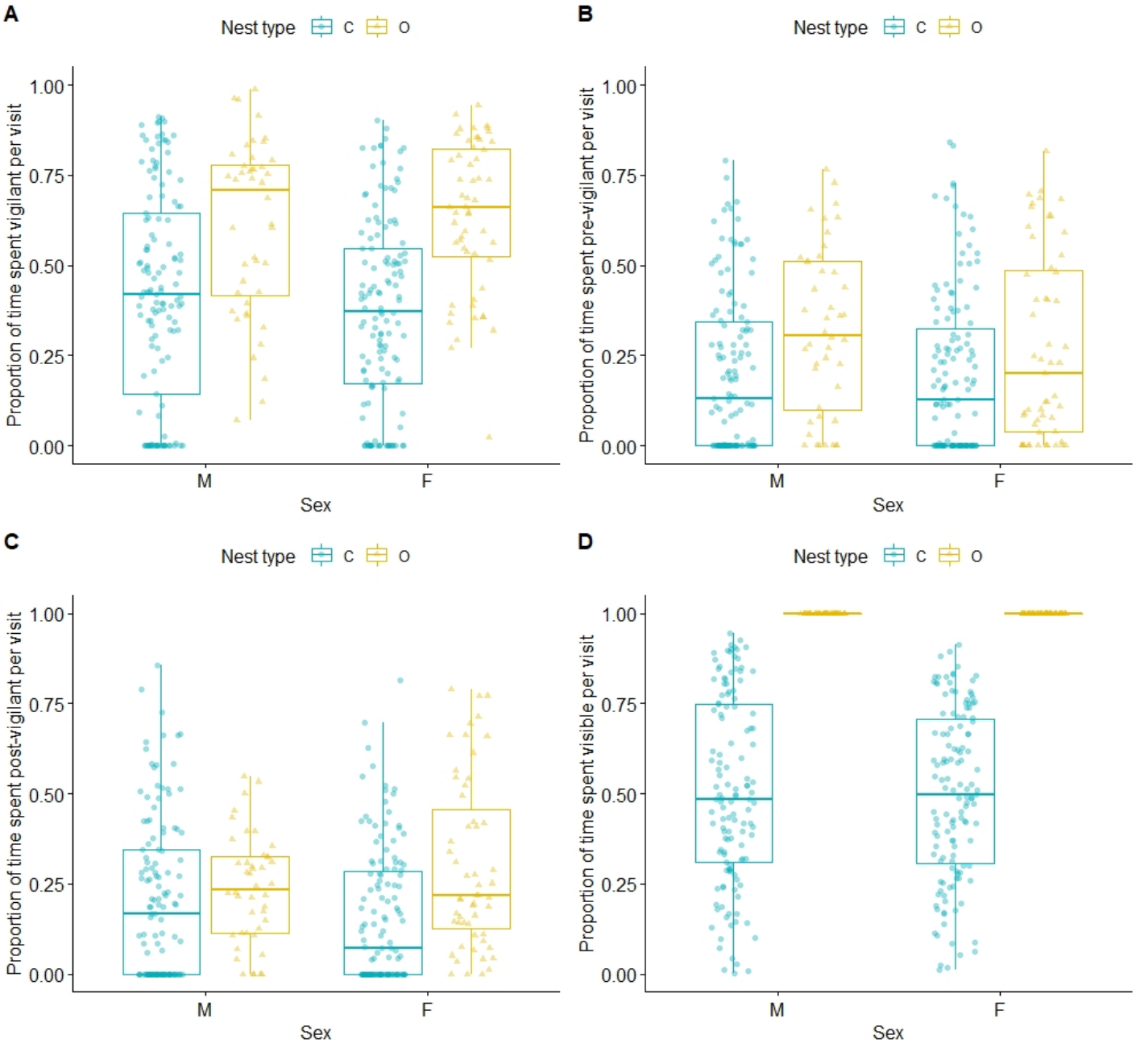


Figure 3: The proportion of time per nest visit male and female titipounamu (*Acanthisitta chloris*) spent on different behaviours across nests of varying exposure (open or closed). A) The proportion of time spent vigilant at the nest between male and female titipounamu, across open and closed nests. B) The proportion of time spent pre-vigilant (vigilant before feeding) between male and female titipounamu, across open and closed nests. C) The proportion of time spent post-vigilant (vigilant after feeding) between male and female titipounamu, across open and closed nests. D) The proportion of time spent visible per visit between male and female titipounamu, across open and closed nests. Note that birds spent all their time visible at open nests. For each sex, the blue, left boxplot corresponds to the closed nest type (nests where birds are not visible while feeding), while the yellow, right boxplot corresponds to the open nest type (nests where birds are visible while feeding). Boxplots show the median values (bold middle line), the interquartile range (box), and the range values (whiskers) including some outliers. Each dot represents the proportion of observations an individual bird was observed performing a behaviour while visiting their nest to feed chicks.

Table 5: Binomial generalised linear mixed effects model results for the following variables: the proportion of time spent vigilant per nest visit, proportion of time spent pre-feeding vigilant per nest visit, the proportion of time spent post-feeding vigilant per nest visit and the proportion of time spent visible per nest visit. The fixed effects include sex, nest stage and nest type, as well as the interaction terms sex*nest type and sex*nest stage. Values represent estimates from each model with standard error (in brackets). Asterisks mark significant results (see note). Nest and individual identification were included as random factors for all models.

	Dependent variable:			
	Proportion of time spent vigilant	Proportion of time spent vigilant before feeding (pre-feeding fvigilant)	Proportion of time spent vigilant after feeding (post-feeding vigilant)	Proportion of time spent visible per visit
	(1)	(2)	(3)	(4)
Sex	0.190	0.179	1.126	-0.213
	(0.296)	(0.306)	(0.661)	(0.289)
Nest stage			1.218**	
			(0.511)	
Nest type	2.006***		1.617***	
	(0.599)		(0.490)	
Sex:Nest type	-0.488		-2.145**	
	(0.579)		(0.834)	
Sex:Nest stage			-0.595	
			(0.715)	
Constant	-0.746**	-1.898***	-3.370***	0.050
	(0.323)	(0.287)	(0.518)	(0.349)
Observations	358	358	358	259
Log Likelihood	-206.601	-152.153	-120.125	-158.863
Akaike Inf. Crit.	425.201	312.306	256.251	325.727
Bayesian Inf. Crit.	448.485	327.828	287.295	339.954
Note:				**p<0.05; ***p<0.01

4.4.3. Differences in vigilance behaviour across nest type and stage

Birds spent a significantly greater proportion of time vigilant at open nests (62.4% on average ± SE = 2.2%) compared to closed nests (39.1% on average ± SE = 1.7%; Table 5). When I split total vigilance into vigilance before and after feeding, I found that there were no differences in the proportion of time spent pre-feeding vigilant across nest type ($p = 0.120$), but birds spent a significantly greater proportion of time vigilant after feeding at open nests than closed nests ($p < 0.001$; mean % ± SE at open nests = 29.2% ± 2.5%, compared to closed nests = 19.6% ± 1.4%). There was also a significant interaction between sex and nest type when the proportion of each visit spent on post-feeding vigilance was modelled ($p = 0.011$). Females are significantly more post-feeding vigilant at open nests than they are at closed nests (mean % of time per visit post-feeding vigilant ± SE at open nests = 29.8% ± 3.2%, compared to closed nests = 15.8% ± 1.6%; ($p = 0.005$), whereas there was no significant difference in the time males spent vigilant after feeding at either nest type ($p = 0.862$). Aside from this result, there were no other significant interactions between sex and nest type across proportion of total vigilance ($p = 0.387$) nor pre-feeding vigilance ($p = 0.712$). There were also no significant interactions between sex and nest stage across proportion of total vigilance ($p = 0.887$), pre-feeding vigilance ($p = 0.588$), post-feeding vigilance ($p = 0.406$) nor time spent visible during the visit ($p = 0.544$). Thus, these interaction terms were removed from the models.

Birds were also found to spend a significantly greater proportion of time vigilant after feeding at late-stage nests, when chicks are older ($p = 0.017$). On average, birds spent 19.6% (SE ± 1.4%) of each visit post-feeding vigilant at early nests, compared to 22.8% (SE ± 1.8%) at late nests. There was no significant difference between nest stage and proportion of each visit spent vigilant ($p = 0.884$), pre-feeding vigilant ($p = 0.275$) nor time spent visible per visit ($p = 0.483$).

4.5. Discussion

Contrary to my prediction that one sex would display more anti-predation behaviours at the nest than the other due to their differences in colouration presumably making one sex more conspicuous, I found no sex differences in vigilance nor the time spent visible at the nest. Thus, males and females do not appear to have any differences in their anti-predation behaviour at the nest despite their sexual dichromatism. However, I did find that females were more vigilant after feeding at open nests compared to closed nests, implying an increased need for predator detection when nests are more exposed. Both sexes were also more vigilant after feeding at late-stage nests, suggesting that the need for vigilance increases as the chicks in the nest age and become more vocally conspicuous.

4.5.1. Sex differences in vigilance at the nest

Nests are more likely to be depredated with increasing levels of activity and parental visibility (Martin et al., 2000; Matysiokova & Remes, 2018; Skutch, 1949). Therefore, if one sex is more conspicuous and more likely to attract predators to the nest than the other, they may compensate by increasing their anti-predation behaviours to reduce the risk of detection (Verner & Willson, 1966). The green dorsal plumage of male titipounamu may contrast with their typically brown nest backgrounds more than the brown-yellow dorsal plumage of the females (Hunt & McLean, 1993) as most titipounamu nests are in cavities in trees, tree ferns or the ground (Moran, Loo, & Cain, 2019; Sherley, 1994). However, Chapter 3 found that females were more conspicuous than males, although this was mostly against green backgrounds. Thus, either sex could be more conspicuous and under selection to develop compensatory anti-nest predation behaviours to reduce the risk of drawing predators to the nest. As previous work has shown that both sexes have similar visitation rates (Sherley, 1994), I predicted that the more conspicuous sex, if there is one, may instead increase their vigilance around the nest or reduce the time they spend visible around the nest. However, in

this study I did not find any differences in the proportion of time spent vigilant nor time spent visible between male and female titipounamu. Thus, this species does not appear to be performing any anti-predation behaviours that vary across sex.

