Colour change in New Zealand geckos: a defence against avian predation?

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A thesis submitted to Victoria University of Wellington
in partial fulfilment of the requirements for the degree of
Master of Science in Ecology and Biodiversity

2022

Acknowledgements

This thesis would not have been possible to achieve without the kind support of many people. Firstly my supervisor, Nicky Nelson, who was available and provided kind and encouraging support whenever I needed it, and understood the challenges I faced along my journey. These years have not been easy, but she has been truly wonderful as a supervisor and I have no hesitation in recommending her to all. Sarah Herbert has also been a wonderful mentor and friend throughout this process. Vanessa Cave has helped me learn so much and provided me with excellent support and an amazing friendship.

Other members of Reptile Research Group – Ox Lennon, Brittany Florence-Bennett, Linlin Liu, Chris Woolley, Sue Keall, Sydney Dean, Sarah Lamar, Doug, Liam, Lily Castle-Tidwell, and Ian Blixt have been a wonderfully supportive group and read through some of my draft chapters. Thank you also to Linlin and Sydney for surprising me with snacks as I worked on my final edits. Stephen Hartley was kind enough to lend me trail cameras that I needed for my chapter 3 research and gave me work as a research assistant. Diane Ormsby provided me with materials to learn to make a conference poster and was always friendly and supportive. Patricia Stein was understanding when I needed more time.

Writing a thesis while working and raising children is a challenge, but with the help and support of others it can be done. I am grateful to Brittany Florence-Bennett for helping me out with childcare when I had run out of other options, my parents for providing me with support where they could, my brother for giving me stats resources and watching my children when he was able to visit over Christmas. My children for being the best they could be, and putting up with my need to focus on my thesis or paid work. I look forward to having more time for them again. Geoff for offering to read my thesis and being kind and supportive. Peter for technical support and reading the final draft.

I am also grateful to:
- Mel Dohner for providing me with some of the equipment and teaching me how to use fieldtech, and Paul Roulston for creating a temperature controller unit for the heat mats. Neville Higgison for 3D printing the lizard models.
- Trent Bell, Dennis Keall, and Richard Romijn for talking to me about lizards.
- Morrie Love and Te Atiawa- Taranaki whānui for approving my research

Abstract

Reptilian colouration is important for a number of functions, including predator evasion, social signalling, and thermoregulation. Colour may assist reptiles to avoid predation in several ways, including camouflage, mimicry, aposematism, and deimatic displays. Camouflage is particularly important for avoiding predators that predominantly use vision to detect prey. Evading visually hunting avian and reptilian predators is thought to have influenced the evolution of New Zealand's endemic lizards, therefore it is plausible that their colouration has an anti-predator function. Rapid physiological colour change has been observed in at least seven of New Zealand's 48 endemic gecko species, but the triggers for this phenomenon are poorly understood. I investigated whether rapid colour change in geckos could serve as a defence mechanism against avian predators. Because many geckos are capable of tail autotomy as a defence against predation, and colour has been observed to change differently in the body and tail of two New Zealand gecko species, I also investigated whether colour change in the tail differed from the rest of the body. To achieve this, I (1) measured the colour responses of geckos to predator presence in ngāhere geckos (*Mokopirirakau* 'southern North Island') and Raukawa geckos (*Woodworthia maculata*), and (2) compared the responses of wild birds to model geckos displaying increased brightness and contrast in their tails.

To examine gecko colouration responses to avian predator presence, I presented 15 ngāhere geckos and 20 Raukawa geckos with a randomly ordered series of visual and auditory cues and photographed their skin colour before and after each cue. The four visual cue 'treatments' consisted of a model animal flying by the enclosure, with a fifth control treatment for which no object passed overhead. The models were of a (1) morepork (*Ninox novaeseelandiae*; a nocturnal lizard predator), (2) kingfisher (*Todiramphus sanctus*; a diurnal lizard predator), (3) fantail (*Rhipidura fuliginosa*; a bird that does not eat lizards), and a (4) monarch butterfly (*Danaus plexippus*; an insect that does not eat lizards and is not eaten by geckos). The three auditory treatments were a (1) morepork call, (2) fantail call, and (3) no call. Photographs of geckos were calibrated using an xrite color standard and ImageJ was used to measure skin brightness, contrast, saturation, and hue. A before-after-control-impact (BACI) framework was used for statistical modelling of the repeated measures data taken from each gecko. There was no evidence for differing body and tail colouration in ngāhere geckos, except in the response of saturation to auditory cues. Conversely, there was evidence that brightness and saturation of Raukawa geckos differed between the body and tail. While variation in skin colour of individual geckos was observed across treatments in

both species, the BACI analysis did not provide evidence of colour change in response to predator presence. These results suggest that the tail and body of both ngāhere and Raukawa geckos can be differently coloured when measured at the same time. However, uniformity in colour across the whole body appears to be displayed much more frequently in ngāhere geckos. Changes observed in the skin hue, brightness, and saturation of individual ngāhere and Raukawa geckos provide the first experimental evidence that these species are capable of changing aspects of their colour. The apparent lack of a direct response to simulated predator presence in the experiments may have been due to the experimental design providing insufficient time for skin colour to change substantially between treatments, or it may be that there are limitations to the frequency, magnitude, and speed of colour change in geckos following previous colour changes. It may also be that the colour changes observed in the field were a result of another trigger, such as increasing light levels, stress, or temperature.

To test whether the increased levels of brightness and/or contrast in the tail observed in nature resulted in an increased probability of avian attack on a gecko's tail compared with other body parts, I used trail cameras and model lizards coated in clay. The three treatments were: tails the same colour and brightness as the rest of the body, brighter tails, and more highly contrasted tails. Trail cameras were not effective for capturing avian predator attack behaviour, but I was able to deduce their behaviour from peck marks left in the clay. I calculated area-standardised pecks for the head, body, tail, and limbs of each model type, and investigated which body part was pecked most often within each model. Across the whole gecko model, contrasted-tailed models received more pecks, however more of these pecks were directed at the tail and limbs. There was a weak signal that a similar pattern may be occurring in brighter-tailed models, however this was not statistically significant. The number of area-adjusted pecks to the head and body did not differ significantly between plain-tailed controls and the models with brighter or more contrasted tails. In models with brighter or more contrasted tails, the most-pecked body part was never the head, and most often the tail (at around 1.3 times the rate of the models with plain tails). Rapid colour change observed in geckos could be an effective defence response, but without further data there is insufficient evidence to demonstrate colour change is being utilised in this way. Alternative study designs for predator presentation to geckos may be worth pursuing and colour change may also be triggered by background matching for camouflage, stress, changing light levels, or changing temperature.

Determining the triggers for colour change in geckos is important, as these can affect conservation management decision-making around habitat changes and climate change. As

colour affects thermoregulation, if geckos are matching colouration to the surrounding background, habitat colouration could affect thermoregulation efficiency and limitations. The combination of increasing temperatures through climate change and the colour of the habitat could affect management decisions relating to restoration.

Avoiding avian predation using colour change in New Zealand geckos (Diplodactylidae)

General Introduction

1.1 Avoiding predators

Predation is an evolutionary arms race between predator and prey, where selection pressures are likely to be strongest on prey species, due to the higher cost of being predated than of missing a meal (Pianka & Vitt, 2003; McElroy, 2019). The interactions of predator and prey have shaped their evolutionary journey, and these have resulted in a variety of adaptations and counter-adaptations for both attack and defence (Stephens et al., 2014; Fulgione et al., 2019, McElroy, 2019). Conversely, when prey are subjected to new predators, these prey tend to be naïve and more vulnerable to their predation, as they have not had sufficient time to adapt and develop avoidance behaviours (Worthy & Holdaway, 2002; Salo et al., 2007; King, 2019).

Predator avoidance throughout a potential predation event has five stages, each with differing levels of defence: detection, recognition, approach, pursuit, and capture (Pianka & Vitt, 2003). At each stage, predation may potentially be avoided through prey defences (Fig. 1).

A predation event will not occur if a predator does not detect its prey (Pianka & Vitt, 2003). The first stage for the prey therefore is avoiding detection, which can be achieved by not being active at the same times as their predators (temporal avoidance) (Lima & Bednekoff, 1999), cryptic colouration or morphology, posture and remaining motionless (Pianka & Vitt, 2003). Cryptic colouration may be achieved through positioning the body to best match the background, or through colour change. For example, pipefish (*Syngnathus typhle*) will turn off colour ornaments when a predator approaches (Berglund, 1993; Fuller & Berglund, 1996). The second layer of defence is to avoid recognition, that is, hiding in plain sight. If the predator detects something, but does not recognise it as prey, a predation event may be avoided. Crypsis and mimicry are common second layers of defence to avoid recognition by predators (Pianka & Vitt, 2003). The third stage of defences are used when a predator makes an approach towards the potential prey. These include various evasive and defensive behaviours such as the pursuit deterrence approach (discouraging a predator from pursuing the prey by showing that the prey has detected it and pursuit is not going to be worth the predator's effort; behaving in a threatening or startling manner towards the predator; warning colouration)

(Hasson et al., 1989; Badiane et al., 2018). The fourth stage is pursuit, where a predator has already detected, identified and approached a prey individual, resulting in defence tactics from the prey individual such as fleeing or seeking refuge. In the fifth stage of a predation event the predator captures the prey, which may respond for example with aggression, chemical defences, or tail autotomy (Pianka & Vitt, 2003; Pafilis et al., 2009, Tsasi et al., 2009; Emberts et al., 2019). The predation sequence ends either in a successful predation event for the predator, or escape for the prey (Pianka & Vitt, 2003). However, escape does not always mean survival, as prey may later succumb to injuries sustained from a failed predation attempt.

1.2 How do lizards avoid predation?

The decision on when and how to attempt to escape predators will depend on prey traits, predator traits, habitat situation, and the costs of fleeing (McElroy, 2019). Lizards depend on behavioural thermoregulation for aspects of their physiology such as speed of movement (Huey & Stevenson, 1979; Gates, 1980; Hare & Cree, 2016). At times when they are colder, such as early in the morning, it will be more difficult for lizards to escape their predators by fleeing. As such, other methods to avoid being predated are often used. The predominant method of avoiding predators in geckos is to avoid the interaction with the predator by avoiding detection or recognition (Worthy & Holdaway, 2002; Pianka & Vitt, 2003; Hoare, 2006). This is made possible through a combination of four strategies: temporal avoidance, cryptic colouration, minimising movement, and spatial avoidance through the use of refuges. Spatial avoidance may also be facilitated through differential habitat use depending on where the predators are present, which is seen in Duvaucel's geckos (*Hoplodactylus duvaucelii*) from New Zealand, who avoid habitat preferred by their predators (Hoare et al., 2007). Many New Zealand geckos are nocturnal (van Winkel et al., 2018), while most of the avian predators they have co-evolved with are diurnal (King, 2019c). This facilitates temporal avoidance.
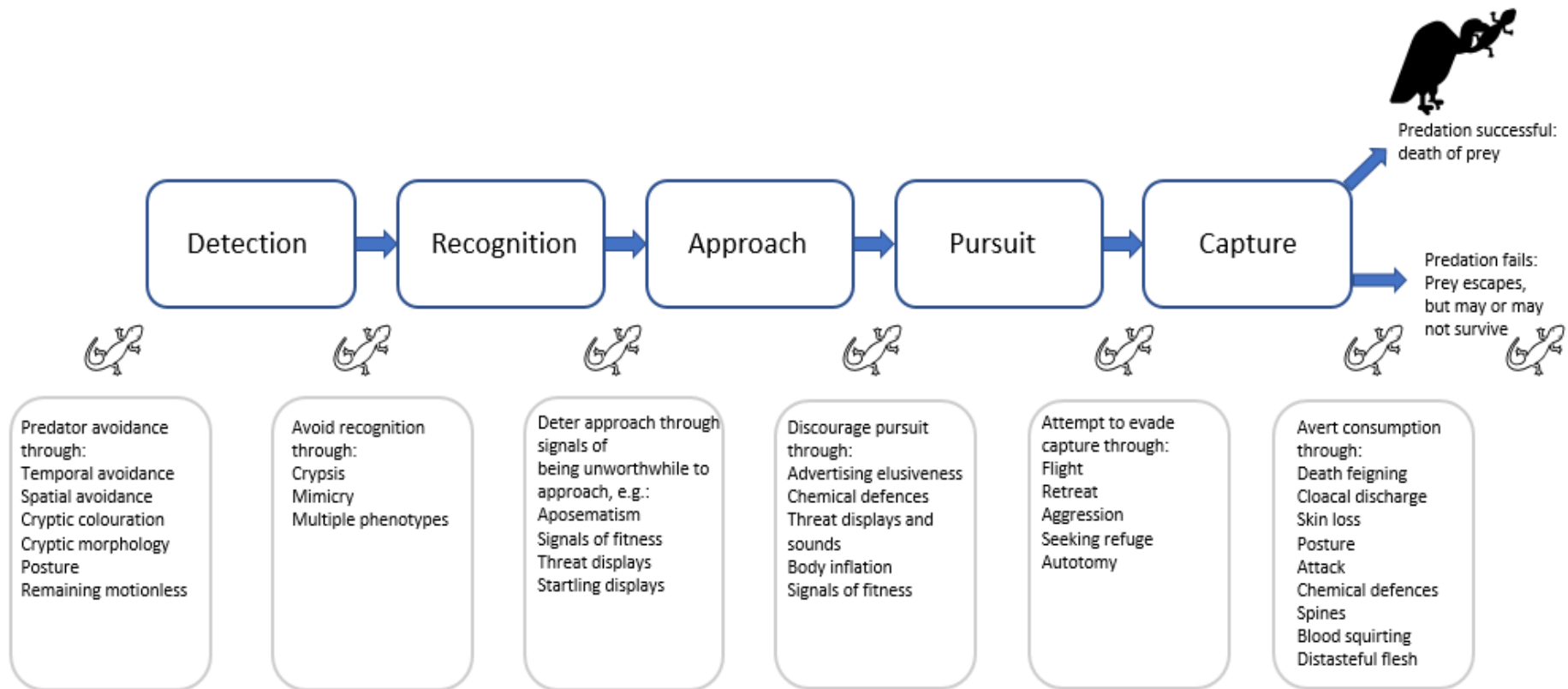
Figure 1.1. A predation sequence and examples of potential avoidance mechanisms of prey for each stage. Figure adapted from Pianka and Vitt (2003), Greene (1988), Lima and Bednekoff (1999), and Ruxton et al. (2018).

Cryptic colouration and minimising movement

In addition to temporal avoidance, one common adaptation is camouflage, used in combination with a freeze response by many species to hide from visually hunting predators such as birds (Hoare, 2006). New Zealand geckos have cryptic colouration that allows them to 'hide in plain sight', and many are sit and wait predators, allowing them to minimise their movements and thus minimise attention to themselves from avian predators (van Winkel et al., 2018). Camouflage can be achieved through a variety of mechanisms, including background matching through selecting backgrounds that match their colouration and patterning, disruptive camouflage where the patterning makes edges difficult to detect, countershading, or through becoming unrecognisable as prey items (e.g. through various forms of mimicry and aposematism) (Ruxton et al., 2018a). The better the camouflage, the greater the chance the reptile has of avoiding detection by predators that hunt visually, such as birds (Isaac & Gregory, 2013).

Refuges

To avoid predation, lizards such as geckos typically seek refuge in tight spaces (refuges) nearby, which may protect them from birds and large predators (Pianka & Vitt, 2003). Unfortunately this often does not protect them from introduced mice (*Mus musculus*) (Norbury et al., 2014). These predators can squeeze into very tight crevices (Day & MacGibbon, 2007) and prefer dark spaces to illuminated ones (Farnworth et al., 2016). They are often active at the same time as many of New Zealand's native lizards (Hut et al., 2011; van Winkel et al., 2018), are capable of killing even animals bigger than themselves (Cuthbert and Hilton, 2004), and have been known to attack even large New Zealand lizards (Norbury et al., 2014). They also nibble on immobile or partially hidden lizards while they are still alive (Adams & Toki, 2019) potentially resulting in injury, infection, or death of lizards (anecdotal photographic evidence: Jewell, 2021).

Autotomy

A further defence strategy commonly used by lizards when other strategies have failed to avert an attack, is autotomy. Autotomy has evolved multiple times throughout Animalia, with lizards being the iconic example (Emberts et al., 2019). The ability of an animal to shed its tail is a widespread antipredator strategy among lizards, though there are differences in this ability between taxa (Pafilis et al., 2009, Tsasi et al., 2009). The lizard sheds its tail in response to a perceived threat or an attack, and, all going well, the predator focusses its efforts on the tail thereby giving the lizard a chance to escape.

While there are many potential costs of autotomy including potential behavioural changes, reduction in home range sizes, reduction in reproductive opportunities, changes in foraging behaviours and success (Emberts et al., 2019), lowered social status (Fox & Rostker, 1982), changes in mobility (Higham, 2019), reduced signalling ability, and losing the fat reserve stored in its tail, these costs are rather less than the rather finite cost of being eaten. One factor thought to influence how readily a gecko will autotomise its tail, is the level of arboreality of the species. Geckos may use their tails to assist them in moving safely between stems. Fitness is strongly related to an animal's ability to move within its environment (Pillai et al., 2020), and anything that affects this ability, such as the loss of a tail, is balanced against the need to escape a predator. Thus one would expect an arboreal gecko to be less quick to autotomise its tail than one where the tail has less of a function in locomotor support. I propose to investigate predator avoidance strategies in New Zealand geckos, and specifically how colour change related to autotomy may impact survival.

1.3 Reptilian colour and its use in predator avoidance

1.3.1 How do we define colour?

To measure colour change in an animal, we first need to define colour. Colour can be defined in several ways. At its most basic, it can be defined as the light reflected from an object, however this is seldom just a single wavelength. It can be defined in the RGB colour space by its levels of red, green, and blue (RGB). The levels (0 = no colour; 255 = maximum colour) of these three primary colours can be varied resulting in 255^3 possible colour combinations (de Farias e Moraes, 2018; Morreale, 2018). The RGB colour space is the one most commonly used by devices capturing and displaying images (Morreale, 2018).

Colour can also be defined in the HSB colour space by its levels of Hue, Saturation, and Brightness, or in terms of HSI - Hue, Saturation, and Intensity. Images of an animal's colouration can also be defined by their contrast. These can all be derived mathematically from the levels of red, green, and blue, which can be consistently measured with the aid of a colour standard (e.g. xrite color standard) using image analysis software such as ImageJ. Hue is defined through the wavelength component of colour and can be defined through the amount of red, green, and blue. Hue is a continuum (0-360°) and can be visualised through the use of a colour wheel (Kennedy, 2020; 0° or 360° corresponds to red, 60° corresponds to yellow, 120° to green, 240° to blue; Morreale, 2018).
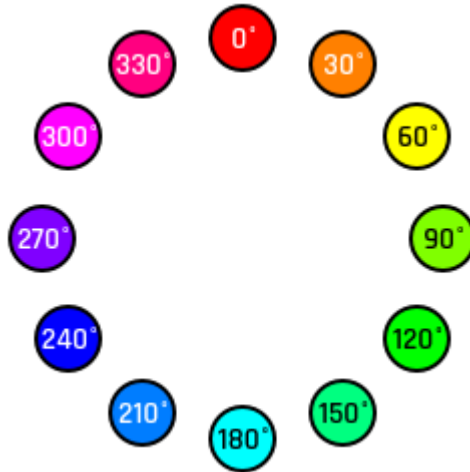
Fig. 1.2. Hue, as shown by the colour wheel (Kennedy, 2020)

Fig. 1.3. Differing levels of saturation (Scott, 2019). The left side of the scale has a higher level of saturation, and the right side shows a low level of saturation.

Fig. 1.4. Differing levels of brightness: left image - reduced brightness, centre image - unedited, right image - increased brightness. Images adjusted using google docs.

Fig. 1.5. Differing levels of contrast: left image - reduced contrast, centre image - unedited, right image - increased contrast. Note that as a result of increased contrast the background has become black. Images adjusted using google docs.

Saturation demonstrates the strength of the colour, e.g. a colour with low levels of saturation will look paler, greyer, and washed out, while a colour with high saturation will show the colour strongly. It is the colourfulness of the stimulus, relative to its brightness. Brightness is determined by how much light is reflected from an object - low brightness will make the object appear dark, while high brightness will make the object appear bright. Brightness depends on amplitude and wavelength, while intensity is a measure of the energy of the wave, which is directly proportional to the square of the amplitude. Intensity is highly correlated with brightness due to the method of calculation: Intensity is calculated as $I = ⅓$ (R+G+B), while brightness is Y' = 0.299 R + 0.587 G + 0.114 B (Where R is the level of red, G the level of green, and Blue the level of blue in the area of interest. Contrast is defined as the maximum intensity minus the minimum intensity of the area of interest. Maximum contrast would be seen as black and white. Perception of colour and its components depend on the environmental light levels, thus for colour analysis it is vital to measure and take into account light levels for a fair comparison. Adding complexity to the measurement of colour in animals, there is the variation in colour across the animal's body and over time, for example through colour change.

1.3.2 The implications of colour and colour change for reptiles

The colour patterns of animals serve three main purposes: thermoregulation, intraspecific communication and evasion of predators (Endler, 1978). These purposes are not mutually exclusive and can be complementary or antagonistic (Cooper & Greenberg, 1992; Stuart-Fox & Moussalli, 2009; Stuart-Fox & Moussali, 2011; Sköld et al., 2012; Baling, 2017). Adding further complexity, some animals are able to manipulate their colour, including variably across different regions of their body, with the classic examples of this being chamaeleons (Cooper & Greenberg, 1992). Different areas of the body (visible vs concealed) may be subject to different selection pressures (Stuart-Fox & Ord, 2004).

There are two types of colour change: morphological colour change (which takes place over days or months) and physiological colour change (which takes milliseconds to hours) (Stuart-Fox & Moussalli, 2011). I will focus on physiological colour change, which is, in vertebrates, mediated by synchronous intracellular transport of pigmented organelles in chromatophores, which are pigment-containing cells (Stuart-Fox & Moussalli, 2011; Sköld et al., 2012). Chromatophores are complex subcutaneous organs consisting of nerves, muscles and sheath cells surrounding tiny sacs of pigment granules and the size of the sacs can be changed by neural impulses to yield various coloured effects (Dawson, 2006). Physiological colour change is important due to its potential effects on thermoregulation, camouflage, and signalling,

not only creating the potential for ectotherms to use colour change to optimise their thermoregulation, but also creating potential conflicts between the need to camouflage and the need to warm up, cool down or communicate. For example, if colour change is used for camouflage, rapid physiological colour change could be important if animals need to move to a better position for thermoregulation, i.e. to warm up or to avoid overheating, so that they can still be camouflaged against the new background.

Colour has an impact on thermoregulation for lizards (Geen & Johnston, 2014; Rowland, 2011, Sköld et al., 2012; Pianka & Vitt, 2003); and, as such, colour change may be initiated by a change in temperature (Stuart-Fox & Moussalli, 2011; Langkilde & Boronow, 2012). When a lizard is too hot, it may cool down by lightening in colour, while when it is too cool, it might increase the efficacy and efficiency of its basking time by becoming darker (Avery, 1979). Colouration has been shown to affect heating and cooling in Blue tongue lizards (Geen & Johnston, 2014), desert lizards (Avery, 1979), and two species of Kenyan Chameleons have been shown to increase their reflectance for visible and near-infrared spectral regions (600-1000 nm) as temperatures increase (Walton & Bennett, 1993).

Thermoregulation is essential, as all physiological processes are a function of temperature including digestion, speed of movement, and duration of pregnancies (Gates, 1980; Lawrence, 1996; Rock et al., 2002; Pianka & Vitt, 2003). However, changing colour to improve thermoregulation may present a trade-off, if it increases a lizard's visibility to predators. Depending on the colour of the background, darkening their body could reduce the time required out openly basking to reach a temperature where they become fast enough to evade predators, but potentially increase the lizard's visibility to predators during that time. Alternatively, a lizard that is background matching while a predator is nearby, could potentially become heat stressed. Some lizards are also known to change colour when under stress (Fitze et al., 2009; Sköld et al., 2012), while others change their thermoregulatory behaviour when stressed or at risk, e.g. a nocturnal species of gecko, *Oedura lesueurii*, Italian Wall Lizards (*Podarcis muralis*), and Raukawa geckos (*Woodworthia maculata*) (Downes & Shine, 1998; Amo et al., 2003; Preest & Cree, 2008).