An explanation for the lack of sex differences in vigilance behaviours may be that increased vigilance may not be a suitable strategy to reduce predation of titipounamu nests. Although increased vigilance could be beneficial in avoiding being depredated, a conspicuous bird spending more time around the nest may increase the risk of them being seen by a predator. Other sexually dichromatic species have adopted alternative strategies (Colombelli-Negrel & Kleindorfer, 2010; Feeney & Langmore, 2015; Vrublevska et al., 2015), such as reducing visitation rate to the nest but maintaining the necessary caloric influx through increasing prey size, quantity or quality (Colombelli-Négrel & Kleindorfer, 2009; Grieco, 2002; Sejberg et al., 2000). For example, the size of larvae delivered by blue tits (*Parus caeruleus*) to the brood increases with the duration of the foraging trip (Grieco, 2002). However, previous studies have shown that titipounamu visitation rate is similar across sexes, with males visiting even more frequently than females at some nests (Khwaja et al., 2017; Sherley, 1994). Reducing visitation rate through bringing larger or more prey per visit may not be feasible for titipounamu due to their size (Sherley, 1993); their small beaks limit them to being single prey loaders, only carrying one insect to the nest at a time (Hunt and McLean, 1993; Sherley, 1990). Prey must also be able to fit into the mouths of chicks, so is constrained by the size of nestlings. Visitation rate may therefore need to stay high to keep nestlings fed, regardless of sex and the threat of predators. However, as titipounamu display biparental care, the advantages of both sexes contributing to all aspects of nest care must outweigh any potential costs linked to conspicuousness at the nest. Likewise, the increased frequency of visits from helper birds due to titipounamu being cooperative breeders must provide ample benefits to mitigate the cost of increased predation risk; helpers increase the amount of food brought to nests and improve juvenile recruitment rates (Preston et al., 2016), and females at nests with helpers were found to have a greater survival rate (Sherley, 1990). The

proportion of time titipounamu spent on vigilance was similar to other bird species (Diehl et al., 2020; Gautheir & Tardif, 1991), including small passerines (Artiss & Martin, 1995; Yasukawa et al., 1992; Yasukawa & Cockburn, 2009), although their vigilance at open nests was at the higher end of the spectrum. Interestingly, the proportion of time spent vigilant at the nest was much higher than some other cavity nesting species such as marsh tits (*Poecile palustris*) and oriental tits (*Parus minor*), which spent only up to 3% of their time vigilant at the nest (Cantarero et al., 2015; Yoon et al., 2016; Yoon et al., 2017). This comparatively high level of nest vigilance in titipounamu compared to other cavity nesters could indicate that vigilance may be important for compensating for the increased activity around their nests.

The lack of differences between male and female anti-predation behaviours could suggest that neither sex is more conspicuous than the other at the nest. Both sexes could be similarly cryptic against their nest backgrounds, or equally as conspicuous. Therefore, neither is under selection to compensate for their colour by becoming more vigilant or less visible at the nest. Although increased perceived risk of nest predation reduced the frequency of visits to the nest in sexually dichromatic blackbirds (*Turdus merula*), there was no difference between males and females despite males likely being more contrasted against their environment (Ibanez-Alamo & Soler, 2017). Thus, Ibanez-Alamo & Soler (2017) predicted that there may be a minimum threshold in which the colouration of each sex must differ for differences in behaviour to be selected for. Although one sex may be slightly more conspicuous against nest backgrounds, male and female titipounamu may be too close in colour, despite their sexual dichromatism, for any differences in anti-predation behaviour to be selected for. As titipounamu are green and brown, they may also match their forest backgrounds more closely in general than other sexually dichromatic species where compensatory nest behaviours have been observed. This prediction is supported by previous work as behavioural differences in the more conspicuous sex have mostly been observed in birds with more exaggerated sexual dichromatism and higher contrast to their

backgrounds, such as the superb fairy wren, *Malurus cyaneus* (Colombelli-Négrel & Kleindorfer, 2009), lined seedeater, *Sporophila lineola* (van den Bemt. et al., 2021), and blue-black grassquit, *Volatinia jacarina* (de Moraes et al., 2020). The assumption that nests provide a mostly brown background for titipounamu to be seen against may also be too simplified; often, the bark around cavities can be covered in moss or lichen that may provide a greener or more patterned background. Thus, the more conspicuous sex may change depending on nest site, resulting in selection for both sexes to have similar anti-predation behaviours.

Predation may also not be a strong enough selection pressure to influence titipounamu anti-predation behaviour at the nest. Potentially, other anti-predation adaptations such as cavity nesting are enough to substantially reduce predation of titipounamu nests, therefore negating the need for differing anti-predation behaviours across sex (Brightsmith, 2005). As avian predators tend to rely on locating prey visually (Mitkus et al., 2018; Potier et al., 2020), concealing the nest through cavity nesting may be a particularly effective strategy for titipounamu, whose main native predators are avian (Higgins et al., 2001). This could also explain why at more open, exposed nests, birds spent more time vigilant, as the benefits of cavity nesting were lessened. However, titipounamu nest predation by long tailed cuckoo has been recorded at an enclosed nest at the site used for this study (Moran et al., 2019), so some nest predation by avian predators does occur despite cavity nesting. Additionally, many other bird species change their nest behaviours when the risk of predation increases (Ghalambor & Martin, 2000); for example, in a study of five insectivorous, socially monogamous, cavity nesting passerines, when perceived predation risk was increased, males reduced how frequently they visited to feed incubating females at the nest (Ghalambor, 2002). Densities of native birds, including predators of titipounamu, have decreased across New Zealand within the last century (Fea et al., 2021); if titipounamu anti-predation behaviours are plastic and change with predator presence or density, the behaviours recorded in this study may not reflect how they behave in higher densities of their

native predators. Some altered behaviour in response to predator presence has previously been demonstrated in titipounamu, with birds increasing their nest defence when exposed to a model owl (Taylor, 1991). This included behaviours such as avoiding the nest and approaching the model predator while performing alarm calls, wing raising and swooping. Future studies may benefit from including perceived predation risk or predator density into investigations of sex differences in anti-predation behaviours in sexually dichromatic species.

4.5.2. Vigilance across nest type

Birds were more vigilant at open nests, where they were visible during the whole visit, compared to closed nests in which they were not visible while feeding. The difference was driven mostly by birds being more post-feeding vigilant, and specifically females being more post-feeding vigilant at open nests. Interestingly, in some other bird species vigilance increases on nests that are more concealed (Gómez-Serrano & López-López, 2014; Javůrková et al., 2011); more concealed nests decrease the distance in which a bird can detect an incoming predator, allowing them less time to escape (Götmark et al., 1995). However, a more exposed nest may also be more likely to be seen by predators than a concealed nest (Koivula & Rönkä, 1998; Wiebe & Martin, 1998; Yoon et al., 2016). As titipounamu's native predators hunt mostly visually, they likely benefit from having more concealed nests (Higgins et al., 2001). Thus, at nests where the birds are more visible during the visit, they may compensate by increasing their vigilance before leaving, allowing them to scan for potential predators that may attack them or the nest once they leave. Females being more post-feeding vigilant at open nests compared to closed nests, but not males, suggests that they may be more cautious than males. This could be because females may be slightly more conspicuously coloured against nests than males (Chapter 3), resulting in them compensating for their colour by increasing their vigilance, but only when the nest is exposed.

4.5.3. Impact of nest stage on vigilance

The stage of a nest may also influence the degree to which birds display anti-predation behaviours. Although there were no sex differences across nest stage, I did find that titipounamu were more vigilant after feeding at late-stage nests than early nests where the chicks are young. Defensive nest behaviours have been shown to increase across the nesting cycle in multiple other species (Greig-Smith, 1980; Knight & Temple, 1986). One potential explanation for this is Trivers' (1972) 'cumulative parental investment' hypothesis, under which parents should increase their nest defence as the nest becomes closer to fledging to protect their investment in their offspring. While the cumulative parental investment hypothesis has some support (Bjerke et al., 1985), it has been challenged by other hypotheses suggesting that nest defence should vary depending on the vulnerability of offspring, and that parents should invest in increased nest defence behaviours only if the benefits of keeping the current nest alive outweigh any future reproductive prospects (Morales et al., 1989; Strnadová et al., 2018). An alternative explanation for the increased post-feeding vigilance in late titipounamu nests is that the increased begging volume of older chicks may increase the risk of attracting a predator while the parent is at the nest (Haff & Magrath, 2011; Strnadová et al., 2018). To mitigate this increased risk, parents have been found to produce alarm calls that silence chicks when predators are nearby and can induce crouching behaviour in chicks to reduce their visibility (Haff & Magrath, 2011; Magrath et al., 2010). However, as titipounamu chicks start begging as the parent arrives and feeds, it could also be beneficial for the parent to spend longer time vigilant after exiting the nest to ensure there are no predators nearby before leaving, although I am not aware of any examples of this occurring.

The majority of time spent vigilant may also not occur at the nest entrance, and instead in surrounding vegetation (Feeney & Langmore, 2015). Titipounamu tended to use the same few perches every time they approached their nest and would spend considerable time moving through the surrounding foliage before arriving at the nest entrance (pers. obs.).

Unfortunately, the nest video could not capture this time spent by adults approaching the nest as the vegetation birds used to approach often covered a wide radius. Other potential variables that could influence anti-predation behaviour include nest characteristics such as height or foliage density (Feeney & Langmore, 2015; Rangel-Salazar et al., 2008; Remes, 2005; Vrublevska et al., 2014). Future studies could explore sex differences in vigilance behaviour before arriving at the nest entrance, or how vigilance is affected by micro-site variables.

4.5.4. Conclusions

In species where one sex is more conspicuous than the other, there may be selection for that sex to compensate for their visibility by increasing their anti-predation behaviours at the nest. Due to their sexual dichromatism, I predicted that one titipounamu sex could be more conspicuous at the nest than the other and therefore have increased anti-predation behaviours such as vigilance and spent less time visible at the nest. However, I found no differences in these behaviours between males and females, potentially suggesting that neither sex is more conspicuous at the nest, or that the difference in colour is too subtle to drive divergence in behaviours. Interestingly, females were more vigilant after feeding at open nests, implying some type of selection driving a sex difference in behaviour, but only when nests are more exposed. Both sexes also increased post-feeding vigilance at late nests when chicks were older. Future studies could focus on exploring the effect of predator density and type on titipounamu nesting behaviour, as well as developing a further understanding of the minimum threshold at which sexual dichromatism can drive differences in nest defence behaviours.

Chapter 5

General discussion

5.1. Summary of key findings

Previous work suggested that titipounamu sexual dichromatism may be driven by sex-specific needs for crypsis against their different foraging environments (Hunt & McLean, 1993). The aim of this thesis was to rigorously test this hypothesis in new ways, including using relevant visual models and in populations more reflective of natural habitat. If crypsis were driving sexual dichromatism, I would expect to see that 1) there are differences in how each sex uses their forest habitat; 2) the plumage of each sex matches the colours or pattern of the environment they are using; and 3) that more conspicuous birds might modify their behaviour during periods of higher predation risk. In Chapter 2, I assessed titipounamu foraging behaviours in a natural, complex habitat to identify any sex differences in where birds forage and the colour of backgrounds that they forage against. In Chapter 3, I analysed titipounamu colour and how closely they match with their background colours from an avian visual perspective, using calibrated digital imaging. In Chapter 4, I examined titipounamu behaviour at the nest to determine whether either sex is compensating for their potentially more conspicuous colouration. Overall, the results undermine the sex-specific crypsis hypothesis, suggesting some other mechanism is likely the main driver of sexual dichromatism in this species.

Chapter 2 focused on sex differences in titipounamu foraging behaviour, and whether this could be driving selection for sexual dichromatism. If sex-specific crypsis is driving the evolution of sexual dichromatism, we would expect the sexes to use their environment differently. I found that males and females used different perch types; males were more

likely to be observed foraging on small branches than females, whereas females were more likely to be observed foraging on trunks than males. Despite this difference in foraging behaviour, both sexes were equally as likely to be observed against green or brown backgrounds. There was also considerable overlap between where each sex foraged; while males used trunks significantly less than females and small branches significantly more, females still used small branches just as often as trunks. This suggests that although males and females forage in different places, they do not forage against backgrounds that match their dorsal colouration. The differences in foraging behaviour may be linked to the ecomorphological differences between the sexes, but do not appear to be correlated with the sex differences in colouration.

In Chapter 3, I assessed whether titipounamu were cryptic in their environment from an avian perspective and if this varied between sex or background type. Using visual modelling, I found that titipounamu dorsal plumage was chromatically and achromatically distinguishable against the tested background types in both UV sensitive passerine and violet sensitive bird of prey visual models. Males were a closer chromatic match than females to green backgrounds (leaves and moss) but were still detectable to both visual models. Females appear to demonstrate higher achromatic contrast to background environments than males, meaning they be more conspicuous to other birds. In contrast, both sexes were a close pattern match to all the different background types, suggesting that they may be cryptically patterned. However, as this cryptic patterning did not vary between sex nor background, it suggests that titipounamu are not differently patterned to match different foraging backgrounds. This supports findings in the previous chapter that showed neither sex is more likely to be seen on different backgrounds substrates nor colours. Overall, titipounamu, particularly females, do not appear to be cryptically coloured but may be cryptically patterned.

In Chapter 4, I explored the idea that the more conspicuous sex may display increased anti-predation behaviours at the nest to compensate for their increased visibility to predators. I

found no sex differences in behaviour at the nest, including vigilance and the time spent visible per visit. This suggests that neither sex perceives higher predation risk resulting from their colouration given the lack of sex differences in vigilance or time spent around the nest entrance. However, birds were more vigilant after feeding at open nests, particularly females, which aligns with Chapter 3 that found females are more conspicuous than males. The lack of sex differences in vigilance behaviour suggests that predation pressure is unlikely to show strong sex biases, supporting the previous finding that the sexes do not differ in conspicuousness.

Taken together, these results do not provide support for the idea that titipounamu have evolved cryptic plumage to match the backgrounds of their different foraging environments. The sex differences in foraging behaviour are likely more to do with ecomorphology than colour, as the larger hind claws and decurved beaks of females may make them better adapted to forage on trunks than males (Hunt & McLean, 1993). The poor colour matching of both sexes suggests that they are not using background matching to increase their crypsis, and it may be that they are displaying a 'compromise' crypsis in which they are not a close match to any specific background in their heterogenous environment but match all their backgrounds to a certain degree (Merilaita et al., 1999; Stevens & Ruxton, 2019). This strategy does not explain their sexual dichromatism, however. Alternatively, the methodologies I used may have been unable to capture some of the smaller colour differences between each sex and their backgrounds, or the model I used is a poor representative of the visual perception of native predators of titipounamu.

5.2. Insights into sexual dichromatism and bird colouration

The existence of sexual dichromatism in avian species is interesting as it requires different selection pressures to be acting on each sex to drive different colourations (Badyaev & Hill, 2003). As colour is used for a wide variety of signalling and concealment strategies (Caro, 2005), exploring the different evolutionary drivers of sexual dichromatism can provide valuable insights into how different evolutionary forces act on each sex and across the different mating and behavioural systems found across birds. Sexual and natural selection can both drive differences in colouration between males and females (Selander, 1972; Shultz & Burns, 2017; Simpson et al., 2020; Soler & Moreno, 2012). Sexual dichromatism is generally thought to be a response to two different, but not mutually exclusive, selection pressures. Dichromatism can arise from sexual selection if colourful traits in one sex are attractive to the other (Andersson & Simmons, 2006; Selander, 1972; Shultz & Burns, 2017). Alternatively, if one sex is under higher predation risk than the other, cryptic colouration may be selected for only in that sex. For example, in many species, female birds are more cryptically coloured than males as they provide more parental care, so more camouflage may reduce predation risk of themselves and their offspring while they are at the nest (Badyaev & Hill, 2003; Gotmark et al., 1997). Alternatively, one or both sexes may experience both sexual and natural selection, resulting in variable colour strategies that take place over time or body regions (Delhey, 2020; Ekanayake et al., 2015; Estep et al., 2006; Gomez & Théry, 2007; Gruson et al., 2021).

I chose titipounamu as my study species as it has been hypothesised that they are an example of a third, less well understood evolutionary force behind sexual dichromatism, where both sexes are under selection to be cryptically coloured but in different habitats. In this context, natural selection may drive different colourations in each sex to increase how cryptic they are in their respective environments. This explanation for sexual dichromatism has been supported by studies on lizards (Medina et al., 2017; Orton & McBrayer, 2018), snakes (Forsman, 1995), and insects (Forsman & Appelqvist, 1999; Ramírez-Delgado &

Cueva del Castillo, 2020), but there are relatively few examples compared to other explanations, particularly in birds. While crypsis mediated sexual dichromatism is common in birds, it is typically driven by selection on one sex to be cryptic, while the other is sexually selected (Badyaev & Hill, 2003; Bossu & Near, 2015; Gotmark et al., 1997; Simpson et al., 2020; Soler & Moreno, 2012). While this thesis did not find evidence for this mechanism being the driver of titipounamu sex differences in colouration, it does identify potential criteria that need to be met for different cryptic colours to be selected for in each sex. For sex-specific cryptic colouration to be selected for, the sex differences in habitat use may need to have minimal overlap and the background colours and substrates in each habitat need to be different. Titipounamu do have differences in where they forage, however, their foraging behaviours overlapped. Furthermore, there were not sex-specific differences in background substrates or colours used while foraging. Despite nests often being against brown backgrounds, neither sex adopted more anti-predation behaviours which also suggests that neither sex was much more conspicuous against the nest background than the other. My results, therefore, suggest that further research is needed to understand why titipounamu are sexually dichromatic.

The foraging analyses conducted in this thesis built on previous research by Hunt and McLean (1993), but in a much more complex and diverse forest that is more representative of typical titipounamu habitat. I found that males and females used different perch types while foraging, but there were no differences in the background colours that each sex was seen against. Thus, different foraging behaviours and environments do not necessarily result in different background colours due to the heterogeneity of habitats such as complex forests. Interestingly, the differences in perch use correlate to sex differences in body size, hind claws, and beak curvature (Hunt & McLean, 1993). Females may be better adapted to foraging on trunks than males due to their large hind claws and decurved beaks, explaining why males used trunks for foraging significantly less than females. Titipounamu, therefore, provide an interesting example of foraging ecomorphology in a sexually dimorphic,

monogamous, and cooperatively breeding forest bird. Sexual dimorphism in trophic structures driven by different uses in foraging environment is common in birds. For example, the sex differences in bill size of many shorebirds may allow for reduced intrasexual competition as each sex probes for prey at different depths (Aplin & Cockburn, 2012; Ferns & Siman, 1994; Nebel et al., 2005). Likewise, in some hummingbirds and woodhoopoes, different bill lengths allow each sex to use different food resources (Radford & Du Plessis, 2003; Temeles et al., 2000; Temeles & Kress, 2003). While my research aligned with results from Hunt and McLean (1993), showing that titipounamu habitat use reflects their physiology, my more detailed foraging analysis allowed me to differentiate between the effects of potential background matching and physiology on where each sex is foraging. This highlights the risk of making assumptions based on data that is not detailed or targeted enough to identify more subtle patterns and differences.

The potential for cryptic patterning in titipounamu found in Chapter 3 is an interesting discovery. Cryptic patterning is a successful strategy in concealing birds from predators, in conjunction with or regardless of colour (Mulder et al., 2021; Robledo-Ospina et al., 2017; Schaefer & Stobbe, 2006; Stevens et al., 2006). Displaying plumage patterns that match the surrounding environment can improve camouflage; for example, nightjar nests are less likely to be depredated when the incubating adult's plumage pattern is a close contrast match to their background (Troscianko et al., 2016). Likewise, eggs with patterns that closely match their nest and environment background have an increased chance of survival across multiple species (Gómez et al., 2018; Lee et al., 2010; Westmoreland, 2008). Species such as the common potoo (*Nyctibius griseus*) and tawny frogmouth (*Podargus strigoides*) also have complex patterns and colours that help improve their masquerade as branches (Cestari et al., 2018; Hedley & Caro, 2021). That male and female titipounamu are differently patterned, and yet were similarly matched across all the different background types is somewhat perplexing, and I do not know of any other literature with a similar example. Previous work has demonstrated that the need for crypsis can drive sexual dichromatism, including

differences in pattern, when each sex is seen against different backgrounds (Ramírez-Delgado & Cueva del Castillo, 2020). However, this explanation may not work for titipounamu as I found a high degree of overlap between where each sex foraged, including their background substrates and colours. Both sexes are also frequently seen against the same, often brown, background of their nest during the breeding season. While the more conspicuous sex in sexually dichromatic species often displays increased anti-predation behaviours (Colombelli-Négrel & Kleindorfer, 2009; de Moraes et al., 2020), there may be a minimum threshold in how conspicuous the more obvious sex had to be for sex differences in behaviour to be selected for (Ibanez-Alamo & Soler, 2017). The lack of sex differences in nest behaviour in titipounamu supports the latter hypothesis, as pattern analyses suggest that both sexes are similarly matched to their backgrounds, while colour analyses found that females were only somewhat more conspicuous than males, mostly against green backgrounds. Therefore, titipounamu may not cross the minimum threshold in how differently conspicuous each sex is at the nest. This could be because both sexes are closely pattern matched to their nest backgrounds. However, my research only focused on a pattern energy analysis, so further pattern analyses, especially those investigating disruptive colouration, are necessary to provide more support for this conclusion. I also only modelled titipounamu colour and backgrounds from 5 meters, which may have been too far for either visual model to distinguish between complex patterns given the relatively low visual acuity of both the modelled species (common buzzard and blue tit). I chose this distance as titipounamu predators likely locate their prey from a distance, but their complex and dense forest habitats reduce visibility across long distances. This may not be appropriate, however, as we do not know much about how titipounamu are hunted by their predators. The visual models used may not capture some of the detail necessary to distinguish between small differences in colour and pattern, particularly as they are only proxies of the vision of actual predators and passerines that titipounamu have evolved alongside.