Light levels and background colour may also affect camouflage and colour change in reptiles. There is evidence that some colour changing species (not just lizards) change to darker colours in low light levels and lighter colours in high light levels, giving them greater camouflage (Endler, 1978; Avery, 1979; Stevens and Merilaita, 2011). Crocodilians have been shown to change colour in different light environments and with different coloured backgrounds, although not

always in the same direction (Staniewicz et al., 2018; Merchant et al., 2018). *Tonistoma* exhibited rapid ventral colour change in juveniles, with significantly darker ventral scales in illuminated vs. dark environments (Staniewicz et al., 2018), while *Crocodylus* lightened substantially when transitioned from dark to white enclosures and two members of the Family Gavialidae showed an opposite response, lightening under darker conditions (Merchant et al., 2018). The changes observed by Merchant et al. (2018) were rapid and reversible (60-90 minutes), visually mediated, and modulated by serum α-melanocyte-stimulating hormone (α-MSH), resulting in redistribution of melanosomes within melanophores (Merchant et al., 2018). Injection of crocodiles with α-MSH caused the skin to lighten (Merchant et al., 2018).

Since lizards, including many geckos, drop (autotomise) their tails as an anti-predator response (Arnold, 1984), it is hypothesised for this (somewhat disposable) part of their body to become brighter and more contrasted in response to a predation threat. This could distract a predator's attention away from the rest of the body and to the tail, thereby potentially increasing the probability of the predator attacking the tail (rather than another indispensable body part) and giving the gecko a better chance to escape after autotomy (Castilla et al., 1999; Ruxton et al., 2018).

Lizards also flick their tails when becoming aware of a predator, which is also likely to increase attention to the tail and thus reduce a lizard's risk of predation (Downes & Shine, 1998; Ruxton et al., 2018). Perhaps because tail loss has costs to lizards including losing fat reserves and therefore a greater risk of starvation, the added investment required in growing a new tail, increased vulnerability to predators until the tail grows back, and reduced mobility in some species, some species are less likely to drop their tails as an antipredator response than others (Ruxton et al., 2018), particularly arboreal species (S. Herbert, pers comm). Tail loss also changes behaviour, e.g. a preference for warmer temperatures during tail regrowth (Ruxton et al., 2018), which would increase the need for basking, whether protected or overt.

1.3.3 Reptilian colour and avoidance of avian predation

Birds are key predators of lizards throughout the world (Martin and Lopez, 1996). Avian predation is often reported to have an important effect on lizard population dynamics and behaviour (e.g. Mirkin et al., 2020; Chejanovski et al., 2017; Schneyer, 2001; Poulin et al., 2001; McLaughlin & Roughgarden, 1989; Munger, 1986; Stuart-Fox et al., 2006; Stuart-Fox et al., 2008; Monks et al., 2019). Predation by visually-orienting predators such as birds may impose a

strong natural selection pressure to evolve a cryptic colour pattern in prey species, or life history traits that improve predator avoidance (Ruxton et al., 2018; Brandley et al., 2014).

It is not yet well understood whether rapid colour change results in ecologically relevant camouflage for an animal (Wuthrich et al., 2022). While most birds' vision is thought to be tetrachromatic, avian colour vision is not as uniform as earlier thought (Kelber, 2019). There are almost as many 'birds-eye views' as there are birds, however some general principles may be applied (Martin, 2017a). For example, eye size is fundamental to both visual resolution (clarity of vision) and sensitivity (minimum light levels in which information can be extracted) (Martin, 2018). While most birds have small eyes, a phylogenetically diverse range of predator species have large eyes, reflecting the importance of vision to those species (Martin, 2018; Potier, 2020). Each species' vision is finely attuned to the perceptual challenges it faces and the tasks it undertakes (Martin, 2017a), though there is a trade-off between visual resolution and sensitivity - as one increases, the other necessarily decreases (Martin, 2018). As a result, subtle differences in tuning (i.e. being well adapted for one task), can have important implications for the ability to gather information for other tasks as well as influencing other facets of a species' behaviour (Martin, 2017a).

The diversity of specialisations in the visual systems of birds suggests a complex interaction between the visual anatomy and ecology of the species, and this may often be unrelated to its phylogeny (Potier, 2020). Even closely related species of birds have differences in visual capabilities that are reflected in differences in their foraging behaviours (Potier et al., 2016). However, despite relatively larger eyes in raptors that are predators, spatial resolution does not differ between predators and scavengers (Potier, 2020).

Differing behavioural tactics used in scanning, prey detection or capture, may be related to differences in the visual capabilities in the birds using these tactics, and differences in rates of head and eye movements can be studied to better understand these (Martin, 2009; O'Rourke et al., 2010a; Fernández-Juricic, 2012; Potier et al., 2016). Visual performance across the visual field varies considerably in birds, with variation in visual resolution and motion detection (e.g. higher in retinal specialisations, lower in the peripheral retina and blind area) (Fernández-Juricic, 2012). This results in information of varying quality across the visual field, meaning that birds need to move their eyes and heads to optimise their visual perception of their field of view (Fernández-Juricic, 2012).

1.4 Study system: New Zealand geckos (Diplodactylidae)

New Zealand's cool temperate lizard fauna is highly diverse. The assembly of squamate reptiles exhibits the highest diversity in the world for this climatic type (Chapple, 2016). It also has some unusual traits, when compared with other lizard faunas. For example, all of New Zealand's native lizard species, bar one skink, are viviparous, an adaptation to cool temperate climates, and many are long-lived, slow breeding species (van Winkel et al., 2018, Cree, 2020). New Zealand has about 126 species of lizard (Knox, 2021), with more being identified as they are found, or as genetic evidence becomes available to support the separation of cryptic species or species complexes. New Zealand's lizards are divided into skinks (*Oligosoma* spp.) and geckos (Diplodactylidae), and all but one species are endemic (van Winkel et al., 2018).

Diplodactylidae are found in Australia, New Zealand, and New Caledonia (Gamble, 2010). New Zealand geckos split from their Australian relatives in the Eocene or Oligocene, about 40.2 million years ago (28.9 - 53.5 mya), with major lineages diverging mainly in the mid to late Miocene (Nielsen et al., 2011). Within the geckos of New Zealand, seven genera have been identified (van Winkel et al., 2018). New Zealand geckos are competent climbers, with variation in toe pad structure thought to be related to the arboreality and habitat use of the species (van Winkel et al., 2018).

1.4.1 Co-evolution of NZ geckos with predators

New Zealand has 31 species of birds that are known to be predators of lizards (Florence-Bennett, 2020), and the dominance of avian and reptilian predators, along with the absence of mammalian predators for millions of years, has had a strong influence on the predator avoidance strategies and adaptations that have evolved in lizards in New Zealand (Worthy & Holdaway, 2002; Hoare, 2006; Monks et al., 2019; King, 2019c). Gecko adaptations to avian predators' acuity of vision have included a freeze response to predators, relying on camouflage to hide themselves (Monks et al., 2019). Geckos are also sit and wait predators, slow cruise foragers, or repeated ambush predators themselves (Bauer 2007), again relying on camouflage to both protect them from predators and keep them hidden from their prey. This strategy works well against avian predators who are more likely to see them if they move - internationally, birds are the most important predators of small to medium-sized diurnal lizards during periods of activity, while mammals and snakes are most important during periods of lizard inactivity (Pianka & Vitt, 2003).

Contrary to the avian acuity of vision, introduced mammalian predators have poorer eyesight and tend to rely on their sense of smell to hunt (Florence-Bennett, 2020). Hiding in plain sight, is of little use against predators who hunt by smell (Hoare, 2006). As a result, camouflage combined with a freeze response to predators is not only not effective against mammalian predators, but makes New Zealand lizards more vulnerable to predation by mammalian predators alongside whom they have have only been evolving for only about 250 years in the case of Norway rats (*Rattus norvegicus*) (Crozet, 1891, cited in Taylor, 1975; King, 2019a) and about 740 years in the case of kiore (*Rattus exulans*) (Wilmshurst et al., 2008; King, 2019b). Prior to this, New Zealand lizards had not encountered mammalian predators for about 16 million years (Wilmshurst et al., 2008; Monks et al., 2019). A predator who hunts by smell dramatically increases the risk of predation for a New Zealand gecko - both out in the open, and hidden away. As ectotherms, geckos are also more vulnerable to predation by mammals when they are cold, as they are not able to move as quickly as when they are warm, and hiding and camouflage do not provide protection against a keen sense of smell and an ability to fit into small spaces such as that seen in mice.

Before the introduction of mammals to New Zealand, the main predators for lizards were birds and reptiles (Baling et al., 2013; Haw & Clout, 1999; van Winkel & Ji, 2012; van Winkel, 2008; Schneyer, 2002; O'Donnell & Hoare, 2009; Monks et al., 2019). Camouflage was probably adapted within the context of avoiding the visual spectrum, visual acuity and the capacity for pattern recognition of those predators, especially given the presence of antipredator freeze behaviour in lizards that have evolved in the absence of mammalian predators (Monks et al., 2019). This antipredator freeze response, when combined with camouflage, may be especially useful when temperatures are cool, given that ectotherms in a cool temperate climate are severely limited by environmental temperature in their ability to escape from a predator (Monks et al., 2019).

New Zealand geckos tend to be sit and wait predators (Dennis Keall, pers. comm.). Camouflage is a highly important component of being a sit and wait predator, but camouflage can be achieved in several ways including selecting the background that best matches body pattern and colouring, and changing colour to match the background (Merilaita & Stevens, 2011). Changing colour to match the background would provide better flexibility in site selection, but can have effects on other matters such as thermoregulation and risk of detection through movement.

1.4.2 Diplodactylidae and colour change

Little has been published on Diplodactylidae and their ability to change colour, but many gekkonid lizards can change their skin colour to attain excellent camouflage (Vroonen et al., 2012, Das et al., 2014, Fulgione et al., 2014; Lapwong, 2021). Within Diplodactylidae, several genera exhibit colourful tails or lining of the mouth (e.g. Melville et al., 2004). Few diplodactylid geckos are known to exhibit colour changes (Johnson et al., 2019), but those that are known to exhibit colour changing abilities are scattered through the family (Rodda, 2020) (Table 1.1). It has been suggested that most New Zealand geckos (except *Naultinus*) can lighten and darken their colouration to facilitate the absorption or buffering of thermal energy (Jewell, 2011), especially some of the species formerly lumped together in *Hoplodactylus* (Rowlands, 2005), which may include Raukawa and ngāhere geckos, although this is unclear.

Rapid colour change has been observed in Raukawa, ngāhere and Minimac geckos (*Woodworthia* "Marlborough mini") during survey work, with observations suggesting they can change levels of contrast, brightness, and hue (pers. obs., T. Bell and S. Herbert, pers. comm.). I have observed rapid physiological colour change in two species of gecko: the ngāhere gecko (*Mokopirirakau* aff. *granulatus* 'Southern North Island', and the Raukawa gecko (*Woodworthia maculata*) (*inter alia* Bell, Herbert, & Kelly, unpubl. observations). These changes took place within around 5 minutes. While the colour of the patterns changed, dramatically in the case of the ngāhere geckos, the overall shapes of the geckos' individual patterns remained the same, which is consistent with other geckos (Allen et al., 2020). When removing ngāhere geckos from closed cell foam covers (artificial refugia used for monitoring) onto a hand, they rapidly changed colour from dark, almost black and orange colouring to a pale green and very pale green colouring within minutes (Kelly & Herbert, unpubl. observations, *inter alia*). Others have also observed them ranging through mahogany and burgundy colouration to pale green and grey, sometimes interspersed with yellow (Bell & Herbert, pers. comm.).

The overall patterns of the Raukawa geckos appear to be unique to each individual and have been used to identify individuals (S. Herbert, pers. comm.). When removing Raukawa geckos from pitfalls and placing them into a relatively translucent white cotton bag, the geckos changed from a black colour to a pale green-grey colour, with their patterning becoming more obvious as their colour lightened, particularly on their tails, where the colour became very bright and highly contrasted. This colour change was also observed over time as they were handled (Kelly & Herbert, unpubl. observations). While more brightly coloured tails than bodies have been observed in the juveniles of a variety of phylogenetically diverse lizard species (Castilla et al.,

1999; Arnold, 1984), colour change specific to the tail has not previously been described in the literature.

Colour change has also been observed in Minimac geckos, again, particularly on their tails where the patterning became highly contrasted (S. Herbert, pers. comm).

Table 1.1 Colour change in the family Diplodactylidae. *denotes a genus endemic to New Zealand

Genus	Records of colour change found
Amalosia	No colour change (Oliver et al., 2012).
Bavayia	Lack colour change (Rodda, 2020).
Correlophus	Anecdotal and indirect evidence only: Crested geckos "fire up" at night (anecdotal evidence, e.g. Kevin N. from mycrestedgecko.com; Squamates Podcast; indirect evidence, e.g. Rooney et al., 2020), but Rodda (2020) says they lack colour change.
Crenadactylus	No specific record found.
*Dactylocnemis**	No specific record found.
Dierogekko	None are documented to show colour change (Rodda, 2020)
Diplodactylus	No specific record found.
Eurydactylodes	At least one species capable of advanced colour change (Rodda, 2020).
Hesperoedura	No specific record found.
*Hoplodactylus**	No specific record found.
Lucasium	Most lack colour change (Rodda, 2020).
Mniarogekko	No specific record found.
*Mokopirirakau**	Most are capable of colour change (75% vs 5% of diplodactylids), and 25% (vs 1.3% of diplodactylids) have advanced colour changing ability (Rodda, 2020). *M. granulatus* can colour change dramatically (van Winkel et al., 2018). *M.* "Roys Peak"can also change their colour tone drastically (van Winkel et al., 2018) in minutes (NZHS, 2021). *M. nebulosus* may undergo minor colour changes (NZHS, 2021). There is also anecdotal evidence *M.* 'Okarito' undergoes colour change when captured (Toki, 2022).
*Naultinus**	The ventral surface of *N. manukanus* changes colour as they mature, and in *N. stellatus* the colouration and patterning of lateral surfaces becomes more complex with maturity (van Winkel et al., 2018), changing to adult colouration at around 18 months to two years old (NZHS, 2021a). In *N. elegans*, juveniles have darker dorsal surfaces, and this darker colour is lost between the first and second moult (NZHS, 2021a).
Nebulifera	No specific record found.
Oedodera	No specific record found.
Oedura	Most undergo significant ontogenetic colour change as they grow. Thought

	to be unique amongst Australian Diplodactylids. Lacking in species such as *O. gemmata* and *O. monilis.* (Oliver et al., 2012). About a quarter of species have significant darkening colour change ability (Rodda, 2020).
Paniegekko	No specific record found.
Pseudothecadactylus	No specific record found.
Rhacodactylus	Bavay noted in 1869 that a New Caledonian species of gecko in the Diplodactylidae, *Rhacodactylus leachianus*, was capable of colour change (cited in Good et al., 1997). Colour change is in the form of darkening in this species (Rodda, 2020).
Rhyncoedura	No specific record found.
Strophurus	Lack colour changing ability (Rodda, 2020).
Toropuku*	*T. stephensi* is capable of rapid colour change, from light tan to dark brown, in minutes (van Winkel et al., 2018).
Tukutuku*	No specific record found.
Woodworthia*	No specific record found in the literature, anecdotal evidence of colour change in *Woodworthia* 'Otago/Southland large' (Christian Chukwuka pers comm, 2020).

1.4.3 Study species

New Zealand reptiles are generally cryptic and can be hard to spot, as they are often hiding out of sight and well camouflaged (from a human's trichromatic colour vision perspective) when in sight (van Winkel et al., 2018). The Raukawa is a good example of the cryptic nature of New Zealand's herpetofauna (Francke, 2005), as is the ngāhere gecko.

Raukawa geckos

Raukawa geckos (*Woodworthia maculata*), a predominantly thigmothermic, diurno-nocturnal species, forage at night with body temperatures of between 10-13 °C, but thermoregulate by day with body temperatures commonly between 18-26°C and occasionally up to 33°C (Werner & Whitaker, 1978; Rock et al., 2002), though they are known to change their thermoregulatory behaviour when stressed (Preest & Cree, 2008). They thermoregulate through indirect or protected basking, with females having average body temperatures 2°C higher than males, probably due to being gravid (Werner & Whitaker, 1978; Rock et al., 2002). Indirect and protected basking is thought to be not only a protection against predators, but also against wind to aid thermoregulation (deWitt, 1962; Werner & Whitaker, 1978). It seems plausible, that for this species, positioning itself underneath objects and in crevices to bask could reduce its need to camouflage against those predators who could not reach them there. In addition, being in the lower light levels of crevices and underneath objects, could allow them to be a darker colour

improving both thermoregulation efficiency and camouflage and potentially increasing the speed at which they would reach a temperature at which they would be fast enough to evade predators (Downes and Shine, 1998) and able to digest their food (Werner & Whitaker, 1978; Rowlands, 2005; Pianka & Vitt, 2003). In addition, visual acuity is limited by lower light levels (Martin, 2017a), making it harder for a visually oriented predator to spot them within the crevice.

Raukawa geckos, previously known as the "common gecko", have broadly expanded toe pads when compared with other more arboreal species such as the ngāhere gecko (*Mokopiriakau* 'Southern North Island') (van Winkel et al., 2018). While Raukawa geckos can be both arboreal and terrestrial, they are more commonly found on the ground and are one of the more terrestrial species (Whitaker, 1996; van Winkel et al., 2018). Raukawa geckos are found in the North Island and northern South Island of New Zealand, often in lowland and coastal habitats (van Winkel et al., 2018; DOC, accessed 2022). Like others in the genus *Woodworthia* they tend to be active at night, but will also bask during the day, both openly and indirectly, hidden, through rocks or crevices (van Winkel et al., 2018; Hare & Cree, 2016). Their diet consists of insects, fruits, nectar, sap, and honeydew, and they are important pollinators and seed dispersers (Whitaker, 1987; Lord & Marshall, 2001; Wotton, 2002; Wotton, 2016; van Winkel et al., 2018). Like many New Zealand geckos, they are a long-lived, slow breeding species, with lifespans of 27 years recorded in the wild, and 37 years in captive individuals, and approximately annual reproduction of 2 young per year (van Winkel et al., 2018). Raukawa geckos are gregarious and will cluster in large social groups when abundant (van Winkel et al., 2018), such as on islands free from mammalian predators. They also have strong site fidelity and move very little - staying at the same site for decades (Whitaker, 1982).

Ngāhere geckos

Mokopirirakau comes from Māori: Moko = lizard, pirirākau = that clings to trees, and this name reflects the habitat use of this gecko (van Winkel et al., 2018). Ngāhere geckos are predominantly arboreal, diurno-nocturnal, and bask openly (Romijn et al., 2014; Jewell, 2011). While they spend an equal amount of time out during the day and the night, they move about more during the day (Romijn et al., 2014). As their name suggests, they are primarily found in forested habitat. They are usually found on vegetation, but may occasionally be found on the ground (Romijn et al., 2014). They are thought to be serial ambushers, that is they are thought to use several sites from which they ambush prey, as they travel an average 9.5m per day (Romijn et al., 2014). The diet of the ngāhere gecko consists of fruit and invertebrates, including moths and flies (Romijn et al., 2014; van Winkel et al., 2018).

1.5 Aims

I aimed to investigate the role of colour change in two species of Diplodactylidae, ngāhere and Raukawa geckos, as a defence against avian predation. Firstly I examined the response of these two species to auditory and visual simulations of avian predators, and secondly I examined the response of birds to model geckos to increased levels of brightness and contrast observed in Raukawa gecko tails. These data are presented in chapters 2 and 3.

In Chapter 2, I simulated the presence of avian predators through bird calls and models to measure whether there was a colour change effect in ngāhere geckos and raukawa geckos. Specifically, I measured change using four aspects of colour: brightness, contrast, saturation, and hue.

In Chapter 3, I created clay-covered model geckos with brighter tails, more contrasted tails, and tails the same colour as the rest of their bodies and placed these in front of trail cameras in the field to address the following questions:

- Does increased **brightness** in the tail region encourage birds to peck this area?
- Does increased **contrast** in the tail area encourage birds to peck this area?
- How does this compare with a control, where the contrast and brightness are the same throughout the lizard model?

In Chapter 4, I summarise the results of chapter 2 and 3, and discuss the evolutionary trade-offs of colour change and autotomy for Raukawa and ngāhere geckos. I then discuss the responses of birds to model prey colour differences. I discuss the limitations of my study, and possibilities for future research directions.

This research helps to provide an insight into the possible evolutionary advantages of different patterns in colour change for two species of geckos in New Zealand, one arboreal, and one predominantly terrestrial. It explores potential colour change responses of geckos to avian predators, and the responses of birds to differing contrast and brightness in the tail of model Raukawa geckos. It discusses the role and importance of tails and the variation in evolutionary pressures relating to the habitat Raukawa and ngāhere geckos inhabit, and how this may have affected differences in colour change between these two species. This research also identifies opportunities for future research that may help to further clarify patterns of colour change in New Zealand geckos.

Chapter 2 - Colour Change in New Zealand Geckos (Diplodactylidae) after simulations of avian predators

2.1 Introduction

Contrary to the range of predators faced by lizards in many other parts of the world, lizards in New Zealand spent most of their evolutionary history experiencing only avian and reptilian predators (lizards and tuatara). Mammals are an evolutionarily recent additional threat. Birds and reptiles mostly have excellent tetrachromatic vision, while mammals have poorer, dichromatic vision and rely more on smell to locate prey than avian and reptilian predators (Bowmaker, 1998). The evolutionary history of New Zealand's lizards with visual predators has resulted in adaptations such as the freeze response, cryptic colouration (allowing lizards to 'hide in plain sight'), cryptic basking or basking beneath the cover of other objects, hiding under the cover of objects such as rocks and bark, and temporal avoidance. Many species of New Zealand lizards also use the predator avoidance mechanism well known for lizards of autotomising their tail, that is, they have the ability to self-amputate their tails when under threat.

While crypsis and colouration are key components of lizard survival, the ability to change colour presents an additional tool for lizards that enables different habitats to be exploited through camouflage and through altering colour to optimise thermoregulation. Colour change enables signals to be provided to potential mates, competitors, or predators including aposematic colouration, deimatic startle display, and other deterrence signals, and for those signals to be turned off at times when they are not advantageous (Stuart-Fox & Moussalli, 2011; Nielsen et al., 2016). Amongst other things, colour change can be used for both camouflage (to prevent detection and recognition) and deterrence - potentially signalling fitness, an unworthwhile meal, or attracting attention to an area of lesser harm (Stevens & Merilaita, 2009). Though few examples of aposematism are known in lizards, they are not unheard of, e.g., *Strophurus*, a diplodactylid gecko found in Australia, combines deimatic startle displays with aposematism (Nielsen et al., 2016; McElroy, 2020; Rodda, 2020). Some colour changes can also be multifunctional, e.g. in tree lizards (*Urosaurus ornatus*), darker colour signals dominance, but also facilitates heat absorption for thermoregulation (Stuart-Fox & Moussalli, 2011). At times, colour can be subject to conflicting selection pressures (Duarte et al., 2017).

Colour change in lizards is facilitated through pigment-containing cells called chromatophores, whose distribution and types determine the pattern and colouration of reptilian skin (Rutland et al.,

2019; Rooney et al., 2020). This occurs through changes in the position of the granules found within these cells (Rutland et al., 2019). Five types are known: iridophores (diffract different wavelengths depending on their arrangement and density in the dermis; produce blue, or green when combined with carotenoid pigments), guanophores (reflect blue, among others), xanthophores (produce pigments important for yellow), erythrophores (contain carotene, important for red), melanophores (deepest within the dermis; produce black, yellow, and grey) (Haisten et al., 2015; Rutland et al., 2019).

Colour is affected by light, circadian rhythm, temperature, background colouration, motion, and physiological state (Stevens & Merilaita, 2009; Stuart-Fox & Moussali, 2009; Vroonen et al., 2012; Cuthill et al., 2017). In some lizards higher light levels result in paler colouration, while lower light levels result in darker colouration (e.g. *Hemidactylus* sp., Das et al., 2014), while in others the opposite pattern is true (e.g. the bearded dragon *Pogona vitticeps,* Fan et al., 2014). It may be that for those species becoming darker in higher light levels, the darker colouration provides better protection against UV (Alfakih et al., 2022). Changes in the length of light and dark cycles can also affect colour (Fan et al., 2014). Similarly, when temperatures are low, many lizards will become darker in colouration, while when temperatures are high, they will become lighter in colouration and increase their reflectance in order to optimise thermoregulation (Langkilde & Boronow, 2012; Smith et al., 2016a; Black et al., 2019). Colour change is affected by background colouration, e.g. in high light levels *Anolis carolinensis* will be dark brown on a black background, and light green on a white background or when moved into low light levels, and the eyes do not regulate this response (Bagnara & Hadley, 1973). Colour change to better match the background colour is another strategy used by lizards, and this strategy is varied depending on the predator faced by the lizard (Stuart-Fox et al., 2006; Wuthrich et al., 2022). Motion can affect both the signal provided by colour, and the ability of the receiver to perceive it (Peters et al., 2007; New & Peters, 2010; Cronin et al., 2014; Cuthill et al., 2017). Colour may fade with physiological stress and ageing, can be indicative of immunocompetence and parasitic load, or of receptivity (Olsson et al., 2013).