My results call into question the suggestion that titipounamu colouration is driven by the need for sex-specific crypsis in different parts of their habitat. What does this suggest about other evolutionary forces that could be driving titipounamu sexual dichromatism? Wallace's female crypsis theory suggests females need increased crypsis to reduce predation while on the nest (Wallace, 1868; Wallace, 1891). I found that both titipounamu sexes were equally cryptic and both performed the same level of anti-predation behaviours while at the nest, suggesting neither sex was more conspicuous and did not perceive higher predation risk. Neither sex being more cryptic against their background environment, as well as the biparental care and cavity nesting traits in titipounamu, make the "female nest crypsis" theory an unlikely explanation for their sexual dichromatism. Alternatively, sexual selection often drives extravagant or conspicuous features in one sex, also resulting in sexual dichromatism (Andersson & Simmons, 2006; Darwin, 1871; Selander, 1972). However, in monogamous species, the effects of sexual selection are often reduced as the choosy sex only selects at mate once per breeding season or less (though extra-pair behaviour can increase the benefits of bright colours) (Dunn et al., 2001; Kirkpatrick et al., 1990). If sexual selection is driving titipounamu sexual dichromatism, their monogamous breeding system and absence of extra-pair parentage (Preston et al., 2013) could explain why neither sex is obviously more ornamented or conspicuous. However, Chapter 3 found that larger females were more conspicuously coloured (brighter) than the smaller males against their background environments to a bird of prey (common buzzard) and a passerine (blue tit) visual model. This could suggest a role reversed sexual selection, where larger and more conspicuous females are more attractive to males (Amundsen, 2000; Tobias et al., 2012). Potentially the yellow-green carotenoid component of female colour signals quality to attract males (Badyaev & Hill, 2000; Blount & McGraw, 2008), while the brown component provides some cryptic patterning to break up the conspicuous yellow (Galván et al., 2017; Stevens et al., 2017; Troscianko et al., 2016; Wilson-Aggarwal et al., 2016). As males often provide more of the investment in nest building and parental care, they may benefit from being 'choosy' and selecting a high-quality female as a partner. The larger body size of females is

proposed to be linked to their large egg to body size ratio rather than sexual selection (Sherley, 1993), but this could make choosing a larger female advantageous. Very little is known about how titipounamu form their monogamous pair bonds, but I observed juvenile birds foraging in male-female pairs and they often appear to pair immediately upon independence (pers. obs.). If the sex differences in adult plumage are driven by sexual selection, it seems unusual that birds would pair while still displaying juvenile plumage, although juvenile plumage only changes colour around the head and breast. Female conspicuousness may be a signal of quality to other titipounamu to maintain their territory (Amundsen, 2000; LeBas, 2006); females do tend to be more territorial and aggressive than males, often chasing away helper birds at the nest (pers. obs.). Sexual selection is also unlikely for males given their monogamy and high parental investment. However, some populations appear to have excess of unpaired males, which may explain why males are more likely to be helpers at nests than females (S. Withers, personal communication, January 25th, 2022). In the Tiritiri Matangi Island population, males were predated more often and potentially then replaced with 'floater' unpaired males (S. Withers, personal communication, January 25th, 2022). Additionally, at Cape Kidnappers and Tiritiri Matangi Island, males were seen dispersing further to find mates and vocalising while alone, presumably to locate potential mates. These behavioural aspects may suggest that male colour could be under sexual selection as females may have a wider choice of potential males to pair with. Male colour could also be driven by competition between males for females to pair with.

Part of what made titipounamu an interesting species to study crypsis as a driver of sexual dichromatism is their green colouration; males have fully green dorsal plumage, whereas females have yellow-green stripes across their crest and mantle. While both green and yellow/brown colouration have often been assumed to increase crypsis, a growing body of work has demonstrated the various other functions of green colouration (Bajer et al., 2011; Grande et al., 2004; Hausmann et al., 2003; Heinsohn, 2008; Kopena et al., 2020; Saks et

al., 2003). Green colour in birds is often produced by carotenoids, which are only obtained through a bird's diet (Pike et al., 2009). Thus, the brightness or hue of the green can be an indication of health and mate or rival quality (Blount & McGraw, 2008; Griggio et al., 2009; Kopena et al., 2020; Saks et al., 2003). There is also some evidence green pigments can help protect feathers from bacterial damage (Grande et al., 2004). The blue structural colouration that often underlies yellow carotenoids to produce green colour has also been linked to quality in some species (Andersson, 1999; Griggio et al., 2009; Siefferman & Hill, 2005). Green colour also often has an ultraviolet component, which can be used for signalling, but is easy to overlook given humans cannot see UV light (Griggio et al., 2009; Hausmann et al., 2003; Heinsohn, 2008). Titipounamu colour is produced a mixture of carotenoids, melanin, and structural blue colour (Thomas et al., 2014; S. Withers, personal communication, January 25th, 2022), thus could be signalling information about their quality to other birds. This thesis provides evidence that green colouration in titipounamu is not as cryptic as previously thought and may, therefore, have another function. This finding defies the assumption that green colouration has predominantly evolved to increase crypsis, providing unique evidence of alternative functions in a green forest bird and basal passerine. This study also demonstrates that accounting for the visual system of the receiver species is essential when studying colouration, as previous research on titipounamu used only human vision for the colour analysis and their results supported a different conclusion (Hunt & McLean, 1993).

The methodologies used in this thesis do have some important limitations to consider while interpreting the results. While using visual models has become well adopted in the literature, and certainly provide a better understanding of how the colour would be viewed by specific receivers than using only human vision (Bennett & Cuthill, 1994; Berg et al., 2020; Eaton, 2005; Håstad et al., 2005), the approach does still have some shortcomings. There is a large research gap when it comes to animal spectral sensitivities, with very few species having the necessary data available to produce a visual model. For example, many papers use the

peacock (*Pavo cristatus*) as a proxy for an avian predator as it has VS vision like most birds of prey (Hart, 2002), and the blue tit to represent UVS passerines (Gomez & Théry, 2007; Hart et al., 2000). However, the class of UV cone varies even with bird families, so predicting the level of UV vision in a species is challenging (Odeen et al., 2011; Ödeen & Håstad, 2013). Thus, studies of colour must rely on proxy species to use for visual modelling that may vary in how well they truly represent the target receiver. Differences in the modelled species vision compared to the target species may hide small differences in how males and females are perceived. Visual models also simplify aspects of animal vision such as cone catch and how photoreceptors are arranged on the retina. Titipounamu retinal anatomy has never been investigated, making it challenging to model colours from their visual perspective. As basal passerines, there are no proxy species that are phylogenetically similar to them to use for modelling (Barker et al., 2002; Worthy et al., 2010). While UV/V vision is determined based on a single point mutation in the SWS1 opsin gene, titipounamu appear to have an unusual mutation downstream and therefore may have different colour perception even when compared to related species (Ödeen & Håstad, 2013). Therefore, as is always the case in animal perception studies, the results from both of my visual models should be interpreted with caution. The scarcity of research in animal perception also means that new information is constantly being published that may make the methodological decisions of colour analyses outdated. For example, growing evidence suggests that most raptors cannot detect UV light (Potier, 2020), despite older behavioural studies implying otherwise (Viitala et al., 1995).

Sexual dichromatism has been well studied in species that display obvious and exaggerated differences in colour, but species with more subtle differences or plumage that is assumed to be cryptic are often overlooked (Eaton, 2005). Thus, we may be missing important evolutionary drivers and patterns that shape colour in these less conspicuous species, a prime example being the lack of study on the New Zealand wren group which represents an important basal group (Barker et al., 2002; Worthy et al., 2010). Crypsis-led sexual

dichromatism has not been focused on as much as dichromatism led by sexual selection (Orton & McBrayer, 2018; Ramírez-Delgado & Cueva del Castillo, 2020), partly as it may be less common, but maybe also because of a bias towards studying species with more exaggerated and conspicuous differences. Although this thesis does not support sex-specific needs for crypsis as the driver of sexual dichromatism in titipounamu, this thesis does provide some insights into what may be necessary conditions for this to occur in other species. Studying basal species such as a titipounamu may also provide revelations into the evolution of songbird colour and sexual dichromatism in general (Webb et al., 2016). The finding that green colour in titipounamu is not particularly cryptic also provides an interesting insight into the evolution and functions of green colour. Green plumage is often assumed to be selected for increased camouflage, especially in forest birds and those with more muted green tones (Gomez & Théry, 2007; Saks et al., 2003). However, this study along with others suggest that green colour has a variety of other functions and may be selected for by sexual or social selection as well as natural selection (Bajer et al., 2011; Griggio et al., 2009; Kopena et al., 2020; Saks et al., 2003). Many of the examples demonstrating functions of green colour have been provided in parrots (Griggio et al., 2009; Heinsohn, 2008; Heinsohn et al., 2005), which often have bright green plumage produced by psittacofulvin pigments unique to the Psittaciformes order (Berg & Bennett, 2016; McGraw & Nogare, 2004), so finding that crypsis may not be driving the green plumage of a forest passerine with carotenoid-based colour is a particularly valuable contribution to the field (Thomas et al., 2014). As New Zealand has many other endemic green birds that have evolved in similar habitats and under the same selection from avian predators, their green colour may also have other functions aside from crypsis. New Zealand's geographical isolation and lack of mammalian predators could have also led to evolution of unique functions of green colour in the endemic avifauna. Lastly, exploring the evolution of sexual dichromatism and how colour can affect behaviour in a monogamous species with biparental care and cooperative breeding provides interesting insights into whether explanations for sexual dichromatism apply to species that have more uncommon breeding systems. Many of the more well-

supported mechanisms for sexual dichromatism focus on species where males are sexually selected, and females do most of the parental care. However, in titipounamu, both sexes are involved in parental care and are monogamous with no extra-pair paternity, which inevitably impacts how selection pressures such as mate choice and predation can influence their colour. Evaluating how different breeding systems and reproductive behaviours conflict with some of the assumptions around common explanations for sexual dichromatism may drive forward new and updated hypotheses.

5.3. Recommendations for future research

Given that the longstanding explanation for sexual dichromatism in titipounamu was not supported by this thesis, further research is clearly needed. Other mechanisms may be important such as cryptic patterning, the visual system of New Zealand birds and potentially sexual selection. I discuss ideas for future approaches below, as well as suggesting ways to advance the field of colour research.

Further pattern analyses are required to conclusively answer whether titipounamu plumage is cryptic and to what extent. These could focus on disruptive colouration and more in-depth comparisons between dorsal pattern and background environments (Cuthill et al., 2005; Robledo-Ospina et al., 2017; Schaefer & Stobbe, 2006; Wuthrich et al., 2022). Finding cryptic patterning in a sexually dichromatic bird that is not a chromatic nor achromatic match to their background environment would be an interesting example of how pattern matching alone can provide a high level of concealment, as well as how pattern can vary between sex. This research could also incorporate more predator visual models to explore how cryptic titipounamu are to their full range of predators, including nocturnal predators and introduced mammalian species. There are currently very few examples of such visual models and none for any New Zealand species, so more research into the vision of different species would be valuable to facilitate future colour analyses. New Zealand species would be interesting to

study as the geographic isolation of the country has resulted in evolution of unique traits across other fields, so the vision of New Zealand species may have also diverged in distinctive ways.

While crypsis is often used to conceal prey from predators, cryptic colouration and patterning can also be used to conceal predators from their prey (Pembury Smith & Ruxton, 2020). While cryptic predators are often ambush predators, which does not align with the constantly moving titipounamu, it could still be interesting to explore how titipounamu appear to their insect prey. This should include analyses of the characteristic wing patterning, which could potentially be used in combination with the constant wing flicking motion titipounamu perform, possibly to stun or confuse insects. Future visual modelling from an insect or arthropod perspective could provide some further insights into the function of titipounamu colour and patterning.

Titipounamu have an unusual opsin gene mutation and are basal passerines (Barker et al., 2002; Ödeen & Håstad, 2013; Worthy et al., 2010), thus it is hard to compare their vision to any other known visual model. The way this species distinguishes colour and pattern, as well as their ability to see within the ultraviolet spectrum, is currently speculative and based on other passerines, as there are no similar or closely related species visual models to use as a proxy. Therefore, to understand how titipounamu view each other, further research must be done to analyse the anatomy of their visual system and create an appropriate visual model. Studying titipounamu vision could be informative for understanding the evolution of bird vision in general, given their place as basal passerines.

Because we found little support for the crypsis hypothesis, this suggests other selective mechanisms are important. Given the potential for signalling via carotenoids or structural colouration (Blount & McGraw, 2008; McGraw & Nogare, 2004; Pike et al., 2009), sexual selection or male-male and female-female competition may be powerful drivers of titipounamu sexual dichromatism. Testing these possibilities would require a better understanding of how titipounamu select partners, and whether there are any attributes that

are preferred in a partner. Additionally, investigating correlates of titipounamu colour may provide more information on how colour may signal aspects of quality and health to conspecifics. Ideally, this would also involve modelling of plumage colours through a titipounamu visual model to see if there are individual or sex differences in colour that are discernible to the birds, although as described above this would not be possible until we have an accurate visual model for the New Zealand wrens. Further research into the evolution of the green plumage in birds more generally may also be valuable to contribute to our understanding of the function of green colour aside from crypsis.

The differences between my results and those of Hunt and McLean (1993) may also imply that titipounamu foraging behaviour is different in complex forest habitats compared to primary successional kānuka (*Kunzea* spp. complex) stands; the potential plasticity in their foraging behaviour based on habitat type could be an interesting avenue for future research on this species. Alternatively, it could be a subspecies differences between the North (*A. c. granti*) and South Island (*A. c. chloris*) titipounamu that is driving the foraging differences between my research and Hunt and McLean's (1993) work; comparing colour and behaviour between the subspecies could help to clarify our contrary results, although to the human eye the two sub-species look virtually identical.

That titipounamu are conspicuous against their environment and show no sex differences in anti-predator behaviour at the nest could be explained by weak natural selection. The degree to which titipounamu are depredated, and by who is not well understood. Published records of predation exist for the Sacred Kingfisher, *Todiramphus sanctus* (Higgins et al., 2001), as well as the long-tailed cuckoo (*Eudynamys taitensis*), which were only recently recorded as titipounamu nest predators (Moran et al., 2019). However, there are no studies that have investigated predation levels in natural populations. Future studies could focus on understanding titipounamu's different predators and how they influence titipounamu behaviour. It may be that titipounamu are not common prey for any of New Zealand's native predators, and thus predation risk is not a strong enough selection pressure to drive colour

or behavioural differences between the sexes. Future research could also identify potential extinct predators that have been overlooked; for example, some of New Zealand's extinct or endangered lizards could have been opportunistic nest predators of titipounamu's small eggs. Titipounamu may have been highly depredated in the past, but with introduced mammalian predators and habitat loss, those predators are now missing from most ecosystems. Incorporating historic predators could be important for all studies focusing on the evolution of colour and behaviour. Other ways to study titipounamu predation could be to test whether titipounamu nest or foraging behaviour changes when there are predator models nearby and if the density of different predators in a habitat changes their behaviour. Future studies could also explore whether birds act differently depending on the microsite characteristics of their nest that could affect nest predation risk, such as nest height and how concealed the nest entrance is.

5.4. Concluding remarks

This thesis showed that titipounamu sexual dichromatism is unlikely to be driven by differing selection for cryptic colour to match their respective foraging environments. My findings challenge previous work and highlight the importance of testing assumptions about colour and evolution. The lack of an explanation for titipounamu sexual dichromatism clearly shows that further work is necessary to increase our understanding of how sex differences in colour evolve. This thesis also demonstrates how vital it is to study colouration through appropriate visual systems to understand the evolution and function of animal colours. It also revealed the value of incorporating both colour and pattern into studies of crypsis, as well as including behavioural observations. My findings defy assumptions around green plumage only being selected for to increase crypsis, contributing a unique example of a green but not cryptic forest bird to the growing body of work showing alternative functions of green colouration in birds. Overall, while the evolution of sexual dichromatism can be challenging to understand

and research, studying it can provide many valuable insights into the evolution of animal colour.

Appendices

Appendix I. Table of all significant pair-wise contrasts from a multinomial logistic regression comparing sex, perch type and status. F and M stand for female and male respectively. Pairwise contrasts were calculated using Tukey adjustment. See Chapter 2 for more details on methodology.

Contrast	Estimate	Standard error	df	t ratio	p value
F ground early chicks - F small branch early chicks	-0.475	0.051	12	-9.381	< 0.001
F ground early chicks - M small branch early chicks	-0.646	0.049	12	-13.142	< 0.001
F ground early chicks - F trunk early chicks	-0.424	0.052	12	-8.174	< 0.001
F ground early chicks - M trunk early chicks	-0.238	0.044	12	-5.436	0.013
F ground early chicks - F large branch late chicks	-0.191	0.036	12	-5.382	0.014
F ground early chicks - M large branch late chicks	-0.193	0.032	12	-6.009	0.006
F ground early chicks - F small branch late chicks	-0.431	0.040	12	-10.707	< 0.001
F ground early chicks - M small branch late chicks	-0.569	0.036	12	-15.629	< 0.001
F ground early chicks - F trunk late chicks	-0.315	0.040	12	-7.960	< 0.001
F ground early chicks - M trunk late chicks	-0.169	0.028	12	-5.988	0.006
F ground early chicks - F small branch nonbreeding	-0.531	0.032	12	-16.776	< 0.001
F ground early chicks - M small branch nonbreeding	-0.657	0.028	12	-23.462	< 0.001
F ground early chicks - F trunk nonbreeding	-0.302	0.030	12	-10.115	< 0.001
F ground early chicks - M trunk nonbreeding	-0.151	0.023	12	-6.615	0.003
M ground early chicks - F small branch early chicks	-0.461	0.054	12	-8.563	< 0.001
M ground early chicks - M small branch early chicks	-0.632	0.054	12	-11.715	< 0.001
M ground early chicks - F trunk early chicks	-0.410	0.054	12	-7.658	0.001
M ground early chicks - M trunk early chicks	-0.224	0.047	12	-4.807	0.033
M ground early chicks - F large branch late chicks	-0.178	0.039	12	-4.617	0.044
M ground early chicks - M large branch late chicks	-0.180	0.035	12	-5.084	0.022
M ground early chicks - F small branch late chicks	-0.418	0.043	12	-9.780	< 0.001

M ground early chicks - M small branch late chicks	-0.556	0.039	12	-14.090	< 0.001
M ground early chicks - F trunk late chicks	-0.301	0.042	12	-7.180	0.001
M ground early chicks - M trunk late chicks	-0.155	0.032	12	-4.845	0.032
M ground early chicks - F small branch nonbreeding	-0.518	0.033	12	-15.492	< 0.001
M ground early chicks - M small branch nonbreeding	-0.643	0.033	12	-19.355	< 0.001
M ground early chicks - F trunk nonbreeding	-0.288	0.033	12	-8.854	< 0.001
M ground early chicks - M trunk nonbreeding	-0.137	0.028	12	-4.901	0.029
F large branch early chicks - F small branch early chicks	-0.446	0.055	12	-8.071	< 0.001
F large branch early chicks - M small branch early chicks	-0.617	0.054	12	-11.469	< 0.001
F large branch early chicks - F trunk early chicks	-0.395	0.057	12	-6.962	0.002
F large branch early chicks - F small branch late chicks	-0.402	0.045	12	-9.010	< 0.001
F large branch early chicks - M small branch late chicks	-0.540	0.039	12	-13.955	< 0.001
F large branch early chicks - F trunk late chicks	-0.285	0.043	12	-6.592	0.003
F large branch early chicks - F small branch nonbreeding	-0.502	0.035	12	-14.156	< 0.001
F large branch early chicks - M small branch nonbreeding	-0.628	0.032	12	-19.504	< 0.001
F large branch early chicks - F trunk nonbreeding	-0.273	0.034	12	-8.058	< 0.001
M large branch early chicks - F small branch early chicks	-0.444	0.057	12	-7.844	0.001
M large branch early chicks - M small branch early chicks	-0.615	0.056	12	-10.992	< 0.001
M large branch early chicks - F trunk early chicks	-0.393	0.055	12	-7.094	0.001
M large branch early chicks - M large branch late chicks	-0.162	0.034	12	-4.780	0.035
M large branch early chicks - F small branch late chicks	-0.400	0.042	12	-9.562	< 0.001
M large branch early chicks - M small branch late chicks	-0.538	0.042	12	-12.920	< 0.001
M large branch early chicks - F trunk late chicks	-0.284	0.042	12	-6.764	0.002
M large branch early chicks - F small branch nonbreeding	-0.500	0.034	12	-14.499	< 0.001
M large branch early chicks - M small branch nonbreeding	-0.626	0.034	12	-18.201	< 0.001
M large branch early chicks - F trunk nonbreeding	-0.271	0.034	12	-8.043	< 0.001