Colour is measured in terms of the three colour channels red, green, and blue. These can be used to mathematically determine hue, saturation, brightness, intensity, and contrast (see Chapter 1). Hue (0-360°) is defined through the wavelength component of colour, saturation (0-255) demonstrates the strength of the colour, brightness (0-255) is determined by the quantity of light reflected by an object and depends on the amplitude and wavelength, intensity (a measure of the energy of the wave, which is directly proportional to the square of the amplitude) is highly correlated with brightness, and contrast (0-255) is defined as the maximum minus the minimum intensity of the area of interest (see Chapter 1). Considering the complexity of colour and its ability to change based on physical and physiological circumstances, standardised methods for measuring colour

and colour change must include careful consideration of the conditions under which colour is observed, including lighting, methods of data capture, for example, photos, and situational context, including capacity of focal species to detect colour aspects.

Little is known about colour change in New Zealand geckos, however it has been suggested that most species can darken and lighten their bodies for thermoregulation purposes (Jewell, 2011). Of the seven genera known in New Zealand, I found records of physiological colour change for *Mokopirirakau* and *Toropuku* in the literature, and anecdotal evidence for *Woodworthia*. I also found records of morphological colour change in *Naultinus* (Table 1.3.1 Chapter 1). I found no records for the other genera.

I have observed colour change in two species of gecko from New Zealand: ngāhere geckos (*Mokopirirakau* 'southern North Island'), a predominantly arboreal species, and Raukawa geckos (*Woodworthia maculata*), a semi-terrestrial species. When retrieved from a retreat, the ngāhere gecko changed colour from black and orange to pale green and grey (fig 2.1a), while the Raukawa gecko became brighter and more highly contrasted, particularly in the tail region (fig 2.1b).

Potential hypotheses for these changes include exposure to a potential predator, changes in light levels, a change in temperature, and a change in background colour. While these were tested for, time constraints (relating to the considerable time required for photo analysis) meant that this data was unable to be analysed for inclusion in this thesis. However this data will be analysed in coming years to form the basis for future publications.

Lizards are able to visually discriminate between different species of predators, and adjust their defensive behaviours accordingly (McElroy, 2020; Sherbrooke & May, 2008). Raukawa geckos are able to autotomise their tail when under threat from predation. While ngāhere geckos can also autotomise their tails, they are thought to be less likely to do so due to their greater arboreality (S. Herbert, pers. comm.). I hypothesised that the brighter and more highly contrasted tail seen in Raukawa geckos was an anti-predator defence mechanism.

Figure 2.1a Ngāhere gecko. Photos of the same animal, taken 4 minutes apart, after removing the gecko from a closed foam cell cover. Pattern is still clearly visible, despite the colour change. Above: first photo, below: second photo. Photos taken by Florence Kelly, April 2018.

Figure 2.1b Four Raukawa geckos with brighter colour and greater pattern contrast exhibited on the tail, the second individual (top right) has a regrown tail. Photos taken by Florence Kelly, 2018-2019.

I investigated potential drivers for the colour change responses of ngāhere and Raukawa geckos. I compared colour change responses of geckos to auditory and visual simulations of avian predators with simulations using non-predatory species, including analysis of differential responsiveness by body part (body and tail). I defined the body as the upper (dorsal) patterned surface of the gecko, including the head. I excluded the lighter coloured (countershaded) ventral surface (which is less visible to predators from above) and the area around the eyes and snout, as the scalation differed in this area and was more reflective (fig. 2.1c). I considered colour using brightness, contrast, saturation, and hue.

Fig 2.1c Tail, and body areas, manually selected in ImageJ. Photo is of a zoomed in selection of the computer screen. Background colour is standardised, and the colour in the photograph is standardised against a colour standard taken in the same lighting conditions and levels.

2.2 Methods

I used 30 ngāhere geckos and 31 Raukawa geckos from the Wellington region of New Zealand, which is characterised by strong winds, steep, strongly faulted hills, warm summers and mild winters (McEwen, 1987). I collected wild geckos from two locations using retreats that suited their differing habitat types and behaviour. Ngāhere geckos are mainly arboreal and found in trees or crevices. Ngāhere geckos were collected from Zealandia Ecosanctuary (fig 2.2a), which is surrounded by a fence designed to exclude all mammalian predators except mice. Zealandia is a mid-successional forested mainland habitat island dominated by broadleaved species with some podocarps present. The species upon which I found these geckos varied slightly from their habitat use in another study (Yee et al., 2022), which may be important if the geckos have adapted their colouration and ability to change colour to their preferred habitat. A list of species upon which the geckos were found can be found in Appendix 2A. I used foam covers to collect ngāhere geckos as per Bell (2009); sheets of black rubber attached to trees using 6-8 nails with gaps of 20-30 mm between the covers and the tree to allow geckos to use them as retreats. One ngāhere gecko was also collected opportunistically from an onduline artificial cover object (ACO) (Wilson et al., 2007).

Raukawa geckos can be arboreal, ground-dwelling, or even semi-fossorial, though being one of the less arboreal gecko species, they are mainly found on the ground (Whitaker, 1996). Raukawa geckos were collected from the area around Tarakena Bay (fig 2.2b), which is subject to

mammalian predator trapping, with mice not directly targetted, but sometimes caught as bycatch. The geckos were collected from an area with low coastal scrub up to around 2m tall, but mostly below 1m (Appendix 2B). There were no large trees in the study area, only low scrub, with the substrate largely dominated by cobble-sized rocks. Raukawa geckos were collected using two layers of onduline ACOs separated by sticks or stones to create a 10-15mm gap, set over a 4L pitfall trap that was set into the ground flush with the soil surface. The buckets were filled with rocks to the top of the bucket. This was done both with the intention of excluding mice (who are known to predate on lizards, e.g. Newman, 1994) and to allow geckos to enter and leave freely, using the pitfalls as retreats.

I labelled newly captured individuals with a silver non-toxic xylene-free permanent marker (Airline 990XF) on the belly and photographed them for individual ID purposes. For each gecko, I noted field air temperature (at ground level for Raukawa geckos, and foam cover level for ngāhere geckos), light levels, humidity, temperature of the collection spot (i.e. temperature within the Onduline, pitfall, or foam cover), cloud cover and weather conditions, type of retreat used, precise location of capture, and capture time. Field air temperature and humidity were measured using a combined thermometer and hygrometer (QM7312, resolution 0.1°C and ±5% relative humidity).
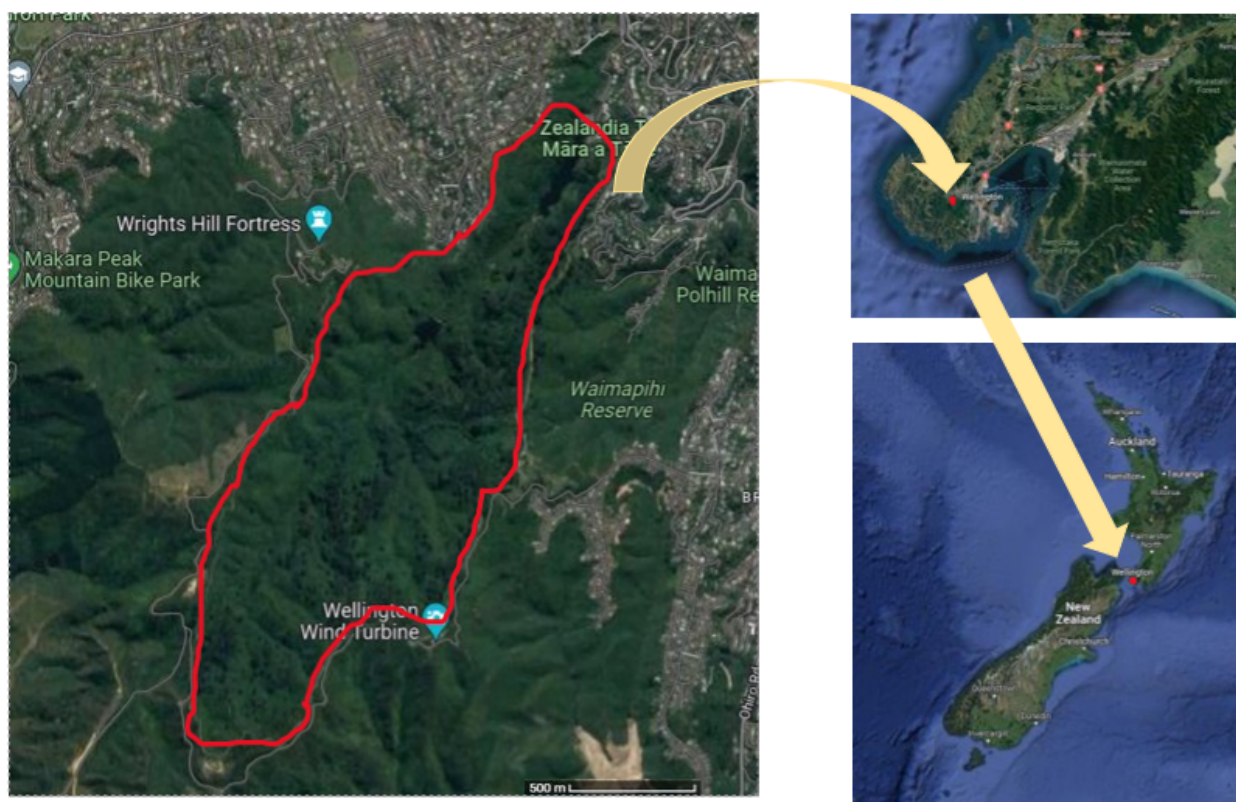
Figure 2.2a Collection site for ngāhere geckos. The red outline shows the Zealandia boundary fence, which is designed to exclude most mammalian predators (Google Maps, data retrieved 24/5/2022).

Figure 2.2b Collection sites for Raukawa geckos (Known as WP2 and WP3 in Herbert, 2020) (Google Maps, data retrieved 24/5/2022).

Temperature was measured using a temperature probe (TP101, resolution 0.1°C) that was calibrated against the combined thermometer and hygrometer. Light levels were measured using a digital lightmeter (QM1587, accuracy 5%). The geckos were then transported to Victoria University of Wellington and taken to the lab for investigation under more standardised conditions than were possible in the field, before being released to their precise point of capture within 24 hours.

Before and after experimentation, captive lizards were individually housed in partially shaded terraria in a windowed room to minimise disturbance to circadian rhythms from artificial light and to avoid overheating. Temperatures were within the 10°C - 25°C range to avoid thermal distress (Hare & Cree, 2016). Geckos were supplied with water, canned pear, and a place to shelter in their terrarium. Terraria were disinfected with 70% ethanol and aired between individuals.

Experiments were conducted in a test aquarium behind a screen to reduce the impact of the human experimenter in the room. The aquarium was set up with an X-rite Color Checker within it and a light meter outside it to standardise the photographs. A thermometer was also placed within the aquarium, and the base was lined with colourless frosted plastic to prevent glare impacting on the photographs. Humidity was also measured. Geckos experienced a settling period of 5 minutes in the aquarium to acclimate, before randomised presentation of the treatments outlined below.

To investigate the potential of geckos to respond to the presence of an avian predator by changing colour, I created life-sized colour print-outs of model avian predators of lizards in New Zealand (morepork - *Ninox novaeseelandiae*, kingfisher - *Todiramphus sanctus*) and species that do not pose a known threat to geckos (North Island fantail - *Rhipidura fuliginosa placabilis*, monarch

butterfly - *Danaus plexippus*) as controls. The morepork is largely a nocturnal predator, while the kingfisher is a diurnal predator. The monarch butterfly was selected as it is not a bird, and not a prey species of the gecko, and does not pose a known threat to the gecko. I attached the model printouts to pieces of corrugated cardboard and bamboo to stabilise them, and to allow them to be flown by the aquarium without the bamboo or the experimenter being seen. I passed the models by the aquarium three times, approximating the speed birds would use to land on a perch. I used these models to simulate an avian predator passing by the enclosure to see whether this elucidated a colour change response.

To test whether auditory simulations of predators provoked a colour change response, I played the territorial call of the morepork (which is also the most common call heard from a morepork) in the vicinity of the enclosure (Brighten, 2015; Morepork song - DOC, accessed 2019). As the control for this experiment, I played the territorial call of a non-threatening species (North Island fantail) (DOC, accessed 2019b). I gave the geckos five minutes between the start of each treatment. One minute before the first treatment and on the 5th minute after each treatment began, I recorded a photo of the "before" state for the next treatment in the BACI (Before After Control Impact, Conner et al., 2016) analysis. Photos were taken using SONY SLT-a33 digital SLR cameras. The flash was not activated. Each gecko experienced each of the six treatments and the settling period consecutively, with the order of treatments randomised. Other treatments to investigate gecko responses to differing light levels, temperatures, and background colouration were also undertaken within the same 24 hour period, but for logistical reasons the results of those experiments have not yet been analysed and are not discussed in this thesis. The after treatment photos were taken every minute within 1-4 minutes of the treatment, and due to processing time constraints the photo exhibiting most change was used for analysis. This was generally 2-3 minutes after treatment.

I recorded the dorsal colour change responses of the geckos to the different treatments using photos taken with SONY SLT-a33 digital SLR cameras. The flash was not used as this would affect the colour of the photographs and likely disturb the geckos. Photos were taken using the JPEG format, as due to advances in technology, it is no longer considered necessary to use only the RAW format. I calibrated the photographs with a photograph of an x-rite colorchecker taken with the same camera, and under the same lighting conditions, as the photograph of the gecko. Initially I did this manually, but once the ijp color calibrator plug-in became available, I adapted my methods on a randomised subset of 20 Raukawa geckos and cross-checked to confirm the results were comparable. I compared the results from the analyses undertaken on all 31 geckos where the photographs had been manually adjusted, with the results from the analyses undertaken on the subset of 20 geckos and found analogous ordering of treatment effects, and the same factors showing statistical significance.
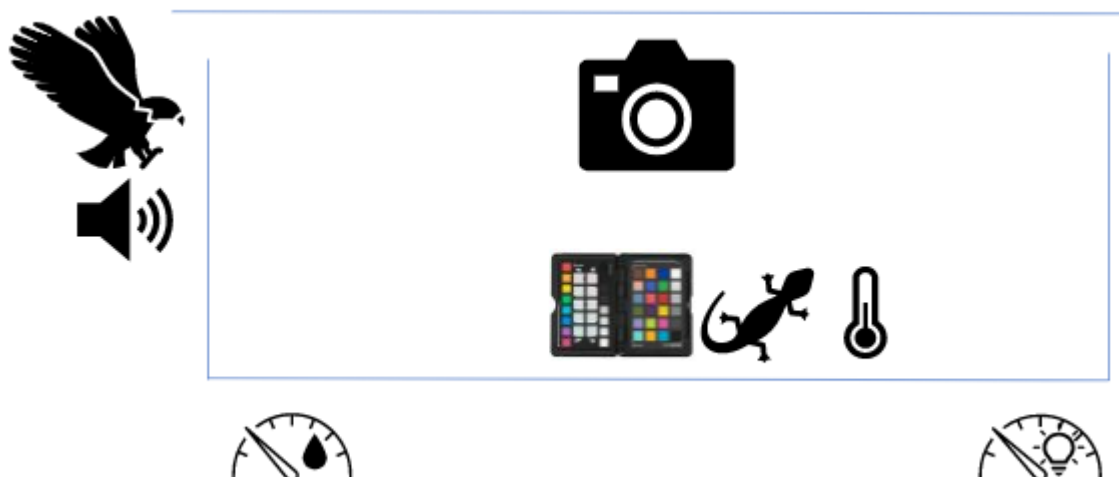
Figure 2.3 Simplified diagram of experimental design in the laboratory setting for the predator experiments, divided into audio and visual experiments. Life size models were used for visual experiments, and recorded bird calls for auditory experiments. A screen was present for all experiments to hide the researcher from the gecko. A camera was remotely triggered during the experiments to record the colour change responses. Temperature, humidity, and light levels were recorded for all experiments, and photographs were calibrated in ImageJ using an x-rite color checker.

Once it became clear that they were comparable, due to logistical constraints relating to the processing time required for each photograph (30-45 minutes per gecko photo and its matching colour standard, 14 photos per gecko, plus 14 matching colour standards), I focussed my efforts on the subset of 20 Raukawa geckos, and a further randomised subset of 15 ngāhere geckos. I used the FIJI plugin ijp-color calibrator (ijp-color v.0.10.2) for the subset of the data to calibrate the photograph of the x-rite colour checker to the x-rite colour standard and applied this calibration to the photograph of the gecko, taken under the same lighting conditions, with the same camera. Lizard colouration was assessed using ImageJ to extract the red, green, and blue values (RGB) from the standardised photographs and using these to calculate brightness, contrast, saturation (all 0-255), and hue (0-360°). I manually selected the regions of interest (dorsal view of body, and dorsal view of tail) using the ROI (Region of Interest) manager tool and used the RGB measure plugin to measure the calibrated levels of Red, Green, and Blue in the selected areas. This gave maximum, mean, and minimum values for each colour channel, as well as for intensity and brightness. I then used the formulae in figure 2 (Saravanan et al., 2016) to calculate the saturation and hue of the regions of interest. I calculated the contrast by subtracting the minimum intensity from the maximum intensity. I compared the values for brightness, contrast, saturation, and hue respectively between the various treatments and with an image taken one minute before each treatment took place.

$$S = 1 - \frac{3}{(R+G+B)} \min(R, G, B)$$

$$H = \cos^{-1} \left(\frac{(R-G) + (R-B)}{2\sqrt{(R-G)^2 + (R-B)(G-B)}} \right) \quad \text{assuming } G > B$$

If $B > G$, then $H = 360 - H$.

Figure 2.4 Formulae used to calculate saturation and hue of areas of interest (Saravanen et al., 2016). S is saturation, H is hue, R is the mean level of red, G is the mean level of green, B is the mean level of blue and min (R,G,B) are the minimum levels of red, green, and blue.

2.2.1 Statistical analysis

While the first set of data was analysed in Genstat, I analysed the subset of data in R (R Core Team, 2020) using linear mixed effects models fitted by maximum likelihood estimation in lme4 (Bates et al., 2015).

My initial analysis was undertaken on all 31 tails of the Raukawa geckos before the ijp color calibrator was available. After the colour calibrator became available, I repeated the analysis. Due to logistical constraints (each individual gecko's photo set took one day to analyse), I sub-sampled randomly from individuals using a subset of 20 Raukawa geckos to determine whether there would be any difference in the results when using the colour calibrator. In addition, I performed more detailed analysis on this subset of data, including BACI analysis (Before After Control Impact, Conner et al., 2016) and whether body parts (Body or tail) responded differently. For the ngāhere geckos, I performed the analysis on a subset of 15 of the 30 geckos.

I undertook analyses in R (R Core Team, 2020) using the AICcmodavg (Mazerolle, 2020), dplyr (Wickham et al., 2021), ggplot2 (Wickham, 2016), ggpubr (Kassambara, 2020), lme4 (Bates et al., 2015), predictmeans (Luo et al., 2021), reshape2 (Wickham, 2007), tidyr (Wickham, 2021), and tidyverse packages (Wickham et al., 2019). I used principal components analysis (PCA) to look at the relationships between variables and determine which variables to investigate further (Appendix 2C). I scaled the variables to have a mean of 0 and variance of 1, so that each variable would have the same influence on the analysis. This allowed me to assess the proportion of the variance attributable to each principal component. The initial variables included the minimum, mean, and maximum levels of red, green, blue, intensity and brightness, as well as the levels of contrast, mean hue, and mean saturation for the body and tail of each individual gecko before and after each treatment.

Next, I repeated the PCA on a subset of the variables (Hue, Saturation, Contrast, Mean Intensity, Mean Brightness, Mean B, Mean R, and Mean G), omitting those that did not contribute much to the model. This allowed me to select the variables contributing most to the first three principal components. Based on this analysis, I decided to investigate the brightness, contrast, saturation, and hue responses further. Brightness and intensity were highly correlated due to their method of calculation, so I omitted intensity from further investigations.

Testing the effects of factors on selected responses

For each species of gecko, after defining my factors (individual ID, treatment, and body part), I undertook exploratory data analyses in which I checked the distribution of the response variables for normality and constancy of variance and looked at residuals vs fit charts. Where data didn't meet the criteria of normality, I also tried logging the data for comparison. However, as it didn't make much difference to the model outcomes, and many of my analyses were quite resilient to non-normal data, I used the unlogged models for comparisons.

For each species of gecko, I analysed the data as two datasets respectively: visual treatments (morepork, kingfisher, fantail, and monarch butterfly models) and auditory treatments (morepork and fantail calls). I created linear mixed models using maximum likelihood to look at whether the effect of body part was important, whether there was a difference in response between body parts before and after treatment, and whether there was a difference in response over the whole gecko (i.e. without differentiating between body parts) before and after treatment. Two models were constructed for the responses of brightness, contrast, saturation, and hue, to visual simulations of predation: an interactive model for the fixed factors *Treatment*, *BA* (before and after simulation), and *Body Part* (body and tail), and an interactive model for *Treatment* and *BA* only. All models included a random effect of individual to account for repeated measures from individual geckos. I used the AICcmodavg package to determine the most parsimonious model.

I also used the predictmeans package to calculate and compare predicted means and undertake pairwise comparisons for the models, adjusted using Fisher's Unprotected Least Significant Difference (Luo et al., 2020). Values of $0.01 < p < 0.05$ describe moderate evidence for a significant influence of factors in analyses. Values of $0.05 < p < 0.1$ describe weak evidence which may indicate a weak signal that may be worth investigating in future analyses with greater sample sizes (Ganesh & Cave, 2008).

2.3 Results

2.3.1 Ngāhere geckos

2.3.1.1 Visual simulations of predators

A total of 300 measurements each of Hue, Saturation, Contrast, and Brightness from 15 individual ngāhere geckos were generated from the visual cue experiments. A *Treatment × Before/After (BA)* model was the most parsimonious for all response variables (Table 2.1). All LMM model summary outputs can be found in Appendix 2D.

Table 2.1 Comparison of AIC$_c$ values for LMMs trialled for each response value describing the colour change response of 15 ngāhere geckos to a visual simulation of predators. The levels for the fixed factor *Treatment* were *Monarch Butterfly* (non-predator), *North Island Fantail* (non-predator), *Kingfisher* (predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *Body Part* were *Body* and *Tail*, and levels for the fixed factor *BA* were *Before* simulation and *After* simulation. All models included a random effect to account for repeated measures from individual geckos.

Response variable	Fixed factor structure of model	AIC$_c$	ΔAIC$_c$	AIC$_c$ weight	N. parameters
Brightness	Treatment × BA	2721.99	0.00	1	12
	Treatment × BA × Body Part	2742.00	20.01	0	22
Contrast	Treatment × BA	2957.39	0.00	1	12
	Treatment × BA × Body Part	2969.31	11.92	0	22
Saturation	Treatment × BA	2488.61	0.00	0.95	12
	Treatment × BA × Body Part	2494.63	6.02	0.05	22
Hue	Treatment × BA	3244.00	0.00	1.00	12
	Treatment × BA × Body Part	3263.00	18.99	0.00	22

For brightness, the random factor *Individual* explained 48.89% of the model variance. There were no statistically significant differences in predicted means for mean brightness before and after treatments (Table 2.2).

Table 2.2 Predicted mean brightness of ngāhere geckos before and after each visual simulation treatment from the model Mean Brightness ~ Treatment*BA+(1|Individual). Figures in square brackets are the 95% Confidence Intervals from the PredictMeans output. The effect size is defined as After minus Before. *p*-values are generated from pairwise comparisons of *Before* and *After* values for each treatment. *p*-values are indicated as follows *p*<0.001***, *p*<0.01**, *p*<0.05*, *p*<0.1'. *p*-values were calculated on 275.02 degrees of freedom.

Treatment	Before	After	Effect size	t	p
Butterfly	65.35 [53.02, 77.68]	73.08 [60.75, 85.41]	+7.73	-1.4892	0.1376
Fantail	74.40 [62.07, 86.74]	69.61 [57.28, 81.95]	-4.79	0.9226	0.3570
Kingfisher	78.31 [65.98, 90.65]	69.78 [57.44, 82.11]	-8.53	1.6449	0.1011
Morepork	65.29 [52.96, 77.63]	66.44 [54.11, 78.78]	+1.15	-0.2212	0.8251
Settling period	66.62 [54.28, 78.95]	64.76 [52.43, 77.09]	-1.86	0.3578	0.7208

For Contrast, the random factor *Individual* explained 17.71% of the model variance. There was weak statistical evidence that predicted mean contrast was higher after the morepork flyover treatment than before (Table 2.3, Fig. 2.5). There was no statistical evidence of a difference in predicted means for contrast before and after the other treatments, or between treatments after treatment (Table 2.3, Fig. 2.5).

Table 2.3 Predicted mean contrast of ngāhere geckos before and after each visual simulation treatment from the model Contrast ~ Treatment*BA+(1|Individual). Figures in square brackets are the 95% Confidence Intervals from the PredictMeans output. The effect size is defined as After minus Before. *p*-values are generated from pairwise comparisons of *Before* and *After* values for each treatment. *p*-values are indicated as follows *p*<0.001***, *p*<0.01**, *p*<0.05*, *p*<0.1'. *p*-values were calculated on 275.02 degrees of freedom.

Treatment	Before	After	Effect Size	t	p
Butterfly	149.90 [136.67, 163.13]	144.97 [131.74, 158.19]	+0.07	0.6210	0.5351
Fantail	157.30 [144.07, 170.53]	152.33 [139.11, 165.56]	+2.66	0.6252	0.5324
Kingfisher	149.67 [136.44, 162.89]	152.83 [139.61, 166.06]	+3.16	-0.3986	0.6905
Morepork	134.20 [120.97, 147.43]	147.90 [134.67, 161.13]	+13.7	-1.7244	0.0857'
Settling period	143.37 [130.14, 156.59]	142.07 [128.84, 125.29]	-1.30	0.1636	0.8701
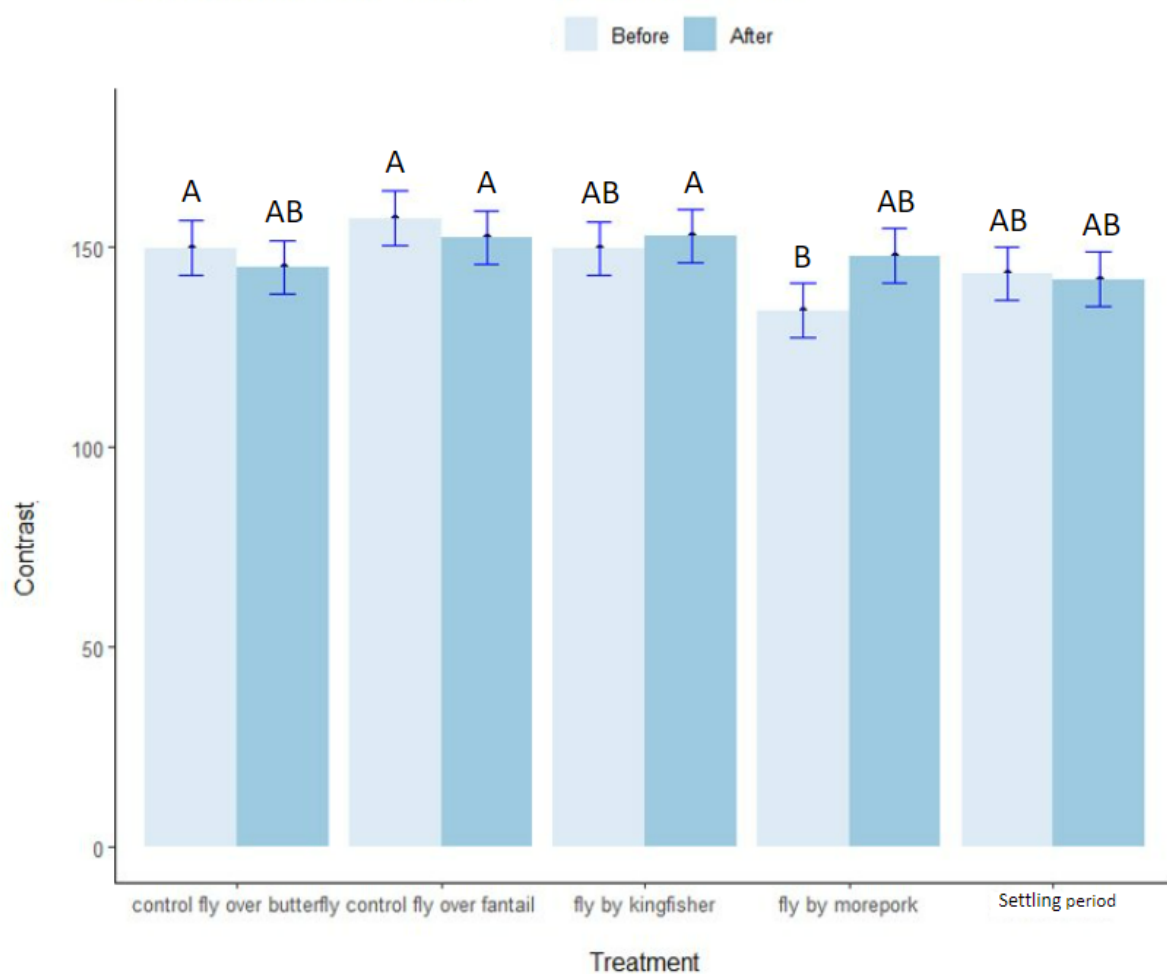
Figure 2.5 Predicted means for contrast (with standard error bars) over the whole body of ngāhere geckos before and after treatment. Differing letters indicate statistically significant differences, while shared letters indicate the differences are not statistically significant at the $p \leq 0.05$ level. None of the treatments differed significantly before and after treatment, and none of the treatments differed significantly from each other after treatment.

For saturation, the random factor *Individual* explained 52.16% of the model variance. There were no statistically significant differences in predicted means for saturation before and after treatments (Table 2.4).

Table 2.4 Predicted mean saturation of ngāhere geckos before and after each visual simulation treatment from the model Saturation ~ Treatment*BA+(1|Individual). Figures in square brackets are the 95% Confidence Intervals from the PredictMeans output. The effect size is defined as After minus Before. *p*-values are generated from pairwise comparisons of *Before* and *After* values for each treatment. *p*-values were calculated on 275.02 degrees of freedom.

Treatment	Before	After	Effect size	t	p
Butterfly	236.23 [227.52, 244.93]	231.46 [222.75, 240.16]	-4.77	1.3600	0.1749
Fantail	231.89 [223.19, 240.60]	232.89 [224.19, 241.60]	+1.00	-0.2849	0.7759
Kingfisher	227.74 [219.04, 236.45]	233.45 [227.74, 242.16]	+5.71	-1.6281	0.1047
Morepork	234.97 [226.26, 234.68]	231.47 [222.76, 240.18]	-3.50	0.9974	0.3194
Settling period	232.80 [224.09, 241.51]	233.35 [224.65, 242.06]	+0.55	-0.1582	0.8744

For hue, the fixed factors *Treatment* and *BA*, and their interaction, displayed a significant effect on hue in comparison to the model intercept (Table 2.5b, Appendix 2D). The random factor *Individual* explained 17.98% of the model variance. The predicted mean hue was significantly higher after the butterfly flyover treatment than before, meaning that hue shifted away from yellow and towards green (Table 2.5, Fig. 2a). Within treatments, there were no statistically significant differences in predicted means for hue before and after the other treatments (Table 2.5).

Table 2.5 Predicted mean hues of ngāhere geckos before and after each visual simulation treatment from the model Hue ~ Treatment*BA+(1|Individual). Figures in square brackets are the 95% Confidence Intervals from the PredictMeans output. The effect size is defined as After minus Before. *p*-values are generated from pairwise comparisons of *Before* and *After* values for each treatment. *p*-values are indicated as follows *p*<0.001***, *p*<0.01**, *p*<0.05*, *p*<0.1'. *p*-values were calculated on 275.02 degrees of freedom.

Treatment	Before	After	Effect size	t	p
Butterfly	53.73 [31.70, 75.76]	88.55 [66.78, 110.31]	+34.82	-2.6472	0.0086 **
Fantail	87.60 [65.84, 109.37]	66.77 [45.01, 88.54]	-20.83	1.5979	0.1112
Kingfisher	77.09 [55.33, 98.85]	60.81 [39.05, 82.58]	-16.28	1.2487	0.2128
Morepork	60.95 [39.19, 82.71]	59.14 [37.38, 80.90]	-1.81	0.1389	0.8896
Settling period	67.35 [45.59, 89.12]	77.61 [55.85, 99.37]	+10.26	-0.7871	0.4319
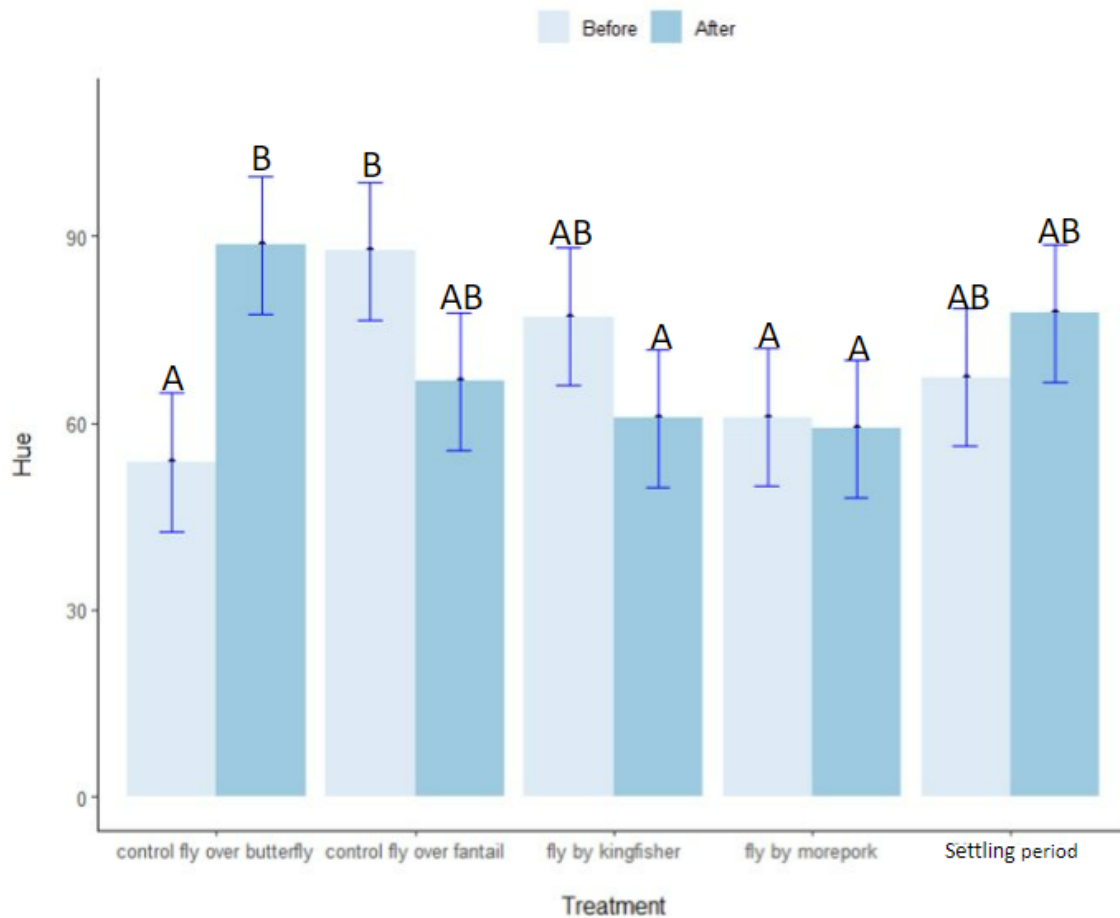
Figure 2.6 Predicted means for hue (with standard error bars) over the whole body of ngāhere geckos before and after treatment. Differing letters indicate statistically significant differences, while shared letters indicate the differences are not statistically significant at the p ≤ 0.05 level.

2.3.1.2 Auditory simulations of predators

A total of 180 measurements each of brightness, contrast, saturation, and hue from 15 individual ngāhere geckos were generated from the auditory cue experiments. Two models were constructed for the responses of brightness, contrast, saturation, and hue, to auditory simulations of predation: an interactive model for the fixed factors *Treatment*, *BA* (before and after simulation), and *Body Part* (body and tail), and an interactive model for *Treatment* and *BA* only (Table 2.6). A *Treatment × BA* model was the most parsimonious for all response variables (Table 2.6). However, in the case of saturation, the difference in AIC$_c$ between the two models was very small (Table 2.6) therefore I chose to report results from the more complex model.

Table 2.6 Comparison of AIC$_c$ values for LMMs trialled for each response value describing the colour change response of 15 ngāhere geckos to auditory simulation of predators. The levels for the fixed factor *Treatment* were *North Island Fantail* (non-predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *Body Part* were *Body* and *Tail*, and levels for the fixed factor *BA* were *Before* simulation and *After* simulation. All models included a random effect to account for repeated measures from individual geckos.

Response variable	Fixed factor structure of model	AICc	ΔAICc	AIC$_c$ weight	N. parameters
Brightness	Treatment × BA	1638.32	0.00	1	8
	Treatment × BA × Body Part	1650.43	12.11	0	14
Contrast	Treatment × BA	1802.40	0.00	0.98	8
	Treatment × BA × Body Part	1810.39	7.99	0.02	14
Saturation	Treatment × BA	1489.88	0.00	0.53	8
	Treatment × BA × Body Part	1490.15	0.27	0.47	14
Hue	Treatment × BA	1989.07	0.00	1	8
	Treatment × BA × Body Part	2000.14	11.07	0	14

For brightness, the random factor *Individual* explained 47.10% of the model variance. There were no statistically significant differences in predicted means for brightness before and after treatments (Table 2.7).

Table 2.7 Predicted mean brightness of ngāhere geckos before and after each auditory simulation treatment from the model Mean Brightness ~ Treatment*BA+(1|Individual). Figures in square brackets are the 95% Confidence Intervals from the PredictMeans output. The effect size is defined as After minus Before. *p*-values are generated from pairwise comparisons of *Before* and *After* values for each treatment. *p*-values were calculated on 160 degrees of freedom.

Treatment	Before	After	Effect size	t	p
Fantail	59.82 [47.95, 71.69]	66.37 [54.50, 78.24]	+6.55	-1.2842	0.2009
Morepork	66.94 [55.07, 78.81]	65.12 [53.25, 77.00]	-1.82	0.3572	0.7214
Settling period	66.62 [54.75, 78.49]	64.76 [52.89, 76.63]	-1.86	0.3643	0.7161

For contrast, the random factor *Individual* explained 17.90% of the model variance. There were no statistically significant differences in predicted means for contrast before and after treatments (Table 2.8).

Table 2.8 Predicted mean contrast of ngāhere geckos before and after each auditory simulation treatment from the model Contrast ~ Treatment*BA+(1|Individual). Figures in square brackets are the 95% Confidence Intervals from the PredictMeans output. The effect size is defined as After minus Before. *p*-values are generated from pairwise comparisons of *Before* and *After* values for each treatment. *p*-values were calculated on 160 degrees of freedom.

Treatment	Before	After	Effect size	t	p
Fantail	142.10 [127.97, 156.23]	136.17 [136.17,164.43]	-5.93	-0.9712	0.3329
Morepork	149.03 [134.90, 163.16]	139.83 [125.70, 153.96]	-9.20	1.0896	0.2775
Settling period	143.37 [129.24, 157.50]	142.07 [127.94, 156.20]	-1.30	0.1540	0.8778

For saturation, the random factor *Individual* explained 46.99% of the model variance. There were no statistically significant differences in predicted means for saturation in either the tail or body before and after treatments (Table 2.9).

Table 2.9 Predicted mean saturation of ngāhere geckos before and after each auditory simulation treatment from the model Saturation ~ Treatment*Bodypart*BA+(1|Individual). Figures in square brackets are the 95% Confidence Intervals from the PredictMeans output. The effect size is defined as After minus Before. *p*-values are generated from pairwise comparisons of *Before* and *After* values for each treatment. *p*-values were calculated on 154 degrees of freedom.

Treatment	Before	After	Effect size	t	p
Fantail Body	240.27 [231.28, 249.25]	239.89 [230.90, 248.87]	-0.38	0.0829	0.9340
Fantail Tail	230.09 [221.10, 239.07]	231.69 [222.71, 240.68]	+1.60	-0.3507	0.7263
Morepork Body	234.65 [225.66, 243.63]	241.16 [232.18, 250.15]	+6.51	-1.4223	0.1570
Morepork Tail	228.98 [219.99, 237.96]	234.09 [225.11, 243.07]	+5.11	-1.1154	0.2664
Settling period Body	235.56 [226.58, 244.55]	234.99 [226.01, 243.97]	-0.57	0.1250	0.9007
Settling period Tail	230.04 [221.05, 239.02]	231.72 [222.74, 240.70]	+1.68	-0.3671	0.7141

For hue, the random factor *Individual* explained 19.88% of the model variance. There were no statistically significant differences in predicted means for hue before and after treatments (Table 2.10).

Table 2.10 Predicted mean hue of ngāhere geckos before and after each auditory simulation treatment from the model Hue ~ Treatment*BA+(1|Individual). Figures in square brackets are the 95% Confidence Intervals from the PredictMeans output. The effect size is defined as After minus Before. *p*-values are generated from pairwise comparisons of *Before* and *After* values for each treatment. *p*-values were calculated on 160 degrees of freedom.

Treatment	Before	After	Effect size	t	p
Fantail	58.35 [34.23, 82.48]	65.87 [41.74, 89.99]	+7.52	-0.5318	0.5956
Morepork	66.50 [42.37, 90.62]	73.83 [49.70, 97.96]	+7.33	-0.5191	0.6044
Settling period	67.35 [43.22, 91.48]	77.61 [53.48, 101.74]	+10.26	-0.7264	0.4687

2.3.2 Raukawa geckos

2.3.2.1 Visual simulations of predators

A total of 400 measurements each of hue, saturation, contrast, and brightness from 20 individual Raukawa geckos were generated from the visual cue experiments. Two models were

constructed for the responses of brightness, contrast, saturation, and hue, to visual simulations of predation: an interactive model for the fixed factors *Treatment*, *BA* (before and after simulation), and *Body Part* (body and tail), and an interactive model for *Treatment* and *BA* only (Table 2.11). The simpler *Treatment × BA* model was the most parsimonious for contrast and hue (Table 2.11). The more complex Treatment x Bodypart x BA model was the most parsimonious for brightness and saturation, although the simpler model for saturation was also strongly supported by the AICc (Table 2.11).

Table 2.11. Comparison of AIC_c values for LMMs trialled for each response value describing the colour change response of 20 Raukawa geckos to visual simulation of predators. The levels for the fixed factor *Treatment* were *Monarch Butterfly* (non-predator), *North Island Fantail* (non-predator), *Kingfisher* (non-predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *Body Part* were *Body* and *Tail*, and levels for the fixed factor *BA* were *Before* simulation and *After* simulation. All models included a random effect to account for repeated measures from individual geckos.

Response variable	Fixed factor structure of model	AICc	ΔAICc	AIC_c weight	N. parameters
Brightness	Treatment × Body Part × BA	3567.11	0.00	0.88	22
	Treatment × BA	3571.06	3.96	0.12	12
Contrast	Treatment × BA	3928.41	0.00	0.87	12
	Treatment × Body Part × BA	3932.31	3.89	0.13	22
Saturation	Treatment × Body Part × BA	3376.18	0.00	0.62	22
	Treatment × BA	3377.20	1.02	0.38	12
Hue	Treatment × BA	4344.00	0.00	1	12
	Treatment × Body Part × BA	4356.26	12.26	0	22

For brightness, the random factor *Individual* explained 64.14% of the model variance. There were no statistically significant differences in predicted means for mean brightness of the body or tail before or after the other treatments (Table 2.12).

Table 2.12 Predicted mean brightness of Raukawa geckos before and after each visual simulation treatment from the model Mean Brightness ~ Treatment*Bodypart*BA+(1|Individual). Figures in square brackets are the 95% Confidence Intervals from the PredictMeans output. The effect size is defined as After minus Before. *p*-values are generated from pairwise comparisons of *Before* and *After* values for each bodypart and each treatment. *p*-values were calculated on 365 degrees of freedom.

Treatment	Before	After	Effect size	t	p
Butterfly Body	50.08 [37.40, 62.75]	49.77 [37.09, 62.44]	-0.31	0.0568	0.9547
Butterfly Tail	59.62 [46.95, 72.30]	57.24 [44.56, 69.91]	-2.38	0.4366	0.6626
Fantail Body	54.99 [42.32, 67.67]	46.52 [33.85, 59.20]	-8.47	1.5514	0.1217
Fantail Tail	61.56 [48.88, 74.23]	53.40 [40.70, 66.06]	-8.16	1.4980	0.1350
Kingfisher Body	54.90 [42.22, 67.58]	54.46 [41.79, 67.14]	-0.44	0.0802	0.9362
Kingfisher Tail	65.98 [53.30, 78.65]	65.07 [52.40, 77.75]	-0.91	0.1656	0.8685
Morepork Body	47.55 [34.88, 60.23]	55.06 [42.39, 67.73]	+7.51	-1.3753	0.1699
Morepork Tail	56.97 [44.29, 69.65]	62.95 [50.28, 75.63]	+5.98	-1.0961	0.2737
Settling period Body	55.04 [42.47, 67.61]	57.63 [45.05, 70.20]	+2.59	-0.4849	0.9034
Settling period Tail	62.90 [50.33, 75.47]	67.76 [55.19, 80.33]	+4.86	-0.9109	0.3629

For Contrast, the random factor *Individual* explained 40.63% of the model variance. The predicted mean contrast was significantly higher after the settling period than before, and there was weak statistical evidence that contrast may be higher after the morepork treatment than before (Table 2.13, Fig. 2.9). There were no statistically significant differences in predicted means for contrast before and after the other treatments (Table 2.13).

Table 2.13 Predicted mean contrast of Raukawa geckos before and after each visual simulation treatment from the model Contrast ~ Treatment*BA+(1|Individual). Figures in square brackets are the 95% Confidence Intervals from the PredictMeans output. The effect size is defined as After minus Before. *p*-values are generated from pairwise comparisons of *Before* and *After* values for each treatment. *p*-values are indicated as follows *p*<0.05*, *p*<0.1'. *p*-values were calculated on 375 degrees of freedom.

Treatment	Before	After	Effect size	t	p
Butterfly	95.55 [81.97, 109.13]	102.15 [88.57, 115.73]	+6.60	-1.0402	0.2989
Fantail	93.95 [80.37, 107.53]	91.98 [78.40, 105.55]	-19.70	0.3113	0.7558
Kingfisher	100.28 [86.70, 113.85]	109.33 [95.75, 112.90]	+9.05	-1.4263	0.1546
Morepork	100.05 [86.47, 113.63]	111.00 [97.42, 124.58]	+10.95	-1.7257	0.0852`
Settling period	97.99 [84.54, 111.44]	110.70 [97.25, 124.16]	+12.71	-2.0533	0.0407*
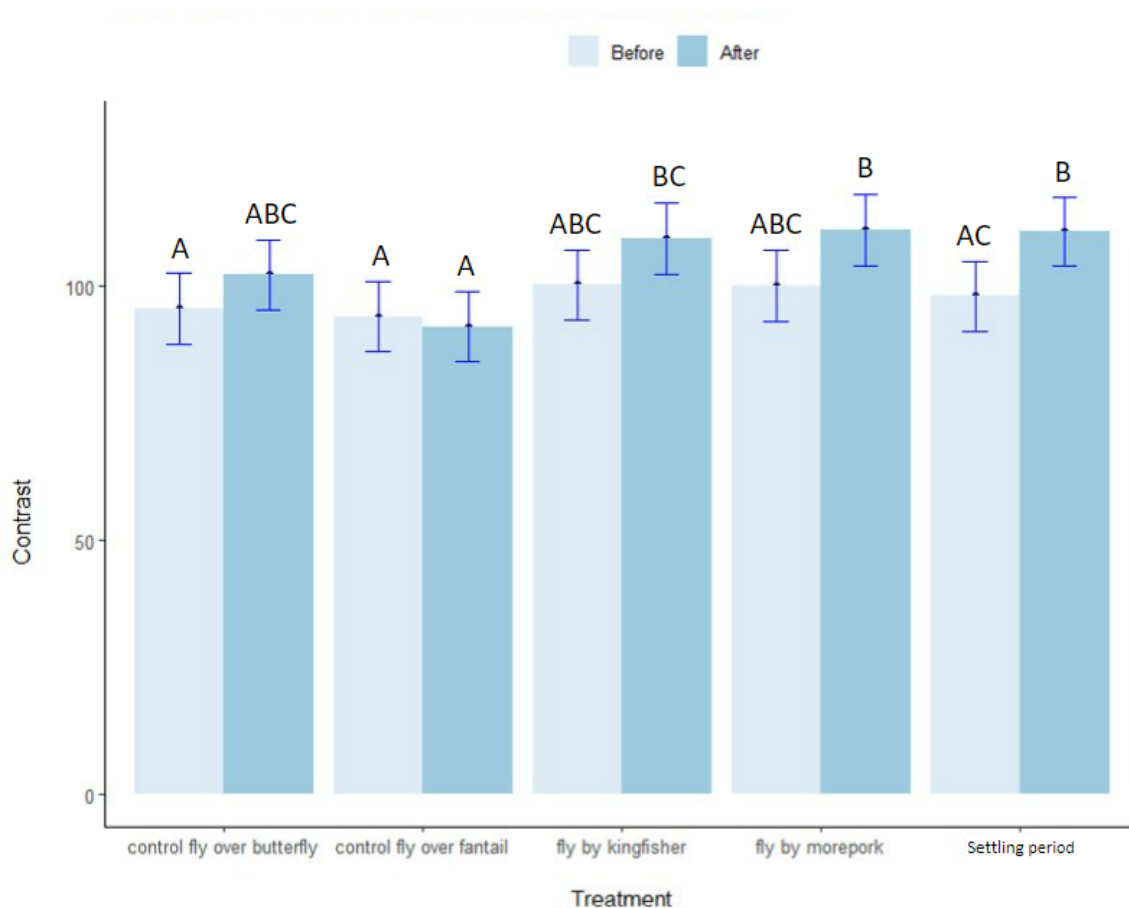
Figure 2.9 Predicted means for contrast (with standard error bars) over the whole body of Raukawa geckos before and after treatment. Differing letters indicate statistically significant differences, while shared letters indicate the differences are not statistically significant at the p ≤ 0.05 level.