F small branch early chicks - M small branch early chicks	-0.171	0.036	12	-4.696	0.039
F small branch early chicks - F ground late chicks	0.484	0.049	12	9.910	< 0.001
F small branch early chicks - M ground late chicks	0.478	0.049	12	9.724	< 0.001
F small branch early chicks - F large branch late chicks	0.283	0.060	12	4.717	0.038
F small branch early chicks - M large branch late chicks	0.281	0.056	12	4.989	0.026
F small branch early chicks - M trunk late chicks	0.306	0.052	12	5.872	0.007
F small branch early chicks - F ground nonbreeding	0.443	0.051	12	8.728	< 0.001
F small branch early chicks - M ground nonbreeding	0.414	0.051	12	8.132	< 0.001
F small branch early chicks - F large branch nonbreeding	0.412	0.051	12	8.025	< 0.001
F small branch early chicks - M large branch nonbreeding	0.416	0.050	12	8.296	< 0.001
F small branch early chicks - M trunk nonbreeding	0.324	0.049	12	6.614	0.003
M small branch early chicks - M trunk early chicks	0.408	0.082	12	4.948	0.027
M small branch early chicks - F ground late chicks	0.655	0.046	12	14.289	< 0.001
M small branch early chicks - M ground late chicks	0.649	0.046	12	13.969	< 0.001
M small branch early chicks - F large branch late chicks	0.454	0.056	12	8.186	< 0.001
M small branch early chicks - M large branch late chicks	0.452	0.056	12	8.132	< 0.001
M small branch early chicks - F trunk late chicks	0.331	0.054	12	6.100	0.005
M small branch early chicks - M trunk late chicks	0.477	0.056	12	8.490	< 0.001
M small branch early chicks - F ground nonbreeding	0.614	0.047	12	13.084	< 0.001
M small branch early chicks - M ground nonbreeding	0.585	0.049	12	11.882	< 0.001
M small branch early chicks - F large branch nonbreeding	0.583	0.047	12	12.300	< 0.001
M small branch early chicks - M large branch nonbreeding	0.587	0.049	12	12.085	< 0.001
M small branch early chicks - F trunk nonbreeding	0.344	0.048	12	7.096	0.001
M small branch early chicks - M trunk nonbreeding	0.495	0.055	12	9.075	< 0.001

F trunk early chicks - M trunk early chicks	0.186	0.036	12	5.151	0.020
F trunk early chicks - F ground late chicks	0.433	0.050	12	8.737	< 0.001
F trunk early chicks - M ground late chicks	0.427	0.050	12	8.560	< 0.001
F trunk early chicks - F ground nonbreeding	0.392	0.051	12	7.653	0.001
F trunk early chicks - M ground nonbreeding	0.363	0.052	12	7.003	0.001
F trunk early chicks - F large branch nonbreeding	0.361	0.052	12	6.982	0.002
F trunk early chicks - M large branch nonbreeding	0.365	0.051	12	7.131	0.001
F trunk early chicks - M trunk nonbreeding	0.273	0.057	12	4.784	0.035
M trunk early chicks - F ground late chicks	0.247	0.041	12	5.988	0.006
M trunk early chicks - M ground late chicks	0.241	0.042	12	5.750	0.008
M trunk early chicks - M small branch late chicks	-0.332	0.057	12	-5.792	0.008
M trunk early chicks - F ground nonbreeding	0.206	0.043	12	4.812	0.033
M trunk early chicks - F small branch nonbreeding	-0.293	0.045	12	-6.514	0.003
M trunk early chicks - M small branch nonbreeding	-0.419	0.054	12	-7.830	0.001
F ground late chicks - F large branch late chicks	-0.201	0.035	12	-5.815	0.008
F ground late chicks - M large branch late chicks	-0.203	0.031	12	-6.564	0.003
F ground late chicks - F small branch late chicks	-0.441	0.039	12	-11.242	< 0.001
F ground late chicks - M small branch late chicks	-0.579	0.036	12	-16.149	< 0.001
F ground late chicks - F trunk late chicks	-0.324	0.039	12	-8.401	< 0.001
F ground late chicks - M trunk late chicks	-0.178	0.027	12	-6.597	0.003
F ground late chicks - F small branch nonbreeding	-0.540	0.030	12	-18.122	< 0.001
F ground late chicks - M small branch nonbreeding	-0.666	0.027	12	-24.958	< 0.001
F ground late chicks - F trunk nonbreeding	-0.311	0.028	12	-11.085	< 0.001
F ground late chicks - M trunk nonbreeding	-0.160	0.021	12	-7.656	0.001
M ground late chicks - F large branch late chicks	-0.195	0.035	12	-5.559	0.011
M ground late chicks - M large branch late chicks	-0.197	0.032	12	-6.163	0.005
M ground late chicks - F small branch late chicks	-0.435	0.040	12	-10.831	< 0.001
M ground late chicks - M small branch late chicks	-0.573	0.037	12	-15.475	< 0.001
M ground late chicks - F trunk late chicks	-0.318	0.039	12	-8.146	< 0.001
M ground late chicks - M trunk late chicks	-0.172	0.028	12	-6.188	0.005
M ground late chicks - F small branch nonbreeding	-0.534	0.030	12	-17.920	< 0.001
M ground late chicks - M small branch nonbreeding	-0.660	0.028	12	-23.382	< 0.001
M ground late chicks - F trunk nonbreeding	-0.305	0.029	12	-10.709	< 0.001
M ground late chicks - M trunk nonbreeding	-0.154	0.022	12	-6.904	< 0.001

F large branch late chicks - M small branch late chicks	-0.378	0.053	12	-7.137	0.001
F large branch late chicks - F small branch nonbreeding	-0.340	0.047	12	-7.209	0.001
F large branch late chicks - M small branch nonbreeding	-0.465	0.040	12	-11.584	< 0.001
M large branch late chicks - M small branch late chicks	-0.376	0.059	12	-6.340	0.004
M large branch late chicks - F ground nonbreeding	0.162	0.033	12	4.901	0.029
M large branch late chicks - F small branch nonbreeding	-0.338	0.040	12	-8.503	< 0.001
M large branch late chicks - M small branch nonbreeding	-0.464	0.042	12	-10.967	< 0.001
F small branch late chicks - M trunk late chicks	0.263	0.055	12	4.804	0.034
F small branch late chicks - F ground nonbreeding	0.400	0.041	12	9.695	< 0.001
F small branch late chicks - M ground nonbreeding	0.370	0.042	12	8.845	< 0.001
F small branch late chicks - F large branch nonbreeding	0.368	0.044	12	8.315	< 0.001
F small branch late chicks - M large branch nonbreeding	0.372	0.038	12	9.707	< 0.001
F small branch late chicks - M trunk nonbreeding	0.280	0.039	12	7.122	0.001
M small branch late chicks - M trunk late chicks	0.401	0.053	12	7.534	0.001
M small branch late chicks - F ground nonbreeding	0.538	0.037	12	14.512	< 0.001
M small branch late chicks - M ground nonbreeding	0.508	0.039	12	13.079	< 0.001
M small branch late chicks - F large branch nonbreeding	0.506	0.036	12	14.201	< 0.001
M small branch late chicks - M large branch nonbreeding	0.510	0.040	12	12.814	< 0.001
M small branch late chicks - F trunk nonbreeding	0.267	0.041	12	6.489	0.003
M small branch late chicks - M trunk nonbreeding	0.418	0.043	12	9.638	< 0.001
F trunk late chicks - F ground nonbreeding	0.283	0.040	12	7.026	0.001
F trunk late chicks - M ground nonbreeding	0.253	0.041	12	6.142	0.005
F trunk late chicks - F large branch nonbreeding	0.251	0.042	12	5.980	0.006
F trunk late chicks - M large branch nonbreeding	0.256	0.039	12	6.523	0.003
F trunk late chicks - M small branch nonbreeding	-0.342	0.042	12	-8.116	< 0.001
M trunk late chicks - F ground nonbreeding	0.137	0.029	12	4.695	0.040
M trunk late chicks - F small branch nonbreeding	-0.362	0.035	12	-10.225	< 0.001
M trunk late chicks - M small branch	-0.488	0.040	12	-12.056	< 0.001

nonbreeding					
F ground nonbreeding - F small branch nonbreeding	-0.499	0.035	12	-14.296	< 0.001
F ground nonbreeding - M small branch nonbreeding	-0.625	0.030	12	-20.711	< 0.001
F ground nonbreeding - F trunk nonbreeding	-0.270	0.032	12	-8.334	< 0.001
F ground nonbreeding - M trunk nonbreeding	-0.119	0.025	12	-4.824	0.033
M ground nonbreeding - F small branch nonbreeding	-0.470	0.034	12	-13.913	< 0.001
M ground nonbreeding - M small branch nonbreeding	-0.596	0.038	12	-15.878	< 0.001
M ground nonbreeding - F trunk nonbreeding	-0.241	0.032	12	-7.463	0.001
F large branch nonbreeding - F small branch nonbreeding	-0.468	0.036	12	-12.878	< 0.001
F large branch nonbreeding - M small branch nonbreeding	-0.594	0.032	12	-18.317	< 0.001
F large branch nonbreeding - F trunk nonbreeding	-0.239	0.034	12	-7.062	0.001
M large branch nonbreeding - F small branch nonbreeding	-0.472	0.034	12	-13.854	< 0.001
M large branch nonbreeding - M small branch nonbreeding	-0.598	0.035	12	-17.011	< 0.001
M large branch nonbreeding - F trunk nonbreeding	-0.243	0.032	12	-7.642	0.001
F small branch nonbreeding - M trunk nonbreeding	0.380	0.039	12	9.754	< 0.001
M small branch nonbreeding - F trunk nonbreeding	0.355	0.041	12	8.557	< 0.001
M small branch nonbreeding - M trunk nonbreeding	0.506	0.043	12	11.899	< 0.001
F trunk nonbreeding - M trunk nonbreeding	0.151	0.029	12	5.208	0.019

Appendix II. Table of all significant pair-wise contrasts from a multinomial logistic regression comparing sex, background substrate type and status. F and M stand for female and male respectively Pairwise contrasts were calculated using Tukey adjustment. See Chapter 2 for more details on methodology.

Contrast	Estimate	Standard error	df	t ratio	p value
F bark breeding - F leaf litter breeding	0.273	0.029	15	9.369	< 0.001
F bark breeding - M leaf litter breeding	0.268	0.030	15	9.034	< 0.001
F bark breeding - F leaves breeding	-0.247	0.055	15	-4.506	0.038
F bark breeding - M leaves breeding	-0.354	0.047	15	-7.589	< 0.001
F bark breeding - F lichen breeding	0.275	0.029	15	9.377	< 0.001
F bark breeding - M lichen breeding	0.267	0.030	15	8.936	< 0.001
F bark breeding - M moss breeding	0.196	0.034	15	5.696	0.005
F bark breeding - F skirt breeding	0.274	0.030	15	9.267	< 0.001
F bark breeding - M skirt breeding	0.268	0.030	15	8.992	< 0.001
F bark breeding - F leaf litter nonbreeding	0.237	0.032	15	7.487	< 0.001
F bark breeding - M leaf litter nonbreeding	0.210	0.033	15	6.399	0.002
F bark breeding - M leaves nonbreeding	-0.280	0.035	15	-8.029	< 0.001
F bark breeding - F lichen nonbreeding	0.277	0.029	15	9.591	< 0.001
F bark breeding - M lichen nonbreeding	0.273	0.029	15	9.375	< 0.001
F bark breeding - F moss nonbreeding	0.180	0.035	15	5.215	0.011
F bark breeding - M moss nonbreeding	0.232	0.030	15	7.818	< 0.001
F bark breeding - F skirt nonbreeding	0.278	0.029	15	9.639	< 0.001
F bark breeding - M skirt nonbreeding	0.276	0.029	15	9.556	< 0.001
M bark breeding - F leaf litter breeding	0.230	0.026	15	8.830	< 0.001
M bark breeding - M leaf litter breeding	0.225	0.027	15	8.440	< 0.001
M bark breeding - F leaves breeding	-0.290	0.047	15	-6.207	0.002
M bark breeding - M leaves breeding	-0.398	0.051	15	-7.823	< 0.001
M bark breeding - F lichen breeding	0.232	0.026	15	8.911	< 0.001
M bark breeding - M lichen breeding	0.224	0.027	15	8.228	0.0001
M bark breeding - M moss breeding	0.153	0.033	15	4.692	0.028
M bark breeding - F skirt breeding	0.231	0.026	15	8.818	< 0.001
M bark breeding - M skirt breeding	0.224	0.027	15	8.293	< 0.001
M bark breeding - F leaf litter nonbreeding	0.193	0.028	15	6.834	0.001
M bark breeding - M leaf litter nonbreeding	0.166	0.030	15	5.490	0.007
M bark breeding - F leaves nonbreeding	-0.241	0.033	15	-7.222	< 0.001
M bark breeding - M leaves nonbreeding	-0.323	0.043	15	-7.596	< 0.001
M bark breeding - F lichen nonbreeding	0.234	0.026	15	9.181	< 0.001
M bark breeding - M lichen nonbreeding	0.229	0.026	15	8.804	< 0.001
M bark breeding - F moss nonbreeding	0.137	0.030	15	4.586	0.033

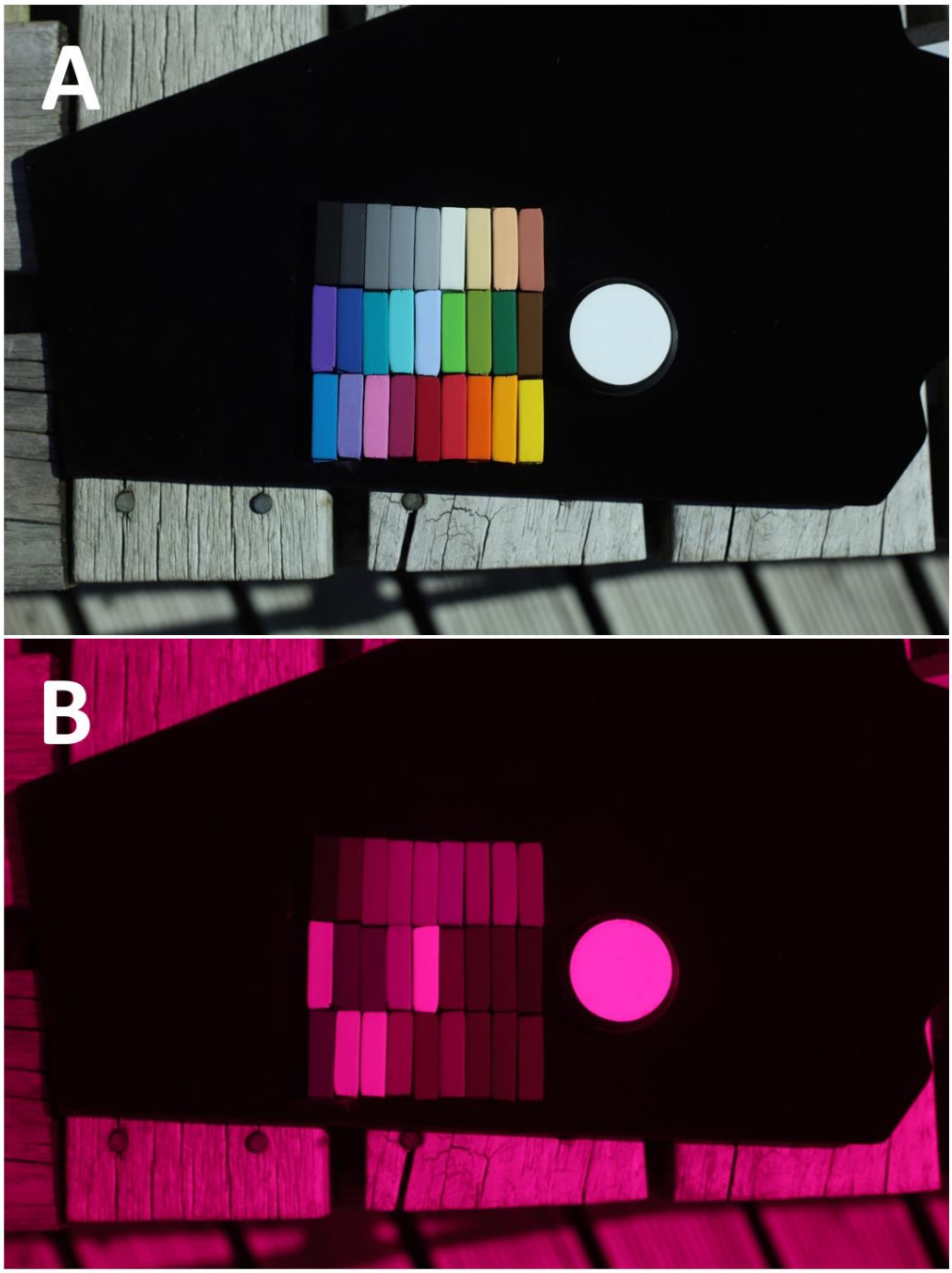
M bark breeding - M moss nonbreeding	0.189	0.029	15	6.558	0.001
M bark breeding - F skirt nonbreeding	0.235	0.025	15	9.227	< 0.001
M bark breeding - M skirt nonbreeding	0.233	0.026	15	9.020	< 0.001
F leaf litter breeding - F leaves breeding	-0.520	0.033	15	-15.856	< 0.001
F leaf litter breeding - M leaves breeding	-0.628	0.030	15	-20.904	< 0.001
F leaf litter breeding - F moss breeding	-0.161	0.027	15	-6.050	0.003
F leaf litter breeding - M moss breeding	-0.077	0.018	15	-4.385	0.047
F leaf litter breeding - F bark nonbreeding	-0.360	0.029	15	-12.547	< 0.001
F leaf litter breeding - M bark nonbreeding	-0.295	0.027	15	-11.140	< 0.001
F leaf litter breeding - F leaves nonbreeding	-0.472	0.030	15	-15.924	< 0.001
F leaf litter breeding - M leaves nonbreeding	-0.554	0.028	15	-19.470	< 0.001
F leaf litter breeding - F moss nonbreeding	-0.093	0.018	15	-5.108	0.014
M leaf litter breeding - F leaves breeding	-0.515	0.033	15	-15.454	< 0.001
M leaf litter breeding - M leaves breeding	-0.622	0.031	15	-20.074	< 0.001
M leaf litter breeding - F moss breeding	-0.155	0.027	15	-5.776	0.004
M leaf litter breeding - F bark nonbreeding	-0.355	0.029	15	-12.336	< 0.001
M leaf litter breeding - M bark nonbreeding	-0.290	0.027	15	-10.594	< 0.001
M leaf litter breeding - F leaves nonbreeding	-0.466	0.029	15	-15.892	< 0.001
M leaf litter breeding - M leaves nonbreeding	-0.548	0.030	15	-18.538	< 0.001
M leaf litter breeding - F moss nonbreeding	-0.088	0.019	15	-4.689	0.028
F leaves breeding - F lichen breeding	0.522	0.033	15	15.818	< 0.001
F leaves breeding - M lichen breeding	0.514	0.033	15	15.392	< 0.001
F leaves breeding - F moss breeding	0.360	0.051	15	7.097	< 0.001
F leaves breeding - M moss breeding	0.443	0.038	15	11.531	< 0.001
F leaves breeding - F skirt breeding	0.521	0.033	15	15.658	< 0.001
F leaves breeding - M skirt breeding	0.515	0.033	15	15.458	< 0.001
F leaves breeding - M bark nonbreeding	0.225	0.036	15	6.199	0.002
F leaves breeding - F leaf litter nonbreeding	0.484	0.035	15	13.807	< 0.001
F leaves breeding - M leaf litter nonbreeding	0.457	0.036	15	12.765	< 0.001
F leaves breeding - F lichen nonbreeding	0.525	0.033	15	16.116	< 0.001
F leaves breeding - M lichen nonbreeding	0.520	0.033	15	15.971	< 0.001
F leaves breeding - F moss nonbreeding	0.427	0.038	15	11.127	< 0.001
F leaves breeding - M moss nonbreeding	0.479	0.032	15	14.874	< 0.001
F leaves breeding - F skirt nonbreeding	0.525	0.032	15	16.173	< 0.001
F leaves breeding - M skirt nonbreeding	0.523	0.032	15	16.159	< 0.001
M leaves breeding - F lichen breeding	0.629	0.030	15	21.072	< 0.001
M leaves breeding - M lichen breeding	0.621	0.032	15	19.631	< 0.001
M leaves breeding - F moss breeding	0.467	0.041	15	11.385	< 0.001
M leaves breeding - M moss breeding	0.551	0.039	15	13.988	< 0.001
M leaves breeding - F skirt breeding	0.628	0.030	15	20.955	< 0.001
M leaves breeding - M skirt breeding	0.622	0.032	15	19.745	< 0.001