For saturation, the random factor *Individual* explained 58.89% of the model variance. There was weak statistical evidence that predicted mean saturation of gecko tails was higher after

treatment in the fantail, settling period, and butterfly experiments, compared to before these treatments (Table 2.14). There were no statistically significant differences in the saturation of gecko tails after the morepork or kingfisher treatments compared to before (Table 2.14). There were no significant differences in saturation of gecko bodies after versus before any of the treatments (Table 2.14).

Table 2.14 Predicted mean saturation of Raukawa geckos before and after each visual simulation treatment from the model Saturation ~ Treatment*Bodypart*BA+(1|Individual). Figures in square brackets are the 95% Confidence Intervals from the PredictMeans output. The effect size is defined as After minus Before. *p*-values are generated from pairwise comparisons of *Before* and *After* values for each bodypart and each treatment. *p*-values are indicated as follows *p*<0.1'. *p*-values were calculated on 365 degrees of freedom.

Treatment	Before	After	Effect size	t	p
Butterfly Body	240.01 [230.61, 249.41]	243.34 [233.95, 252.74]	+3.33	-0.7691	0.4423
Butterfly Tail	231.93 [222.53, 241.33]	239.54 [230.14, 248.93]	+7.61	-1.7560	0.0799'
Fantail Body	236.68 [227.28, 246.08]	242.59 [233.19, 251.99]	+5.91	-1.3638	0.1735
Fantail Tail	230.96 [221.56, 240.36]	238.16 [228.76, 247.56]	+7.20	-1.6609	0.0976'
Kingfisher Body	241.93 [232.54, 251.33]	242.43 [233.03, 251.83]	+0.50	-0.1149	0.9086
Kingfisher Tail	234.35 [224.96, 243.75]	231.21 [221.82, 240.61]	-3.14	0.7248	0.4690
Morepork Body	242.04 [232.64, 251.44]	241.99 [232.59, 251.39]	-0.05	0.0116	0.9908
Morepork Tail	237.19 [227.79, 246.59]	236.47 [227.07, 245.86]	-0.72	0.1669	0.8675
Settling period Body	230.53 [221.22, 239.84]	237.12 [227.82, 246.43]	+6.59	-1.5595	0.1197
Settling period Tail	224.37 [215.06, 233.68]	231.49 [222.18, 240.80]	+7.12	-1.6823	0.0934'

For hue, the random factor *Individual* explained 49.08% of the model variance. There was weak statistical evidence that predicted mean hue may be lower after the fantail treatment than before, meaning a shift in hue from green and towards yellow (Table 2.15, Fig. 2e). There were no statistically significant differences in predicted means for hue before and after the other treatments (Table 2.15).

Table 2.15 Predicted mean hues of Raukawa geckos before and after each visual simulation treatment from the model Hue ~ Treatment*BA+(1|Individual). Figures in square brackets are the 95% Confidence Intervals from the PredictMeans output. The effect size is defined as After minus Before. *p*-values are generated from pairwise comparisons of *Before* and *After* values for each treatment. *p*-values are indicated as follows *p*<0.1'. *p*-values were calculated on 375 degrees of freedom.

Treatment	Before	After	Effect size	t	p
Butterfly	101.38 [76.33, 126.43]	102.53 [77.48, 127.58]	+1.15	-0.1097	0.9127
Fantail	111.45 [86.40, 136.50]	91.35 [66.30, 116.40]	-20.10	1.9094	0.0570'
Kingfisher	93.96 [68.91, 119.01]	81.52 [56.47, 106.57]	-12.44	1.1822	0.2379
Morepork	94.56 [69.51, 119.61]	90.83 [65.78, 115.88]	-3.73	0.3539	0.7236
Settling period	69.30 [44.44, 94.16]	59.32 [34.46, 84.18]	-9.98	0.9717	0.3318
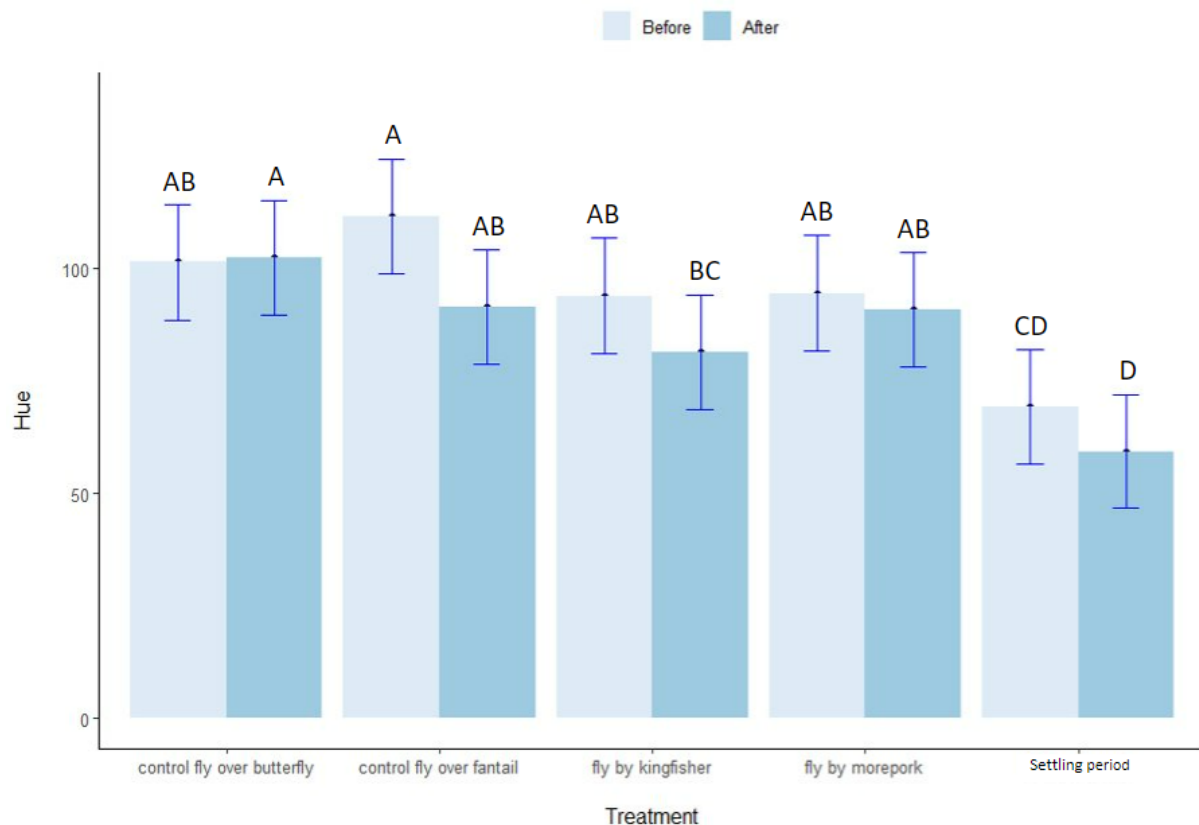
Figure 2.10 Predicted means for hue (with standard error bars) over the whole body of Raukawa geckos before and after treatment. Differing letters indicate statistically significant differences, while shared letters indicate the differences are not statistically significant at the p ≤ 0.05 level.

A total of 240 measurements each of hue, saturation, contrast, and brightness from 20 individual Raukawa geckos were generated from the auditory cue experiments. Two models were constructed for the responses of brightness, contrast, saturation, and hue, to visual simulations of predation: an interactive model for the fixed factors *Treatment*, *BA* (before and after simulation), and *Body Part* (body and tail), and an interactive model for *Treatment* and *BA* only (Table 2.16). A *Treatment × BA* model was the most parsimonious for contrast and hue (Table 2.16). For brightness and saturation the Treatment x BA x Bodypart model was most parsimonious, although the less complex model was moderately supported for brightness (Table 2.16).

Table 2.16 Comparison of AIC_c values for LMMs trialled for each response value describing the colour change response of 20 Raukawa geckos to auditory simulation of predators. The levels for the fixed factor *Treatment* were *North Island Fantail* (non-predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *Body Part* were *Body* and *Tail*, and levels for the fixed factor *BA* were *Before* simulation and *After* simulation. All models included a random effect to account for repeated measures from individual geckos.

Response variable	Fixed factor structure of model	AICc	ΔAICc	AIC_c weight	N. parameters
Brightness	Treatment × BA × Body Part	2183.22	0.00	0.77	14
	Treatment × BA	2185.60	2.38	0.23	8
Contrast	Treatment × BA	2374.65	0.00	0.99	8
	Treatment × BA × Body Part	2383.69	9.04	0.01	14
Saturation	Treatment × BA × Body Part	2030.50	0.00	0.92	14
	Treatment × BA	2035.42	4.92	0.08	8
Hue	Treatment × BA	2689.51	0.00	0.98	8
	Treatment × BA × Body Part	2697.74	8.23	0.02	14

For brightness, the random factor *Individual* explained 59.25% of the model variance. There were no statistically significant differences in predicted mean brightness of gecko tails or bodies between treatments before and after treatment (Table 2.17).

Table 2.17 Predicted mean brightness of Raukawa geckos before and after each visual simulation treatment from the model Mean Brightness ~ Treatment*Bodypart*BA+(1|Individual). Figures in square brackets are the 95% Confidence Intervals from the PredictMeans output. The effect size is defined as After minus Before. *p*-values are generated from pairwise comparisons of *Before* and *After* values for each bodypart and each treatment. *p*-values were calculated on 215 degrees of freedom.

Treatment	Before	After	Effect size	t	p
Fantail Body	51.88 [40.08, 63.68]	50.86 [39.06, 62.66]	-1.02	0.1875	0.8514
Fantail Tail	61.19 [49.39, 72.99]	60.64 [48.84, 72.44]	-0.55	0.1013	0.9194
Morepork Body	60.73 [48.93, 72.53]	55.71 [43.91, 67.51]	-5.02	0.9294	0.3537
Morepork Tail	68.14 [56.34, 79.94]	62.75 [50.95, 74.56]	-5.39	0.9963	0.3202
Settling period Body	54.92 [43.23, 66.61]	57.60 [46.01, 69.19]	+2.68	0.5130	0.6085
Settling period Tail	62.78 [51.09, 74.07]	68.04 [56.45, 79.63]	+5.26	-1.0085	0.3144

For contrast, the random factor *Individual* explained 48.22% of the model variance. The predicted mean for contrast across the whole body was significantly higher after the settling period than before (Table 2.18, Fig. 2.12). There were no statistically significant differences in predicted means for contrast across the whole body before and after the other treatments (Table 2.18).

Table 2.18 Predicted mean contrast of Raukawa geckos before and after each auditory simulation treatment from the model Contrast ~ Treatment*BA+(1|Individual). Figures in square brackets are the 95% Confidence Intervals from the PredictMeans output. The effect size is defined as After minus Before. *p*-values are generated from pairwise comparisons of *Before* and *After* values for each treatment. *p*-values are indicated as follows *p*<0.05*. *p*-values were calculated on 221.03 degrees of freedom.

Treatment	Before	After	Effect size	t	p
Fantail	98.00 [84.11, 111.89]	96.23 [82.33, 110.12]	-1.77	0.3013	0.7635
Morepork	109.00 [95.11, 122.89]	100.43 [86.53, 114.32]	-8.57	1.4555	0.1470
Settling period	96.81 [83.03, 110.60]	109.53 [95.84, 123.23]	+12.72	-2.2351	0.0264*
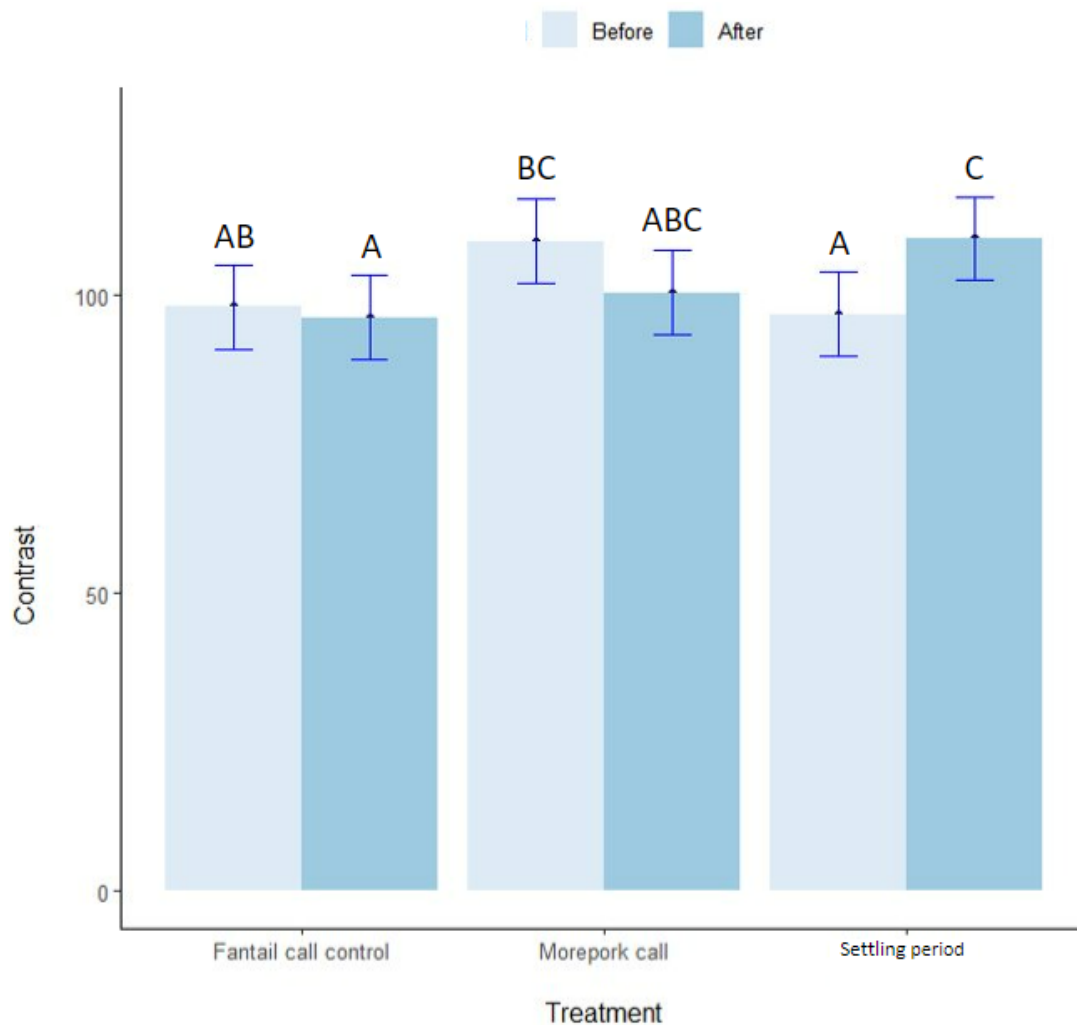
Figure 2.12 Predicted means for contrast (with standard error bars) over the whole body of Raukawa geckos before and after treatment. Differing letters indicate statistically significant differences, while shared letters indicate the differences are not statistically significant at the p ≤ 0.05 level.

For saturation, the fixed factors *Treatment* and *Bodypart*, and their interaction, displayed a significant effect on saturation in comparison to the model intercept (Table 2.19b, Appendix 2D).

The random factor *Individual* explained 71.15% of the model variance. There were no statistically significant differences in predicted means for saturation before and after treatments (Table 2.19).

Table 2.19 Predicted mean saturation of Raukawa geckos before and after each auditory simulation treatment from the model Saturation ~ Treatment*Bodypart*BA+(1|Individual). Figures in square brackets are the 95% Confidence Intervals from the PredictMeans output. The effect size is defined as After minus Before. *p*-values are generated from pairwise comparisons of *Before* and *After* values for each bodypart and each treatment. *p*-values are indicated as follows $p<0.001$***, $p<0.01$**, $p<0.05$*, $p<0.1$'. *p*-values were calculated on 215 degrees of freedom.

Treatment	Before	After	Effect size	t	p
Fantail Body	240.21 [230.14, 250.29]	239.09 [229.01, 249.16]	-1.12	0.2909	0.7714
Fantail Tail	231.29 [221.22, 241.36]	230.95 [220.88, 241.03]	-0.34	0.0871	0.9307
Morepork Body	234.33 [224.26, 244.40]	235.83 [225.75, 245.90]	+1.50	-0.3859	0.6999
Morepork Tail	227.81 [217.74, 237.89]	231.11 [221.04, 241.18]	+3.30	-0.8494	0.3966
Settling period Body	230.41 [220.40, 240.42]	235.82 [225.88, 245.77]	+5.41	-1.4447	0.1500
Settling period Tail	224.25 [214.25, 234.26]	230.25 [220.30, 240.20]	+6.00	-1.5998	0.1110

For hue, the fixed factor *BA*, and its interaction with *Treatment*, displayed a significant effect on hue in comparison to the model intercept (Table 2.20b, Appendix 2D). The random factor *Individual* explained 36.07% of the model variance. The predicted mean hue was significantly higher after the fantail call treatment than before, meaning that hue shifted away from yellow and towards green (Table 2.20, Fig. 2.14). There were no statistically significant differences in predicted means for hue before and after the other treatments (Table 2.20).

Table 2.20 Predicted mean hues of Raukawa geckos before and after each auditory simulation treatment from the model Hue ~ Treatment*BA+(1|Individual). Figures in square brackets are the 95% Confidence Intervals from the PredictMeans output. The effect size is defined as After minus Before. *p*-values are generated from pairwise comparisons of *Before* and *After* values for each treatment. *p*-values are indicated as follows $p<0.001$***, $p<0.01$**, $p<0.05$*, $p<0.1$'. *p*-values were calculated on 221.05 degrees of freedom.

Treatment	Before	After	Effect size	t	p
Fantail	83.92 [60.79, 107.05]	110.77 [87.63, 133.90]	+26.85	-2.3592	0.0192*
Morepork	84.01 [60.88, 107.15]	84.88 [61.75, 108.11]	+0.87	-0.0762	0.9394
Settling period	71.81 [48.91, 94.70]	60.35 [37.67, 83.04]	-11.46	1.0419	0.2986
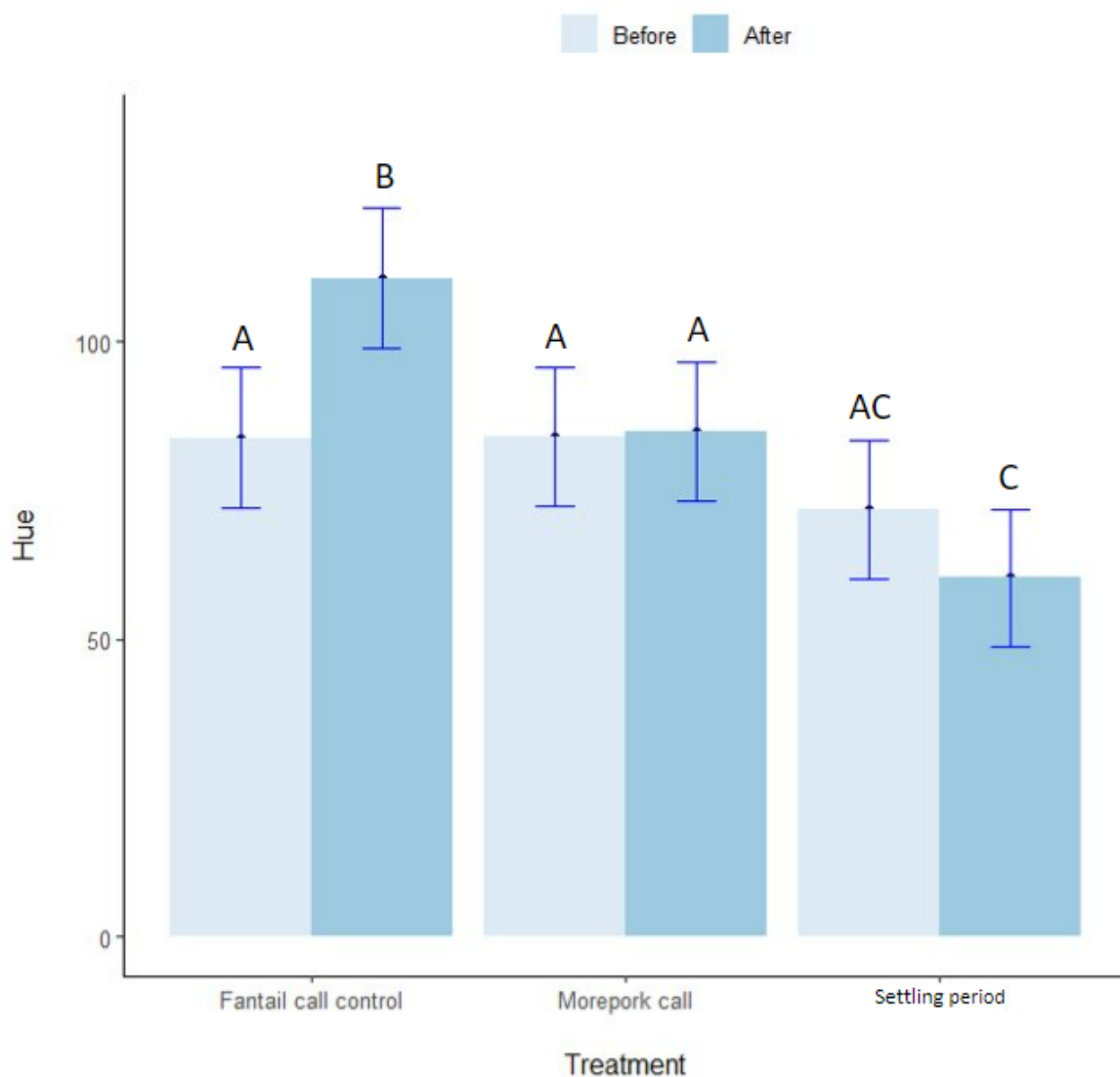
Figure 2.14 Predicted means for hue (with standard error bars) over the whole body of Raukawa geckos before and after treatment. Differing letters indicate statistically significant differences, while shared letters indicate the differences are not statistically significant at the p ≤ 0.05 level.

2.3.3 Overview and summary of results

There was a difference in response to simulated avian predators between the ngāhere and Raukawa geckos. From the BACI results, across the whole body of ngāhere geckos, hue increased after butterfly treatments, meaning they become more green and less yellow (Table 2.21). There was weak evidence that contrast may have increased across the whole body after the morepork visual simulation. There were no statistically significant differences between before and after auditory simulations for this species (Table 2.22). However, there was evidence of a difference in saturation between body and tail for saturation before auditory simulations of

fantails, and weak evidence that there may also be a difference afterwards (Table 2.9b Appendix 2D).