M leaves breeding - F bark nonbreeding	0.267	0.036	15	7.461	0.0003
M leaves breeding - M bark nonbreeding	0.332	0.044	15	7.611	0.0002
M leaves breeding - F leaf litter nonbreeding	0.591	0.032	15	18.671	< 0.001
M leaves breeding - M leaf litter nonbreeding	0.564	0.034	15	16.727	< 0.001
M leaves breeding - F lichen nonbreeding	0.632	0.029	15	21.584	< 0.001
M leaves breeding - M lichen nonbreeding	0.627	0.030	15	20.981	< 0.001
M leaves breeding - F moss nonbreeding	0.535	0.032	15	16.485	< 0.001
M leaves breeding - M moss nonbreeding	0.586	0.033	15	17.767	< 0.001
M leaves breeding - F skirt nonbreeding	0.633	0.029	15	21.630	< 0.001
M leaves breeding - M skirt nonbreeding	0.630	0.030	15	21.256	< 0.001
F lichen breeding - F moss breeding	-0.162	0.027	15	-6.092	0.003
F lichen breeding - M moss breeding	-0.079	0.018	15	-4.459	0.041
F lichen breeding - F bark nonbreeding	-0.362	0.029	15	-12.615	< 0.001
F lichen breeding - M bark nonbreeding	-0.297	0.027	15	-11.112	< 0.001
F lichen breeding - F leaves nonbreeding	-0.473	0.029	15	-16.047	< 0.001
F lichen breeding - M leaves nonbreeding	-0.555	0.029	15	-19.322	< 0.001
F lichen breeding - F moss nonbreeding	-0.095	0.018	15	-5.174	0.012
M lichen breeding - F moss breeding	-0.154	0.027	15	-5.664	0.005
M lichen breeding - F bark nonbreeding	-0.354	0.029	15	-12.118	< 0.001
M lichen breeding - M bark nonbreeding	-0.289	0.028	15	-10.459	< 0.001
M lichen breeding - F leaves nonbreeding	-0.465	0.030	15	-15.590	< 0.001
M lichen breeding - M leaves nonbreeding	-0.547	0.030	15	-18.415	0
M lichen breeding - F moss nonbreeding	-0.086	0.019	15	-4.491	0.039
F moss breeding - F skirt breeding	0.161	0.027	15	6.003	0.003
F moss breeding - M skirt breeding	0.155	0.027	15	5.715	0.005
F moss breeding - F bark nonbreeding	-0.200	0.039	15	-5.095	0.014
F moss breeding - F leaves nonbreeding	-0.311	0.040	15	-7.683	< 0.001
F moss breeding - M leaves nonbreeding	-0.393	0.037	15	-10.663	< 0.001
F moss breeding - F lichen nonbreeding	0.165	0.026	15	6.290	0.002
F moss breeding - M lichen nonbreeding	0.160	0.026	15	6.036	0.003
F moss breeding - F skirt nonbreeding	0.166	0.026	15	6.335	0.002
F moss breeding - M skirt nonbreeding	0.163	0.026	15	6.216	0.002
M moss breeding - F bark nonbreeding	-0.283	0.032	15	-8.865	< 0.001
M moss breeding - M bark nonbreeding	-0.218	0.032	15	-6.777	0.001
M moss breeding - F leaves nonbreeding	-0.394	0.032	15	-12.417	< 0.001
M moss breeding - M leaves nonbreeding	-0.476	0.035	15	-13.726	< 0.001
M moss breeding - F lichen nonbreeding	0.081	0.017	15	4.739	0.026
M moss breeding - F skirt nonbreeding	0.082	0.017	15	4.807	0.023
M moss breeding - M skirt nonbreeding	0.080	0.017	15	4.581	0.034
F skirt breeding - F bark nonbreeding	-0.361	0.029	15	-12.517	< 0.001
F skirt breeding - M bark nonbreeding	-0.296	0.027	15	-10.999	< 0.001

F skirt breeding - F leaves nonbreeding	-0.472	0.030	15	-15.945	< 0.001
F skirt breeding - M leaves nonbreeding	-0.554	0.029	15	-19.169	< 0.001
F skirt breeding - F moss nonbreeding	-0.093	0.018	15	-5.050	< 0.001
M skirt breeding - F bark nonbreeding	-0.355	0.029	15	-12.173	< 0.001
M skirt breeding - M bark nonbreeding	-0.290	0.028	15	-10.523	< 0.001
M skirt breeding - F leaves nonbreeding	-0.466	0.030	15	-15.643	< 0.001
M skirt breeding - M leaves nonbreeding	-0.548	0.030	15	-18.499	< 0.001
M skirt breeding - F moss nonbreeding	-0.087	0.019	15	-4.563	0.035
F bark nonbreeding - F leaf litter nonbreeding	0.323	0.033	15	9.807	< 0.001
F bark nonbreeding - M leaf litter nonbreeding	0.296	0.033	15	9.089	< 0.001
F bark nonbreeding - M leaves nonbreeding	-0.193	0.044	15	-4.432	0.043
F bark nonbreeding - F lichen nonbreeding	0.364	0.028	15	12.794	< 0.001
F bark nonbreeding - M lichen nonbreeding	0.360	0.029	15	12.511	< 0.001
F bark nonbreeding - F moss nonbreeding	0.267	0.037	15	7.237	< 0.001
F bark nonbreeding - M moss nonbreeding	0.319	0.031	15	10.259	< 0.001
F bark nonbreeding - F skirt nonbreeding	0.365	0.028	15	12.860	< 0.001
F bark nonbreeding - M skirt nonbreeding	0.363	0.029	15	12.728	< 0.001
M bark nonbreeding - F leaf litter nonbreeding	0.259	0.029	15	8.775	< 0.001
M bark nonbreeding - M leaf litter nonbreeding	0.231	0.034	15	6.892	0.001
M bark nonbreeding - M leaves nonbreeding	-0.258	0.051	15	-5.048	0.015
M bark nonbreeding - F lichen nonbreeding	0.299	0.027	15	11.252	< 0.001
M bark nonbreeding - M lichen nonbreeding	0.295	0.027	15	10.818	< 0.001
M bark nonbreeding - F moss nonbreeding	0.202	0.032	15	6.245	0.002
M bark nonbreeding - M moss nonbreeding	0.254	0.030	15	8.480	< 0.001
M bark nonbreeding - F skirt nonbreeding	0.300	0.027	15	11.308	< 0.001
M bark nonbreeding - M skirt nonbreeding	0.298	0.027	15	11.093	< 0.001
F leaf litter nonbreeding - F leaves nonbreeding	-0.435	0.034	15	-12.744	< 0.001
F leaf litter nonbreeding - M leaves nonbreeding	-0.517	0.031	15	-16.409	< 0.001
M leaf litter nonbreeding - F leaves nonbreeding	-0.408	0.033	15	-12.223	< 0.001
M leaf litter nonbreeding - M leaves nonbreeding	-0.490	0.037	15	-13.135	< 0.001
F leaves nonbreeding - F lichen nonbreeding	0.476	0.029	15	16.286	< 0.001
F leaves nonbreeding - M lichen nonbreeding	0.471	0.030	15	15.953	< 0.001
F leaves nonbreeding - F moss nonbreeding	0.379	0.038	15	9.923	< 0.001
F leaves nonbreeding - M moss nonbreeding	0.430	0.032	15	13.268	< 0.001
F leaves nonbreeding - F skirt nonbreeding	0.476	0.029	15	16.361	< 0.001
F leaves nonbreeding - M skirt nonbreeding	0.474	0.029	15	16.192	< 0.001
M leaves nonbreeding - F lichen nonbreeding	0.558	0.029	15	19.385	< 0.001
M leaves nonbreeding - M lichen nonbreeding	0.553	0.030	15	18.712	< 0.001
M leaves nonbreeding - F moss nonbreeding	0.461	0.035	15	13.242	< 0.001
M leaves nonbreeding - M moss nonbreeding	0.512	0.033	15	15.621	< 0.001

M leaves nonbreeding - F skirt nonbreeding	0.558	0.029	15	19.456	< 0.001
M leaves nonbreeding - M skirt nonbreeding	0.556	0.029	15	19.121	< 0.001
F lichen nonbreeding - F moss nonbreeding	-0.097	0.018	15	-5.427	0.008
M lichen nonbreeding - F moss nonbreeding	-0.092	0.018	15	-5.017	0.016
F moss nonbreeding - F skirt nonbreeding	0.098	0.018	15	5.501	0.007
F moss nonbreeding - M skirt nonbreeding	0.096	0.018	15	5.298	0.010

Appendix III. Explanation of how the camera calibration was performed for Chapter 3 colour analyses, following guidelines from Troscianko and Stevens (2015) and the micaToolbox user guide (Troscianko, 2019). Images A and B show the range of 27 different coloured soft pastels used for camera calibration photographed in the visual light spectrum and ultraviolet spectrum respectively, alongside a 99% reflectance standard. See Chapter 3 for more information about the camera and photography methods.



Ultraviolet and visible spectrum photos were taken of 27 MUNGYO soft pastels arranged in a grid against a black velvet background alongside a 99% reflectance standard, outdoors on an overcast but bright day with fairly consistent light levels (See image A and B). Each pastel was cleaned with a piece of paper so that one side was uniform and diffuse in colour. I also removed any fluorescent pastels, as these may interfere with the light source. The spectral reflectance of the same pastels was then measured with an Ocean Optics 2000 spectrophotometer, with the probe held at 45-degree angle to the surface of the pastel using a mount designed to keep the probe still and at a consistent distance from the pastel. The resulting spectral data was binned into 1nm increments across 300-700nm and normalised, then entered into the “Cone Mapping > Charts” folder in the micaToolbox plugin.

After creating a mspec. image combining the visual spectrum and ultraviolet photos and calibrating with the 99% reflectance standard, the pastel chart was measured using the “Camera Calibration > Measure Chart” tool in the micaToolbox (Troscianko et al., 2015). A 9x3 grid was overlayed on the image to measure each pastel individually. The results were saved and used for the next step, which was “Camera Calibration > Generate Cone Mapping from Chart”. The camera name, Canon EOS RP, was inputted, alongside either blue tit 300-700nm or common buzzard 300-700nm as the receptors. The illuminant selected was the D65 300-700 as the images were taken outside. The MUNGYO pastel chart was selected for the chart reflectance spectra. The resulting cone mapping model was then used for further image analyses.

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