Table 2.21 Summary of BACI results from visual simulation experiments on ngāhere geckos

Treatment Type	Treatment	Measurement	Body part	Δ predicted means After - Before	Statistical evidence (*p*)
	Settling period	Brightness Contrast Saturation Hue	Whole body Whole body Whole body Whole body	-1.86 -1.3 +0.55 +10.26	0.7208 0.8701 0.8744 0.4319
Non-predator	Butterfly	Brightness Contrast Saturation Hue	Whole body Whole body Whole body Whole body	+9.73 +0.07 -4.77 +34.82	0.1376 0.5351 0.1749 0.0086**
Non-predator	Fantail	Brightness Contrast Saturation Hue	Whole body Whole body Whole body Whole body	-4.79 +2.66 +1.00 -20.83	0.3570 0.5324 0.7759 0.1112
Predator	Kingfisher	Brightness Contrast Saturation Hue	Whole body Whole body Whole body Whole body	-8.53 +3.16 +5.71 -16.28	0.1011 0.6905 0.1047 0.2128
Predator	Morepork	Brightness Contrast Saturation Hue	Whole body Whole body Whole body Whole body	+1.15 +13.70 -3.50 -1.81	0.8251 0.0857' 0.3194 0.8896

Table 2.22 Summary of BACI results from auditory simulation experiments on ngāhere geckos

Treatment Type	Treatment	Measurement	Body part	Δ predicted means After - Before	Statistical evidence (*p*)
	Settling period	Brightness Contrast Saturation Hue	Whole body Whole body Body only Tail Whole body	-1.86 -1.30 -0.57 1.68 +10.26	0.7161 0.8778 0.9007 0.7141 0.4687
Non-predator	Fantail	Brightness Contrast Saturation Hue	Whole body Whole body Body only Tail Whole body	+6.55 -5.93 -0.38 +1.6 +7.52	0.2009 0.3329 0.9340 0.7263 0.5956
Predator	Morepork	Brightness Contrast Saturation Hue	Whole body Whole body Body only Tail Whole body	-1.82 -9.20 +6.51 +5.11 +7.33	0.7214 0.2775 0.1570 0.2664 0.6044

From the BACI results, for the Raukawa geckos, after the settling period, contrast increased across the whole body (Table 2.23). There was weak evidence that saturation may also have increased in the tail area after both the settling period and the fantail visual simulation. After the fantail visual simulation, hue decreased across the whole body, meaning the gecko became more yellow and less green. After the morepork visual simulation, there was weak evidence that contrast may have increased across the whole body.

Table 2.23 Summary of BACI results from visual simulation experiments on Raukawa geckos

Treatment Type	Treatment	Measurement	Body part	Δ predicted means After - Before	Statistical evidence (p)
	Settling period	Brightness	Body only	+2.59	0.9034
			Tail	+4.86	0.3629
		Contrast	Whole body	+12.71	0.0407*
		Saturation	Body only	+6.59	0.1197
			Tail	+7.12	0.0934'
		Hue	Whole body	-9.98	0.3318
Non-predator	Butterfly	Brightness	Body only	-0.31	0.9547
			Tail	-2.38	0.6626
		Contrast	Whole body	+6.6	0.2989
		Saturation	Body only	+3.33	0.4423
			Tail	+7.61	0.0799'
		Hue	Whole body	+1.15	0.9127
Non-predator	Fantail	Brightness	Body only	-8.47	0.1217
			Tail	-8.16	0.1350
		Contrast	Whole body	-1.97	0.7558
		Saturation	Body only	+5.91	0.1735
			Tail	+7.20	0.0976'
		Hue	Whole body	-20.10	0.0570'
Predator	Kingfisher	Brightness	Body only	-0.44	0.9362
			Tail	-0.91	0.8685
		Contrast	Whole body	+9.05	0.1546
		Saturation	Body only	+0.5	0.9086
			Tail	-3.14	0.4690
		Hue	Whole body	-12.44	0.2379
Predator	Morepork	Brightness	Body only	+7.51	0.1699
			Tail	+5.98	0.2737
		Contrast	Whole body	+10.95	0.0852'
		Saturation	Body only	-0.05	0.9908
			Tail	-0.72	0.8675
		Hue	Whole body	-3.73	0.7236

After the settling period, contrast increased across the whole body of Raukawa geckos (Table 2.24). After fantail calls, hue also increased across the whole body.

Table 2.24 Summary of BACI results from auditory simulation experiments on Raukawa geckos

Treatment Type	Treatment	Measurement	Body part	Δ predicted means After - Before	Statistical evidence (p)
	Settling period	Brightness	Body only	+2.68	0.6085
			Tail	+5.26	0.3144
		Contrast	Whole body	+12.72	0.0264*
		Saturation	Body only	+5.41	0.1500
			Tail	+6.00	0.1110
		Hue	Whole body	-11.46	0.2986
Non-predator	Fantail	Brightness	Body only	-1.02	0.8514
			Tail	-0.55	0.9194
		Contrast	Whole body	-1.77	0.7635
		Saturation	Body only	-1.12	0.7714
			Tail	-0.34	0.9307
		Hue	Whole body	+26.85	0.0192*
Predator	Morepork	Brightness	Body only	-5.02	0.3537
			Tail	-5.39	0.3202
		Contrast	Whole body	-8.57	0.1470
		Saturation	Body only	+1.50	0.6999
			Tail	+3.30	0.3966
		Hue	Whole body	+0.87	0.9394

2.4 Discussion

While there were some differences in colour, the BACI analysis did not provide evidence of the dramatic changes in hue observed upon capturing ngāhere geckos in the field. There was however some evidence that tails sometimes differed from bodies in saturation for ngāhere geckos, and that they were able to change the hue of their colour. While the BACI analysis did not provide evidence that this was the result of predator simulations there are several reasons why this may be the case. From a human visual perspective of the photographs taken, colour changes appeared to be strongest approximately 2-3 minutes after the simulations had taken place. On the 5th minute after treatment, the before photograph for the next treatment was taken. However, it seems likely that this was insufficient time for the geckos to either change to some baseline level or recover from the potential stress of a predator flying over their enclosure or calling nearby. This may mean that the baseline "Before" for each treatment was not representative of a "resting" or "recovered" state. To a limited extent, this could be analysed in future analyses of the complete dataset by looking at the treatment order as a covariate, and by analysing all of the photos taken in the minutes following each treatment. Future research should allow greater time between treatments, a longer settling period, and subject geckos to fewer treatments as there may also be limitations to the frequency and magnitude of colour

changes. It may also be that the frequency, magnitude, and/or speed of colour change declines after one or more colour changes, as there can be costs to colour change.

For example, in guppies, where yellow colouration is both costly to express and is an honest signal of fitness (foraging ability - Kodric-Brown, 1989; speed and viability of sperm - Locatello et al., 2006; food intake and behavioural decisions - Rodgers et al., 2013). Stressed guppies become paler in colouration. When moved into a predator free environment, female preference was also a strong driver for increasing orange colouration in guppies in only three generations (Gordon et al., 2015). In Anoles, carotenoid-based dewlaps are found predominantly in full shade, where the ambient spectrum is yellowish-green after filtering through the leaves of the canopy (Macedonia et al., 2000).

For ngāhere geckos there was weak evidence that contrast may have increased across the whole body after morepork simulations. Further research would be required to determine whether this potential pattern would remain with a larger sample size, and whether this had any impact on the behaviour or avian predators, or their ability to detect them. To test whether birds are more or less likely to attack ngāhere geckos if contrast increases across the whole body, model geckos could be created and placed in the field.

In terms of brightness, ngāhere geckos did not darken their bodies in response to bird calls, as seen in Madagascan giant day geckos (*Phelsuma grandis*) (Ito et al., 2013). As colour can affect thermoregulation, there may be costs to changing levels of brightness (e.g. overheating as a result of darkening or having insufficient energy to escape as a result of brightening). It may also be that if the saturation levels were to be assessed for the Day geckos that a difference might be found. However, the Day geckos changed their level of brightness after exposure to the avian alarm calls that indicated the presence of a predator, which the authors asserted indicated that the Day gecko was using the alarm calls as a warning. My approach differed in that I played the (non-alarm) calls of a predator and a non-predator, however it would be interesting to investigate whether ngāhere geckos also respond specifically to the alarm calls of non-predator birds that share a predator with geckos. Colour changes could also be compared against the colours and light spectra of their natural environment and the visual capabilities of these specific predators.

For Raukawa geckos, bodies and tails varied in saturation and brightness. However, the BACI analysis did not provide evidence that differences in brightness were the result of predator simulations. While there was weak evidence that saturation may have varied between body and

tail before visual simulations of kingfishers, after treatment, this difference in saturation increased to become statistically significant evidence (p = 0.01, t = 2.5887, df = 365, table 2.14c Appendix 2D) of a difference between body and tail. While Raukawa geckos demonstrated changes in contrast and hue across the whole body, the BACI analysis only showed weak evidence that contrast may have increased across the whole body after visual simulations of moreporks. However contrast also increased across the whole body after the settling period. As for the ngāhere geckos, further research, with greater time between treatments, a longer settling period, fewer treatments, and more individuals are needed to determine effects of avian predators on colour change.

While the results from the BACI analysis were unable to explain the colour changes initially observed, It may be that there was insufficient time between treatments, and that resulted in the "Before" comparisons not being representative of either a resting or recovered state. Future investigations should leave more time between treatments, and subject geckos to fewer treatments. It may be that geckos are limited in the frequency and magnitude of colour changes they can achieve within a time period, and it may be that either the frequency, speed, or magnitude declines after one or more changes. It may also be that the changes observed were not a response to predators, but a response to the change in light levels or temperature geckos were exposed to after capture, or a different stress response unrelated to predators.

With regard to the settling period, it may be that it was insufficient time for the geckos to adjust to their environment, and that despite not showing obvious signs of stress, their stress levels were still sufficiently elevated to affect their colour. These results alone are not sufficient to make statements about the direction of any change because a difference was not able to be discerned between before and after treatments. However with a different experimental design allowing more time between treatments, and fewer treatments per gecko, it may be that a pattern could be found.

Though this was not part of the experimental design, I noted that both ngāhere and Raukawa geckos appeared to respond behaviorally to auditory and visual simulations of predators - either with a freeze or flight response, compared with walking slowly within the enclosure at other times. However, while ngāhere geckos and Raukawa geckos may differ in colour change responses, and a clear before and after effect was not discernible using the BACI analysis.

Although I was not able to elicit significant colour change in ngāhere geckos, it does not mean they are incapable of significant colour change. For example, colour change in ngāhere geckos

might be used for conspecific communication, as it is in male veiled chamaeleons (Ligon, 2015). Colour is used by many animals for both inter- and intraspecific communication. In some animals, such as anoles (*Anolis* spp.), the colour used for communication is hidden from the sight of predators, and only flashed when the anole feels safe enough to do so (Fleishman, 1992; Fleishman & Persons, 2001). The role of colour in social behaviour is also yet to be addressed for ngāhere geckos, but could be tested experimentally.

When colour change is considered, the time of day that the animal is active, and the structure of its habitat may be relevant to how this colour change is perceived or visible to avian predators. Ngāhere geckos are active both during the day and the night, with peak travel activity occurring during the middle of the day (Romijn et al., 2014). The habitat in which they are generally found will also affect their vulnerability to predation. Ngāhere geckos are usually arboreal in trunks and branches of trees and shrubs (Romijn et al., 2014), but can occasionally be found on the ground (pers. obs., Trent Bell & Sarah Herbert, pers. comm.). The structure and colour of the habitat in which they are found will affect which colouration and patterning provides the most effective camouflage. In addition, the structure of the habitat will affect the light levels, which in turn will affect the spatial resolution available to birds, which declines rapidly as light levels decrease (Mitkus, 2015). In avian vision, there is a tradeoff between resolution and sensitivity (Pollard, 2009). Thus, in lower light levels greater sensitivity is required, but a loss of resolution follows (Pollard, 2009). To an extent, larger eyes help with this, and as a result, nocturnal species tend to have larger eyes (Pollard, 2009). Spatial resolution is measured in cycles per visual degree, which provides an indication of how many lines can be seen per degree of visual field, without blurring (Cronin et al., 2014; Martin, 2017a). Low spatial resolution is seen in birds like the common barn owl (2.3-4.5 cycles per visual degree), and high spatial resolution in birds like the wedge-tailed eagle (138 cyc/deg) (Reymond, 1985; Harmening et al., 2007; Mitkus, 2015). Moreporks may have low spatial resolution too, given their nocturnal nature, and that several species of owls may use hearing to a large extent in hunting, perhaps to compensate their visual limitations (Payne, 1971; Pollard, 2009). However the active period of moreporks extends either side of dusk and dawn, they have large eyes, they don't display auditory bilateral asymmetry (important to owls hunting by sound) and their hearing frequency range has not been studied (Norberg, 1977; Brighten, 2015; Mikola, 1983, Olsen, 2011 both cited in Brighten, 2015). For kingfishers, the other species simulated in this study, spatial resolution is known to be somewhere in the middle of the range with 26 cyc/deg (Moroney & Pettigrew, 1987; Mitkus, 2015).

Future analysis to investigate whether ngāhere geckos are able to match various background colours, and the effects of light levels and temperature on their colouration could provide evidence for a camouflaging response. As ngāhere geckos have a New Zealand Threat Conservation Status of 'At risk-declining' (Hitchmough et al., 2021), these areas will be an important consideration when designing habitat enhancement and restoration projects. Because ngāhere geckos only use retreats irregularly (Romijn et al., 2014), their ability to match their background is particularly important in order to maximise their chances of avoiding avian predation. An example of the consequences of not being able to adequately match the background can be seen in Shore skinks (*Oligosoma smithii*), where translocations to a different environment resulted in a reduction of phenotypic diversity to just one colour morph – a likely reduction in genetic diversity, as not all founders had survived (Baling et al., 2016).

While the BACI analysis was not able to support the field observations of increased tail brightness and contrast in Raukawa geckos, this may be the result of insufficient time between treatments. Other studies have shown that lizards may sometimes undergo an ontogenetic change in tail colour (from colourful to less colourful) as they adopt less risky behaviours (Hawlena, 2009). This type of colour change is not rapid, as seen in ngāhere and Raukawa geckos, but refers instead to a change as a lizard transitions from being a neonate or juvenile to adulthood. In this case, the immature lizards are already more vulnerable to predation due to being more active and spending longer time out in risky habitats, making it worthwhile to draw the predator's attention to the tail (Hawlena, 2009). Contrary to ngāhere geckos, Raukawa geckos are a cryptic species who have small home ranges, bask cryptically (Werner and Whitaker, 1978), and have low average movements (c. 2m) (Green, 2001), though they also disperse seeds up to 9.3m from source plants (Wotton, 2002). For a cryptic and not highly active species like the Raukawa gecko, continuously having a bright and contrasted tail may not be advantageous, as it may draw attention to the gecko when the gecko might otherwise not be detected. However, changing colour only when under threat could be advantageous. If the predator attacks the tail first, the gecko can autotomise its tail, giving it a second chance to escape. Whether having a brighter or more contrasted tail would be effective in drawing birds to attack this area will be tested in chapter 3.

My study focussed on simulations of predators for colour change, but there are several other mechanisms that may drive colour change in New Zealand geckos. These include temperature, light levels, humidity, background colouration, and social signalling. Considering the extent of colour change observed in the field, and not within these results, these potential triggers warrant further investigation. Future research into these potential mechanisms will help us to better

understand the extent and triggers of colour change in New Zealand geckos. A better understanding of the extent and triggers of colour change can be utilised to better understand habitat requirements for optimal camouflage against avian predation, optimising thermoregulation, and using this knowledge to inform restoration and habitat management strategies.

Chapter 3 - Could rapid colour change by geckos be an effective defence against avian predators?

3.1 Introduction

Predation pressure, and the suite of predators targeting prey species, influence both animal physiology and behaviour (Case & Bolger, 1991; Hoare, 2006; Massaro et al., 2008; King 2019c). For those oceanic islands that lack indigenous mammalian predators, like New Zealand, predator guilds are dominated by avian and reptilian predators with a high acuity of vision, and who tend to rely on vision to hunt (Meyer-Rochow, 1988; Meyer-Rochow & Teh, 1991; DuMont, 2015; King, 2019c). For example, Tuatara (*Sphenodon punctatus*) rely on visual rather than acoustic or olfactory cues to hunt (Meyer-Rochow, 1988), can hunt at very low light levels, and are better at catching conspicuous than camouflaged prey (Meyer-Rochow & Teh, 1991). Visually-orienting predators may impose strong selection pressure on prey to evolve cryptic colouration, or life history traits that improve avoidance of such predators (Brandley et al., 2014; DuMont, 2015; Kuriyama et al., 2016; Ruxton et al., 2018; King, 2019c). This situation has resulted in a large number of flightless species, with good camouflage, a freeze response, and a large number of nocturnal prey species (King, 2019c; Hoare, 2006). Strategies such as camouflage and a freeze response are thought to be effective against visually oriented predators, because well-camouflaged prey are less likely to be visually detected if they remain motionless (Heatwole, 1968; Ydenberg & Dill, 1986). Many avian predators are diurnal, though not all (King, 2019c). Colour vision and spatial resolution are however limited by low light levels, therefore nocturnal lifestyle, combined with the use of camouflage and a freeze response, provides greater protection against avian predators (Boström et al., 2016; Martin, 2017a).

New Zealand lizards have co-evolved with avian and reptilian predators for around 28.9-53.5 million years (Nielsen et al., 2011), before the recent introduction of a suite of invasive mammalian predators which includes three species of rats (*Rattus norvegicus, R. rattus, R. exulans*), mice (*Mus musculus*), cats (*Felis catus*), ferrets (*Mustela furo*), stoats (*M. erminea*), weasels (*M. nivalis*), hedgehogs (*Erinaceus europaeus*), and possums (*Trichosurus vulpecula*) (Hoare, 2006; King, 2019c). Conversely to avian and reptilian predators, introduced mammalian predators have poorer eyesight (Osorio & Vorobyev, 2005) and tend to rely on their sense of smell to hunt (Worthy & Holdaway, 2002; Hoare, 2006; Bateman et al., 2017). As a result, cryptic colouration and camouflage are likely of little use against these predators (King, 2005; DuMont, 2015). Due to their co-evolutionary history with predominantly visually-oriented

predators, I would expect New Zealand lizards to be adapted more strongly towards avoiding these types of predators. Here I explore the role of colour and colour change in avoiding avian predation.

Colour is used by animals for signalling, thermoregulation, and camouflage (Stuart-Fox & Moussalli, 2011; Langkilde & Boronow, 2012). There are many examples of lizards and other species using colour to startle, deflect, or distract a predator, in order to increase their chances of escape and thus increase their chances of survival. For example, the Australian blue-tongued skink (*Tiliqua* spp.) exhibits colourful full-tongue displays in the final stages of a predatory attack (Badiane et al., 2018). Waiting until the final stages of a predator attack to startle or distract the predator using displays or colour, has the potential advantage of not drawing attention to themselves before a predator has detected the potential prey.

Conspicuous colouration has a cost. In *Crotaphytus collaris* (Iguanidae) more conspicuous males have greater detection probability by predators and are more frequently predated than less conspicuous females (Husak et al., 2006). Many anti-avian predator responses have been observed in lizards, some of which involve colour change. For example, the Madagascan giant day gecko (*Phelsuma kochi*) has been observed to darken its whole body in response to the alarm calls of birds (Ito et al., 2013), presumably to reduce its own conspicuousness to predators. The dwarf chameleon (*Bradypodion transvaalense*) has been observed to change colour differentially for avian predators than for snake predators, depending on their visual acuity (Stuart-Fox et al., 2006, 2008).

Autotomy is an antipredator trait found in a variety of Animalia, and is thought to be the ancestral state in squamate reptiles (Dunoyer et al., 2020). Autotomisable body parts are frequently more conspicuous than the rest of the body (Ruxton et al., 2018), although comparative phylogenetic analyses have found the ability to autotomise tails in lizards evolved before tail colouration (Murali et al., 2018; Emberts et al., 2019). Some lizard species have permanently brighter or more colourful tails (Watson et al., 2012; Ortega et al., 2014; Bateman et al., 2014; Fresnillo et al., 2015; Murali et al., 2018; Ruxton et al., 2018), which could be more costly a strategy than changing colour after detection. Others display different tail colouration in juveniles and adults, which has been hypothesised in juveniles to deflect imminent attacks to the tail, allow greater activity and more time in open habitats, and to fade as lizards adopt less risky behaviours as adults (Cooper & Vitt, 1985; Castilla et al., 1999; Hawlena et al., 2006; Hawlena, 2009; Nasri et al., 2017; McElroy, 2019). It may also be that in those species that undergo ontogenetic colour change, juveniles tend to be worse at escaping attacks (e.g. less

experienced, slower to detect predators, less able to escape quickly), and that having a more conspicuous tail improves their chance of surviving attacks experienced through potential naïvety or delayed response to danger. In most diurnal lizards, the conspicuous tail is colourful (e.g. blue, green, or red); in nocturnal species, contrasting colours (light and dark bands) make the tail noticeable (Hawlena et al., 2006).

During survey work, tail contrast and brightness in Raukawa geckos (*Woodworthia maculata*) rapidly increased after capture by humans. The trigger for this change is unknown, but I hypothesised that this was a mechanism to attract a predator's attention towards an autotomisable body part. Despite the temporary costs of caudal autotomy, the evolutionary fitness consequences of losing a tail are less severe than the fatal cost of being eaten (Fox & Rostker, 1982; Alibardi & Meyer-Rochow, 1988; Salvador et al., 1995; Emberts et al., 2019). Therefore, in this chapter, I aimed to test responses of wild, free-ranging birds (as measured using pecking behaviour) to increased brightness and/or contrast in gecko tails using clay models.

I applied three treatments to the models: 1. Tail the same colour and brightness as the rest of the body (the plain-tailed "Control"); 2. Tail brighter than the rest of the body; and 3. Tail more contrasted than the rest of the body. I used these models to address the following questions: Does increased **brightness** in the tail region encourage birds to peck this area in preference to other areas of the body, and compared to the evenly coloured control model? Does increased **contrast** in the tail area encourage birds to peck this area in preference to other areas of the body, and compared to the evenly coloured control model? Previous research has shown that birds tend to aim for the head in uniformly coloured models of lizards (Florence-Bennett, 2020; Marshall et al., 2015), therefore I predicted that a more conspicuous tail would disproportionately attract predation attempts by birds.

3.2 Methods

3.2.1 Lizard model construction

Thirty lizard models were constructed from 3D printed models covered in clay (fig. 3.1). These were based upon models of shore skinks (*Oligosoma smithii*) previously used by Baling (2017) and Florence-Bennett (2020) in studies of bird predation behaviour on New Zealand lizards. The 3D-printed models were constructed from acrylonitrile butadiene styrene filament using a 3D printer (UP BOX+, 3D Printing Systems). The method for printing the models was as per

Florence-Bennett (2020), but the models were resized (maintaining proportions) to have a snout-to-vent length (SVL) of 68 mm (largest Raukawa gecko used in Chapter 2).

The models were coated with approximately 8 g of non-toxic animation clay (Newplast, Newclay Products Ltd, Devon) to approximate the shape and natural coloration of a Raukawa gecko. The main body of each model and the tails of 'Control' (plain-tailed) and 'Contrasted' models were coated in pale khaki-green clay (Newplast "Ginger"). Tails of 'Bright' models were coated in a 50/50 mixture of Newplast "Ginger" and Newplast "White" clay. Patches of Newplast "White" and Newplast "Dark Brown" clay were added to Contrasted model tails (fig 3.1).
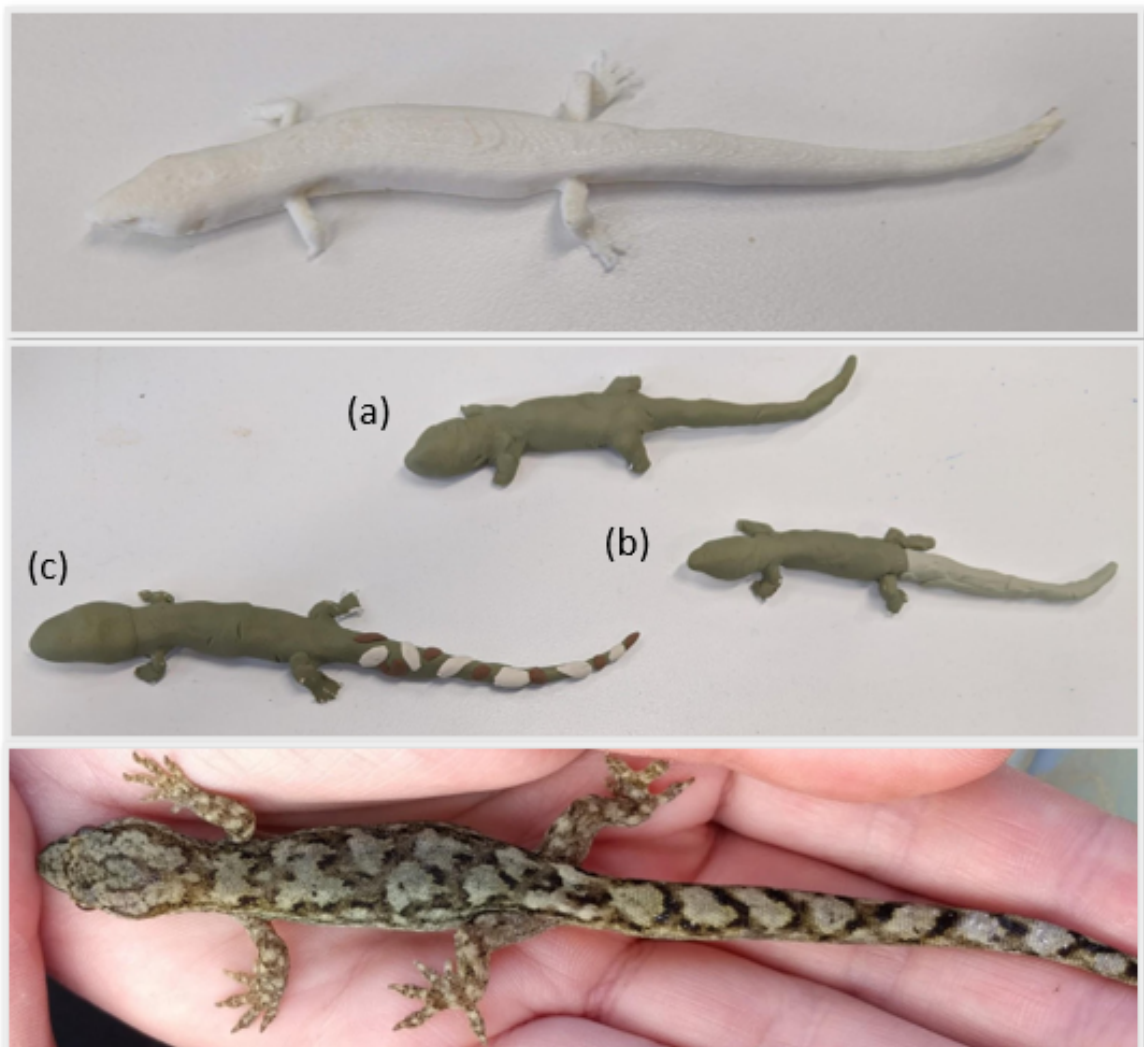
Figure 3.1 Top image: 3D-printed model frame. **Middle image:** Completed models of Raukawa geckos consisting of a 3D-printed frame covered with animation clay; (a) Control (plain-tailed) model, (b) Bright-tailed model, and (c) Contrasted-tailed model. **Bottom image:** A Raukawa gecko exhibiting a brighter and more contrasted tail on handling (see Chapter 2).

The models were glued to rocks measuring approximately 20 mm high x 110-150 mm long x 110-120 mm wide (grey Beach Flats medium size from The Goods Shed, Wellington) using Uhu universal standard adhesive glue. This was done to standardise the background and reduce the risk of models being removed by predators (Florence-Bennett, 2020). A unique number was written at the base of each rock to keep track of models during the field experiment.

3.2.2 Field experiment

The field experiment was carried out across three study sites located on Wellington City Council-managed public land on the Southern coast of the Miramar Peninsula, Wellington, New Zealand (fig. 3.2). These sites were in the same general location used for collecting Raukawa geckos for Chapter 2, and for other studies on Raukawa gecko populations and avian predation of lizards (Florence-Bennett, 2020; Herbert, 2020). Thus the birds found in this area may be the same populations and community of birds predating on the lizard populations sampled for chapter 2, and the same community that participated in Florence-Bennett's study on avian predation of lizards. Vegetation at these sites comprised a mixture of low coastal shrubs, vines, sedges, grasses, and herbs ranging between 10 cm and 2 m in height. The dominant indigenous plant species at the sites were taupata (*Coprosma repens*), pohuehue (*Muehlenbeckia complexa*), and wharariki (*Phormium cookianum*). These were interspersed with weedy exotic species including tree lupin (*Lupinus arboreus*), gorse (*Ulex europaeus*), boneseed (*Chrysanthemoides monilifera*), and *Bromus diandrus*. The substrate at each site varied from cobbles to rocky/sandy soil. All sites were within the Predator Free Miramar mammalian pest control area (Predator Free Wellington, 2022), though mice are not a target of this programme and thus not controlled. Sites supported Raukawa geckos, northern grass skinks (*Oligosoma polychroma*) and/or copper skinks (*O. aeneum*).

The field experiment consisted of three sampling sessions in May, June, and July of 2020. During each session, all thirty lizard models ($n_{Plain(Control)} = 10$, $n_{Bright} = 10$, $n_{Contrasted} = 10$) were deployed across the three study sites using a block design (figs 3.3 and 3.4). At the start of each sampling session, fresh clay was applied to each model, and the treatments were swapped so that each model had each treatment applied once (fig 3.3). The models were placed out in relatively flat areas and paired with a motion-triggered trail camera to record bird behaviour. A mixture of trail camera models was used; 15 Reconyx 600 Hyperfire, 9 Bushnell Aggressors, and 6 Bushnell Trophy Cameras (Brown, Model 119436). The different camera models were divided equally amongst sites, so that each site had the same number of each type of camera. Cameras were secured to vegetation with a black zip tie at a height of 0.3 m to 1.8 m from the ground to optimise security of camera attachment and view of the lizard models.

Figure 3.2 Gecko models were deployed across three study sites on the Southern coast of the Miramar Peninsula, Wellington, New Zealand. These were adjacent to capture locations for geckos captured in Chapter 2 demonstrating colour change capacity. Map created using Google maps.

Lizard models were placed between 0.5 and 2 metres from the cameras to optimise the visibility of the lizard models via the cameras. Cameras were pointed down to face the lizard models and signage was erected in the area to alert people to the presence of cameras. I noted GPS locations of the cameras, noted the surrounding vegetation, and took photographs to ensure cameras and models were placed identically for each session. Each camera model used was tested for appropriate distancing and settings in a suburban garden prior to use. The camera settings used are shown in Appendix 3.1. Cameras and models were deployed for three sessions of three days each. Following each session, I photographed the models *in situ* to record peck mark locations, and collected the models and cameras from the field. After each sampling session, treatments were swapped around between sites so that all treatments took place in each sampling session, with one treatment per site (n = 10 models per site per session, see fig 3.3).
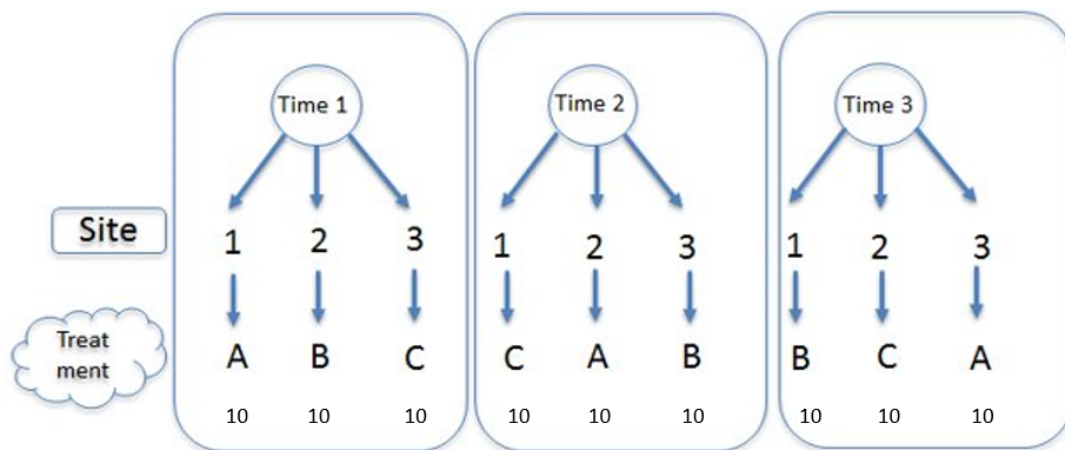
Figure 3.3 Experimental design. Where treatment A = Bright, B = Contrasted, and C = Plain/Control. Ten models and cameras were placed at each of the three sites during each survey (total = 30), and rotated amongst sites at the start of each session.

3.2.3 Statistical analysis

Trail camera photographs were categorised according to whether they contained birds, mice, or neither (Table 3.1). Garden snails were also seen feeding on the clay of the models, but these were not systematically counted, as although they are frequently found in high numbers in pitfall traps left for lizards, they are not a known predator of geckos. Images containing birds were further divided into subcategories by apparent behaviour captured in order to undertake exploratory analysis (Table 3.1). The number of photographs per subcategory were tallied. The dependent variables were the number of photos of each behaviour, and the independent variable was the treatment, i.e. the tail being plain (control - the same colour as the rest of the body), bright (brighter than the rest of the body), or contrasted (more contrasted than the rest of the body).

Peck data were analysed in R (R Core Team, 2020) as a generalised linear mixed effects model using the R packages "Predictmeans", "lme4", "nlme", and "lmerTest" (Bates et al., 2015; Kuznetsova et al., 2017; Luo et al., 2021; Pinheiro et al., 2021). All models included a fixed effect for 'Treatment' and the random effects 'Site' and 'Trial' (i.e. which of the three sampling sessions, or trials), but the response variable differed between tests. For my model, the dependent variables were 1) the total number of pecks for each model, or 2) the number of pecks by area for each body part. The fixed effect was the treatment (Plain (Control), Bright, or Contrasted tails), with random effects of site and trial. Normality of response variables were appraised using the "qqnorm" function.

Table 3.1 Categories of photos and subcategories of bird behaviour captured in the photos captured by trail cameras.

	All photos, including those not containing birds or mice			
Category	Photos containing birds potentially interacting with the model	Photos containing birds not interacting with the model	Photos containing mice	Other photos
Subcategory	Bird pecking model	Bird flying away		
	Bird looking at model	Bird walking past		
	Bird blocking model*	Bird perched nearby		
	Bird vocalising while perched on model	Bird looking at camera		
		Bird standing nearby		
		Bird feeding nearby		
		Bird walking away		

*Where the bird was blocking the model, the bird was blocking the camera's view of the model. It was bending down towards the model, but whether it was pecking it and where, or just looking at it, was not visible in the photo.

Peck marks on models were identified by the presence of v- and u-shaped imprints in the clay, which are easily distinguishable from other marks, such as, the bite and scrape marks left by mouse incisors (Florence-Bennett, 2020). The total number of peck marks on a model per trial were compared using a Poisson GLMM, with pairwise comparisons of treatments using the Tukey Honest Significant Difference Test. For examination of the distribution of peck marks across models, the locations of the peck marks were classified into four areas of interest: the head and neck, the body, the limbs, and the tail (fig 3.4). To avoid the size of the body part influencing the results, the area of each body part was calculated for each trial as the average number of pixels from three repeated measurements taken in ImageJ, and pecks were expressed as an area-standardised variable: the natural logarithm of the number of pecks per 10,000 pixels, with the addition of a constant equal to half the smallest non-zero value, to allow transformation of all values, including those equal to zero. Standardised pecks were compared between treatments using a Gaussian GLMM with an interaction between 'Treatment' and 'Bodypart'. I then undertook pairwise comparisons using the "Predictmeans" package. Lastly, I looked at which body part had the most pecks for each model type.
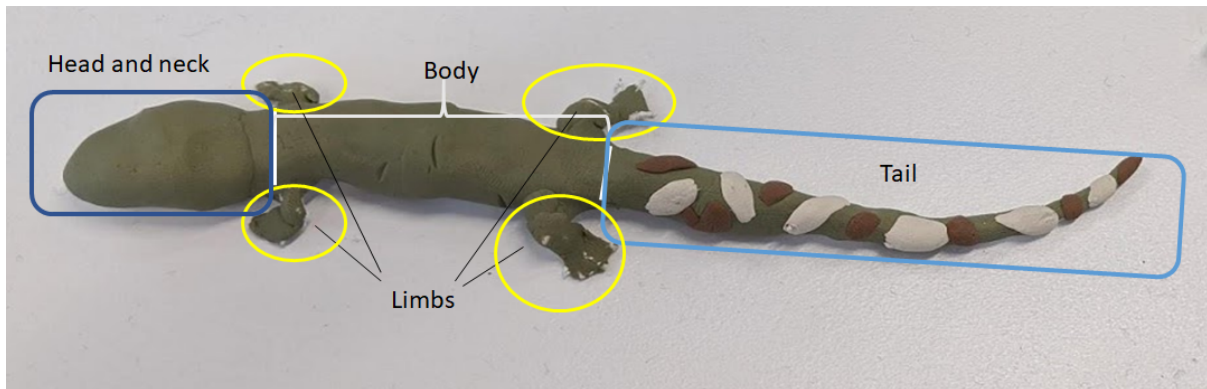
Figure 3.4 Areas of interest for assessing pecks on lizard models.

3.3 Results

3.3.1 Trail camera footage

Trail cameras captured 12,558 photographs, of which 364 (2.9%) were photographs of birds and 441 (3.5%) of the photographs contained house mice (*Mus musculus*). Half of the photos of birds (n = 182) indicated a potential interaction with a model. Of these, only 38 (21%) showed birds pecking the model. A further 40 (22%) showed birds looking at the model, 103 photos (57%) showed birds standing in front of the model and blocking the camera view of the model (so that one could not see the part they were looking at and/or pecking), and one (0.5%) showed a bird vocalising while perched on the model (fig 3.5). In the photographs where the bird was blocking the view of the model, the exact nature and position of the potential interaction could not be seen due to the angle of the camera and the position of the bird, however, the bird was bending down towards the model.
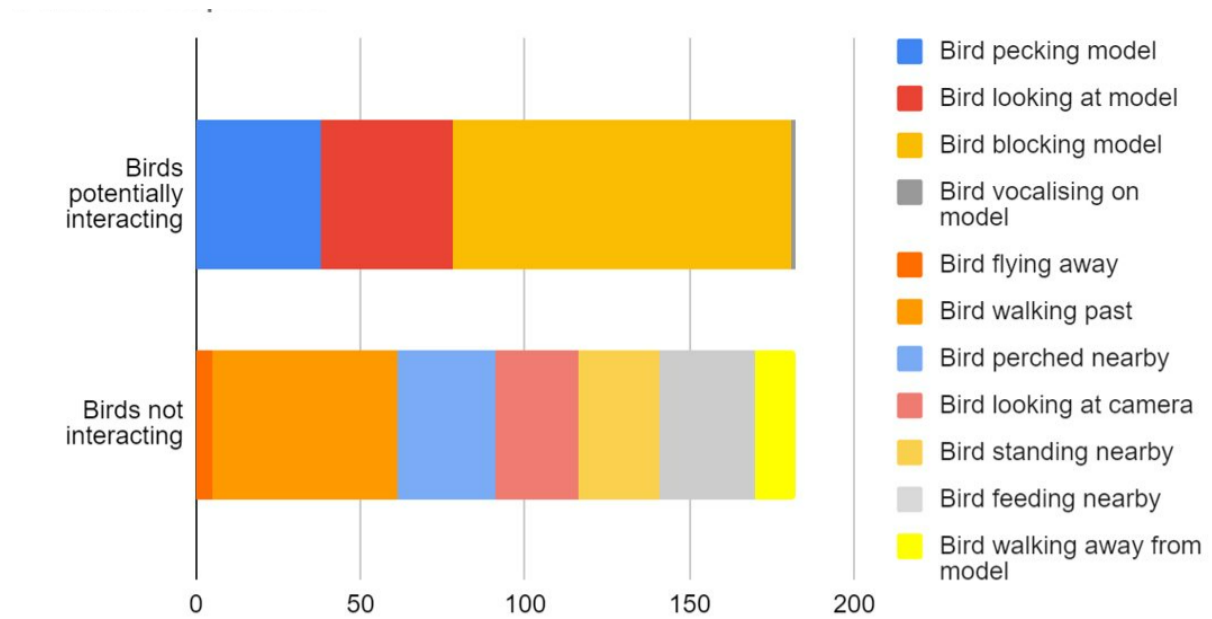
Figure 3.5 Number of photographs captured by trail cameras of apparent bird behaviour near model lizards (n = 364), classified by behavioural type. More detail can be found in Appendix 3B.

Nine bird species were photographed by trail cameras in close proximity with the models (fig 3.6). Blackbirds (*Turdus merula merula*) were the most commonly photographed species, had the most photographed interactions with the models, and only blackbirds and song thrushes (*Turdus philomelos clarkei*) were observed pecking the models (figs. 3.6 and 3.9). Only two native species were captured in five photographs: little penguins (*Eudyptula minor*) and silvereyes (*Zosterops lateralis*). These birds did not appear to interact with the models (fig. 3.6).

The majority of potential interactions captured (n = 142, 78%) took place on the models with plain tails, with only 19 (10%) potential interactions being photographed in models with brighter tails, and 21 (12%) in models with more highly contrasted tails (fig. 3.7). In most photographs the body part being pecked could not be determined, due to the speed of the motion and the photographs being taken one second apart.
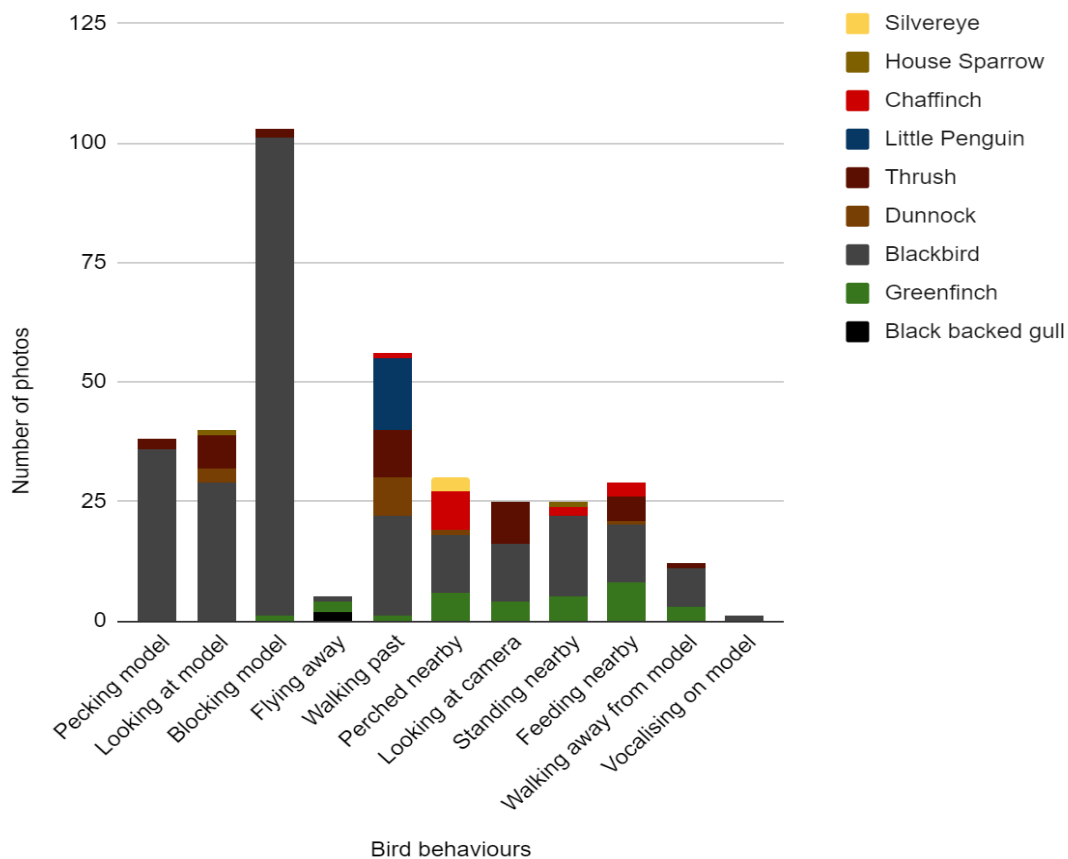
Figure 3.6 The number of photographs captured of each species of bird (above), for each behaviour type, by species.
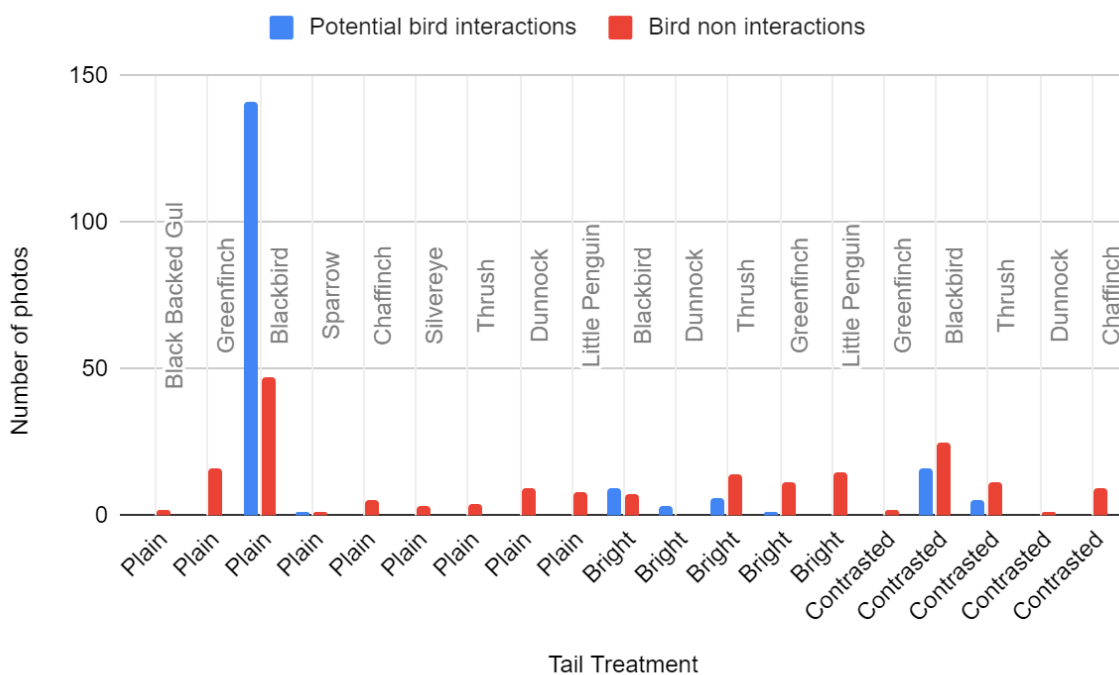
Figure 3.7 Number of photographs of potential interactions with lizard models captured of each species of bird for each model lizard tail treatment.

Figure 3.8 Bird turning towards the brighter tail of a model after initially looking at head/body.

07-27-2020 11:23:45

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Figure 3.9 Bird pecking the head of a plain tailed model.

3.3.2 Peck marks on lizard models

Plain-tailed (control) models received pecks on 24/30 models (80%), bright-tailed models received pecks on 29/30 models (97%), and contrasted-tailed models received pecks on 30/30 models (100%). Treatment had a significant effect on the total number of pecks over the entire model per trial (Poisson GLMM: $F_{2, 84}$ = 6.598, p = 0.002). Control models had, on average, 4.4 fewer pecks per trial than Contrasted models (Tukey HSD 95% confidence level(CI) = -1.5, -7.3; p = 0.002, fig 3.10). Though controls had 2.7 fewer pecks per trial than Bright models, statistical evidence of a difference between them was weak (Tukey HSD 95% CI = 0.2, -5.6; p = 0.080; fig. 3.10). There was no significant difference between the number of pecks per trial on Contrasted and Bright models (Tukey HSD 95% CI = 1.2, -4.6; p = 0.335; fig. 3.10).
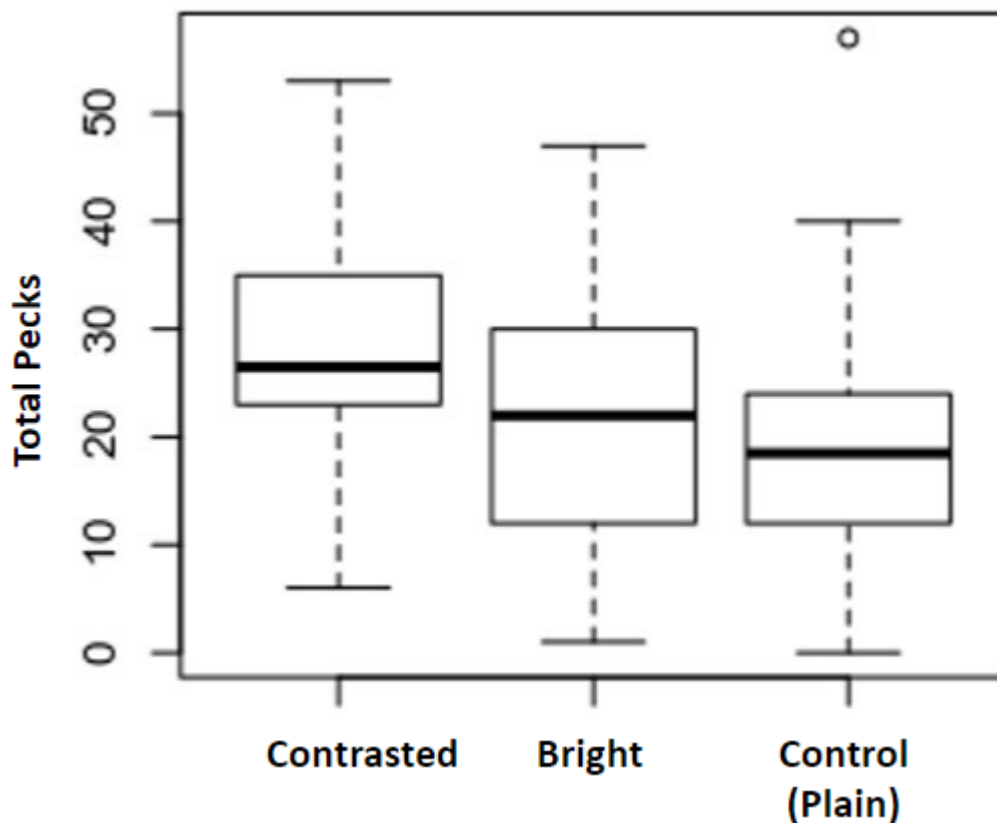
Figure 3.10 Boxplots of total number of pecks over an entire lizard model. N trials = 90. Control models receive fewer pecks than contrasted models (p=0.002).

3.3.3 Effect of treatment on the number of pecks per area-adjusted body part

There were significantly more pecks on the tails of Contrasted models than Control models (t = 3.494, p <0.001, fig. 3.11, table 3.2, table 3.3). While there were also more pecks on the tails of

Bright models than Control models, this difference was not statistically significant (t = 1.625, *p* = 0.106, fig. 3.11, table 3.2, table 3.3). The bodies of Contrasted models had a greater number of pecks than both Bright and Control models, but the difference was only significant between Contrasted and Bright models (fig. 3.11, table 3.3). The limbs of Contrasted models had significantly greater numbers of pecks than both Bright and Control models. There was no statistically significant difference between treatments in the number of pecks to the head and neck of models (fig. 3.11, table 3.6).

Table 3.2 Estimates of the effect sizes of fixed factors from a Gaussian GLMM for the effect of tail treatment on the area standardised number of pecks by body part after accounting for any effects of site, trial, and model. The model formula was: pecks ~ Treatment * Bodypart + (1|Site) + (1|Trial) + (1|Model). The levels for the fixed factor *Treatment* were *Plain* (Control), *Bright*, and *Contrasted*. Levels for the fixed factor *Body Part* were *Head and neck, Body, Limb*, and *Tail*. SE = standard error, DF = degrees of freedom. *p*-values are indicated as follows $p<0.001$***, $p<0.01$**, $p<0.05$*, $p<0.1$'.

Fixed factor	Estimate	SE(Estimate)	DF	t	*p*
(Intercept)	-0.2263	0.2746	4.1809	-0.824	0.4542
Bright	0.2750	0.1693	263.9305	1.625	0.1054
Contrasted	0.5914	0.1693	263.9305	3.494	0.0006 ***
Head	-0.2492	0.1414	260.9991	-1.763	0.0791 '
Body	-0.2221	0.1414	260.9991	-1.571	0.1174
Limb	0.1204	0.1414	260.9991	0.852	0.3952
Bright × Head	-0.3696	0.1999	260.9991	-1.849	0.0656 '
Contrasted × Head	-0.4027	0.1999	260.9991	-2.014	0.0450 *
Bright × Body	-0.4101	0.1999	260.9991	-2.052	0.0412 *
Contrasted × Body	-0.2960	0.1999	260.9991	-1.481	0.1398
Bright × Limb	-0.0977	0.1999	260.9991	-0.489	0.6255
Contrasted × Limb	0.0361	0.1999	260.9991	0.181	0.8569
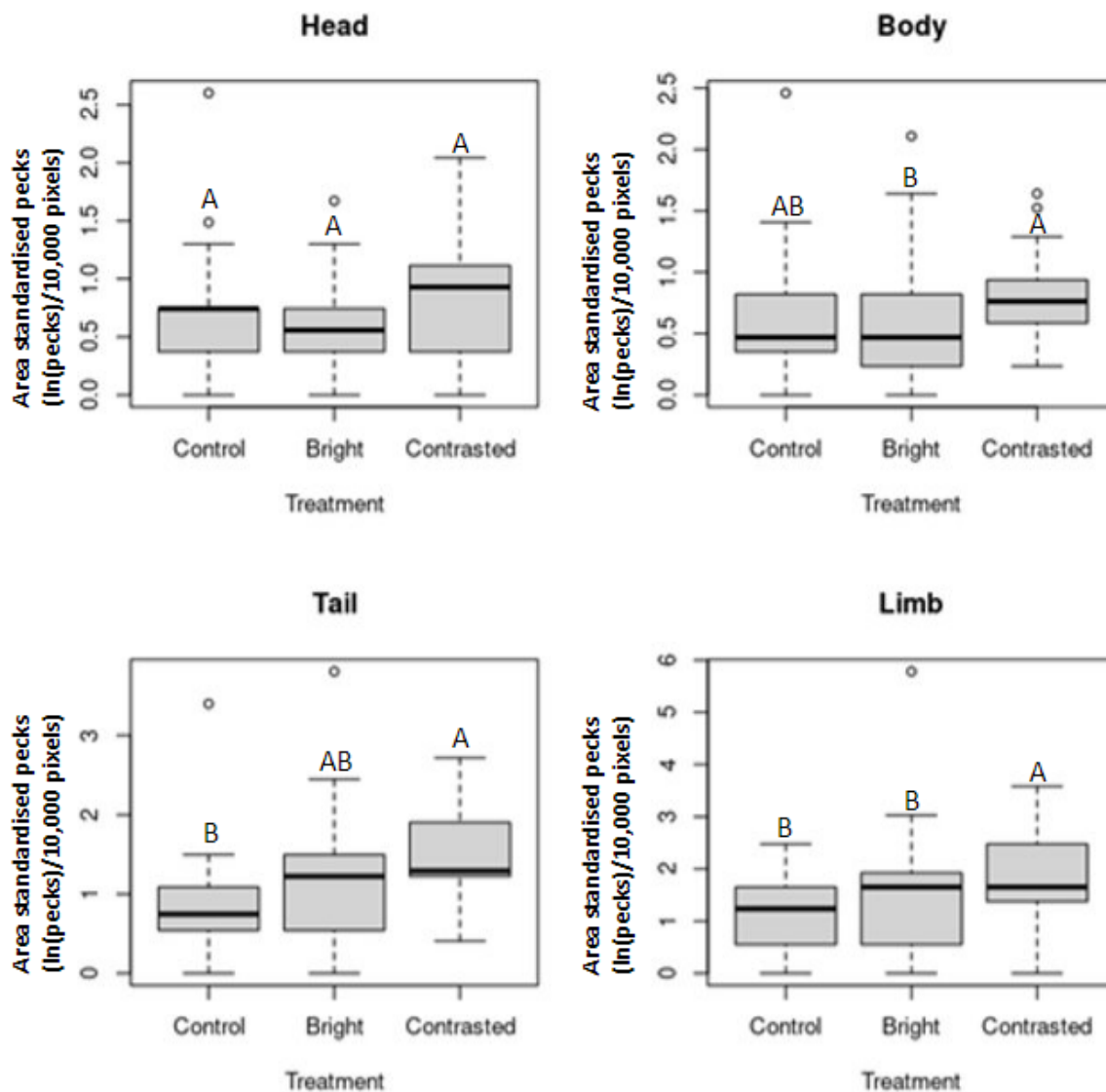
Figure 3.11 Pecks adjusted for area (natural log transformed pecks per 10,000 pixels) for each body part and tail treatment. Shared letters indicate differences in predicted mean area standardised pecks within a body part are not statistically significant at the p<0.05 level.

Pairwise comparisons: Body parts

For the **tails** of each model, there was evidence of a statistically significant difference between plain (control) and contrasted tail treatments (p=0.0006) with more area adjusted pecks on contrasted tails, and weak statistical evidence that there may be more pecks on contrasted tails than on bright tails (p=0.0627). There was no evidence of a statistically significant difference between plain and bright treatments (table 3.3).

For the **head** and neck area of each model, there was weak statistical evidence that there may be more area-adjusted pecks to the head and neck in contrasted than bright treatments (p =

0.0955) and no evidence of a statistically significant difference in number of pecks to the head and neck (by area) between other treatments (table 3.3).

For the **body** of each model, there was statistically significant evidence of a greater number in area-adjusted pecks to the body in contrasted than in bright treatments (p = 0.0116), and weak statistical evidence that there may be more area-adjusted pecks in contrasted than plain treatments (p = 0.0822). There was no evidence of a statistically significant difference between the plain and bright treatments (table 3.3).

For the **limbs** of each model, there was statistically significant evidence of a greater number of area-adjusted pecks in contrasted than plain (p = 0.0003) and bright (p = 0.0083) treatments (table 3.3). There was no evidence of a statistically significant difference between the models with brighter tails and the plain-tailed controls (p = 0.2956). These results are summarised in Fig 3.12.

Table 3.3 Pairwise comparisons of predicted means for area-standardised pecks (natural log-transformed pecks per 10,000 pixels) between treatments for each body part of model Raukawa geckos. The standard error is 0.2746. P-values were calculated on 261 degrees of freedom. p-values are indicated as follows $p<0.001***$, $p<0.01**$, $p<0.05*$, $p<0.1$'.

Body part: Tail	Effect size and direction	t	p
Plain vs Bright	0.2750	-1.6250	0.1054
Plain vs Contrasted	0.5914	-3.4940	0.0006***
Bright vs Contrasted	0.3163	-1.8690	0.0627'
Body part: Head and neck			
Plain vs Bright	-0.0945	0.5585	0.5770
Plain vs Contrasted	0.1887	-1.1179	0.2659
Bright vs Contrasted	0.2832	−1.6733	0.0955'
Body part: Body			
Plain vs Bright	-0.1351	0.7979	0.4256
Plain vs Contrasted	0.2954	-1.7450	0.0822'
Bright vs Contrasted	0.4304	-2.5429	0.0116*
Body part: Limb			
Plain vs Bright	0.1774	-1.0479	0.2956
Plain vs Contrasted	0.6275	-3.7072	0.0003***
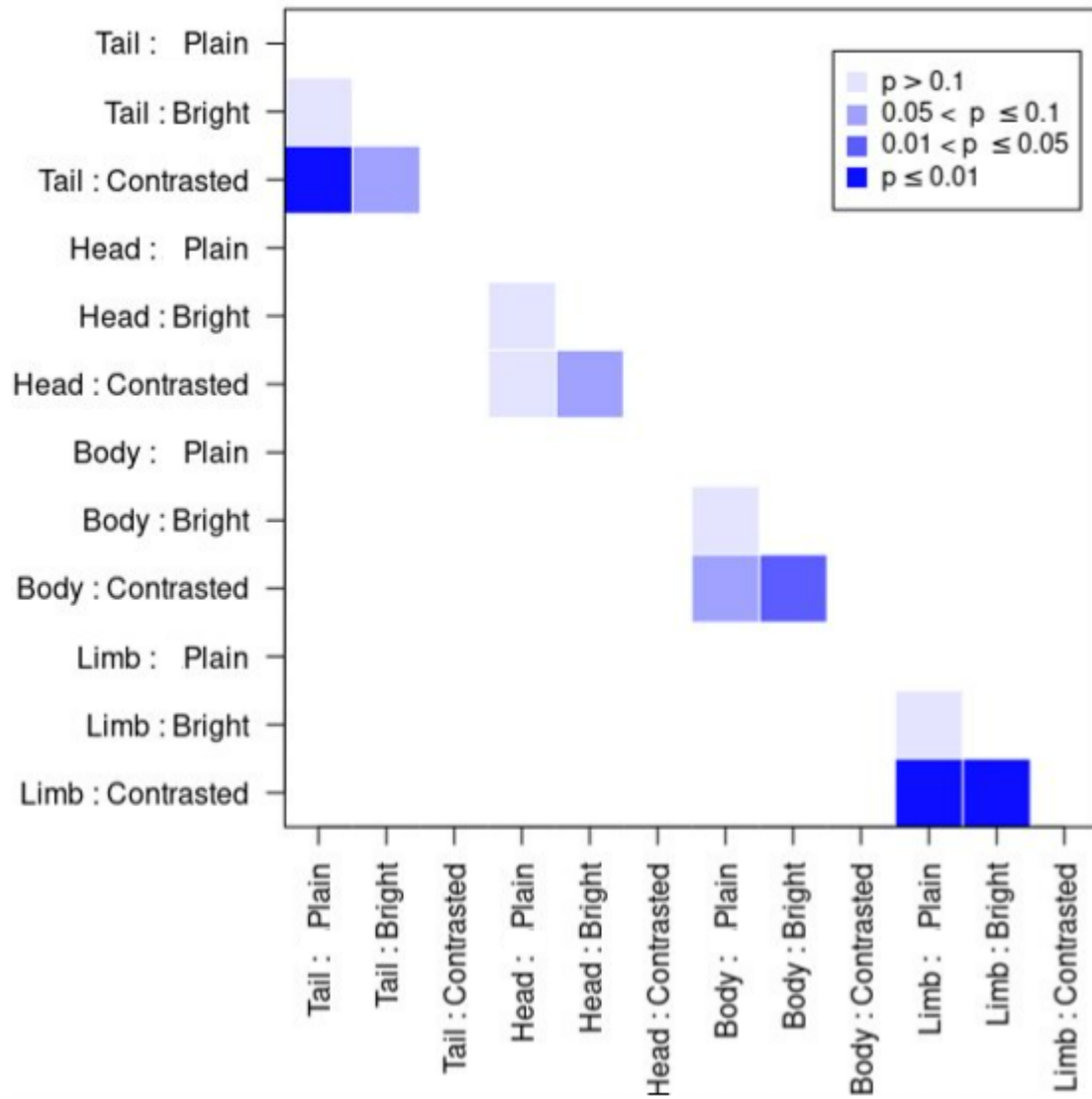
Figure 3.12. Pairwise comparisons comparing differences in pecks (adjusted for area) between treatments within a body part.

How do mean pecks by area differ from predicted means?
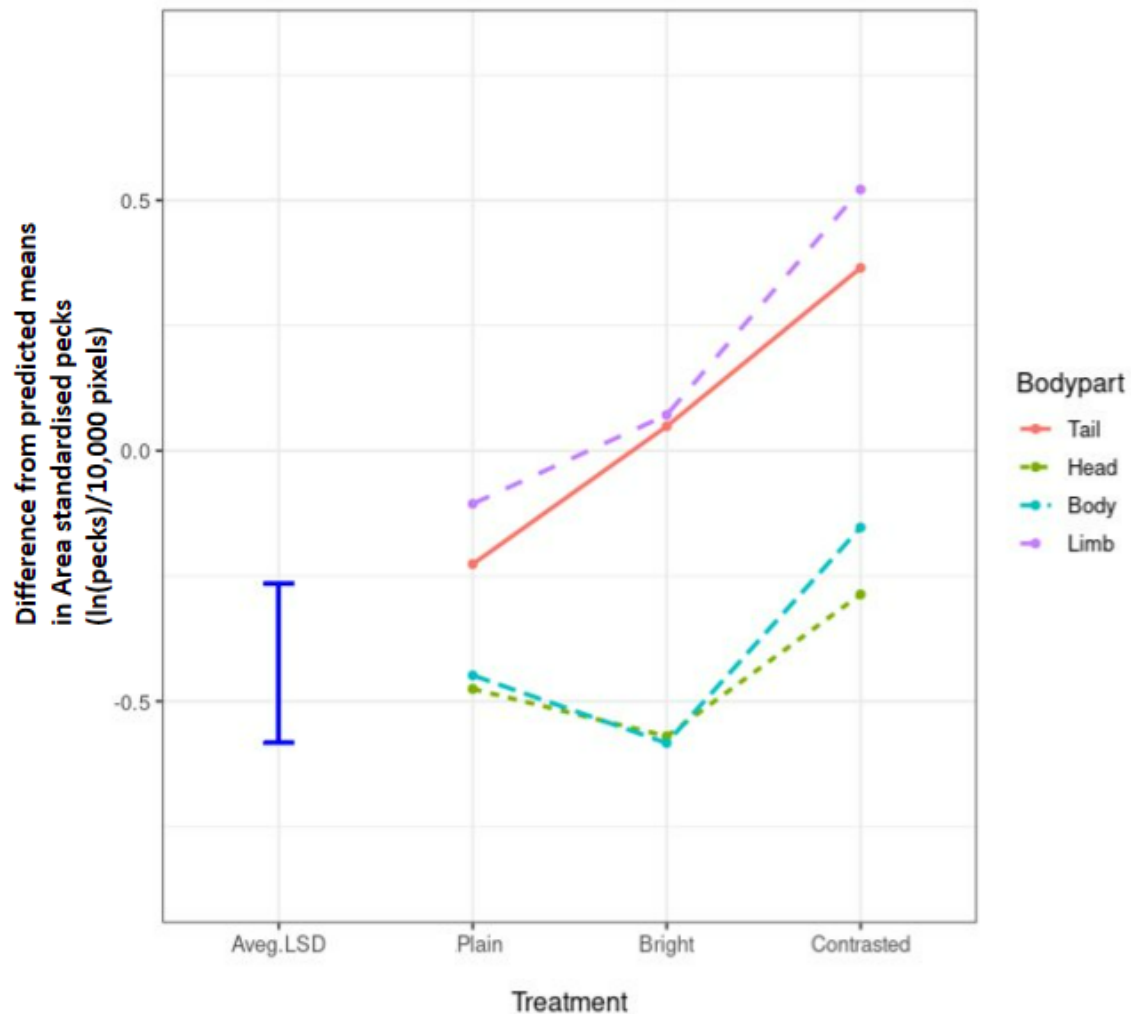
Figure 3.13. Difference from predicted means for each treatment by body part with the average Fisher's unprotected least significant difference (significance level 0.05) marked as a bar in blue on the left-hand side of the chart.

The predicted mean number of pecks for each treatment is higher for the tail and the limbs than for the body and head, but that the difference is greater for the bright tail, and particularly the contrasted tail treatments, than for the plain-tailed control (Fig 3.13). For all treatments the predicted mean pecks for the head and body are lower than would be expected for the head and body if all body parts and treatments were equal.

Within each treatment, the predicted mean number of pecks was highest in the tail and limbs (fig. 3.13; Appendix 3F). However, the magnitude of these differences varied between treatments (fig. 3.13). The limbs of Control models had significantly more pecks than heads ($p = 0.010$) and bodies ($p = 0.016$; fig. 3.13; Appendix 3F). There was weak statistical support for a greater number of area-adjusted pecks to the tails than the heads in Control

models (*p* = 0.079), with the limbs and tail receiving the most pecks (fig. 3.13; Appendix 3F). The limbs and tails of Bright models received significantly more pecks than the heads and bodies (all p < 0.001; fig. 3.13; Appendix 3F), with higher levels of statistical significance than for the control models. The limbs and tails of Contrasted models also received significantly fewer pecks than the heads or bodies (all p < 0.001), but the magnitude of these differences may have been greater than in the Bright models (fig. 3.13).

Side note
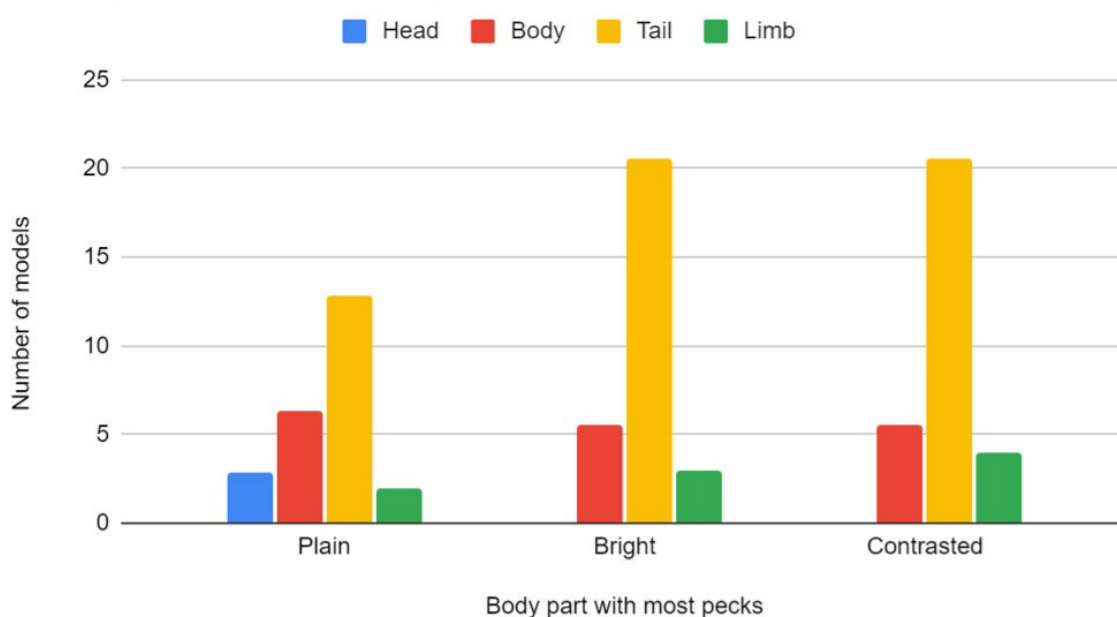
Figure 3.14 Body part with the most pecks. NB: not all models received pecks. Plain - 24/30 received pecks, Bright - 29/30 received pecks, Contrasted - 30/30 models received pecks.

The number of pecks found on the models were highly variable. To combat this large variability in number of peck marks, I also looked at which body part had been pecked the most for each individual model, and found that the tails of both the brighter and more contrasted models were pecked the most in approximately 1.3x more of the models than in the models with plain tails, when adjusted for differing numbers of models pecked (fig 3.19, table 3.10). I also found that the most frequently pecked body part in both the brighter and the more contrasted was never the head, while it sometimes was in the plain models. In terms of the body, this was the most pecked area for similar numbers of models between treatments, while for the limbs, this was the most pecked in slightly more of the bright and contrasted models.

Table 3.10. Body part with most pecks, as a ratio against the plain-tailed controls.

Treatment/Body part	Plain	Bright	Contrasted
Head	1	0	0
Body	1	0.72	0.69
Tail	1	1.32	1.28
Limb	1	1.24	1.60

3.4 Discussion

Fewer plain-tailed models received pecks, but those that did received fewer pecks to the tail and limbs than contrasted-tailed, with weaker evidence of plain-tailed models also receiving fewer pecks across the whole body than bright-tailed models (fig 3.10, Table 3.3). This suggests that a contrasted tail is more effective than a bright tail in luring the birds that interacted with the models in this study (blackbirds and thrushes) towards the tail. While more bright-tailed and contrasted-tailed models received pecks, more of these pecks were received to the tail and limbs than to the head and body (fig 3.11; Appendix 3F). As the models with contrasted tails attracted more pecks, there is an evolutionary trade-off between luring the avian predator to a specific body part when the gecko has already been detected, and overall conspicuousness to the avian predator. This supports the idea that changing colour in the tail to become more conspicuous through increasing contrast in times of danger, rather than continuously having a more contrasted tail, would be advantageous. Continuously brighter or more contrasted tails attract more attention in the form of more pecks across the whole body, though the evidence for a statistical difference was weak for brighter tails. Maintaining more cryptic colouration until detected may avoid some detections, but once detected, the gecko can change colour to attract attention towards the tail and away from vital body parts. The limited trail camera footage that showed where the pecks were occurring supported this idea, however there was insufficient evidence from trail camera footage alone due to the limited number of such photos captured. As such, the peck data captured through marks in the clay was vital to the results. While the trail camera footage provided limited information on where the pecks were occurring, it did show which species were interacting with the models in this study.

3.4.1 Trail camera footage

Nine species of birds were caught on camera. This compares with 5 minute bird count data from the area indicating the presence of 16 species of bird (Florence-Bennett, 2020) and iNaturalist research grade records of 9 species (iNaturalistnz, 2021), with some of the species overlapping

those recorded by Florence-Bennett (2020), and some species recorded likely being infrequent visitors to the area. Ray and McArthur (2018) found 20 species of bird over the entire Miramar peninsula, of which 11 were native, and 9 introduced. Between the above sources, and the trail camera photographs, 22 species of bird have been recorded for the sites, of which 5 are known lizard predators (Appendix 3D).

Only one of the known lizard predators from the area was observed on camera to be pecking the model, the blackbird. However, another species, the song thrush was also captured on camera pecking the model. This species is not recorded as a known lizard predator yet in New Zealand or overseas, and its known diet consists of invertebrates and fruit (MacFarlane et al., 2016; Chaplygina et al., 2019). While this may simply be an example of exploratory behaviour, it would be interesting to undertake dietary research to investigate whether the song thrush is indeed a lizard predator in New Zealand, especially given that blackbirds, a member of the same genus, are a lizard predator.

Blackbirds, the species that most interacted with the models, are already known skink predators (Nilsson et al., 1994), but have not been described as gecko predators in the literature. The data would appear to indicate that blackbirds prefer the plain tailed model, but the 35 photographs of blackbirds, or perhaps one blackbird, pecking a plain-tailed model were all captured by one camera for one model during one trial. Therefore, the power of this information is low, and greater sampling would be needed to be able to draw conclusions from trail camera data. In addition, blackbirds' frequent movement and flight over distances of tens to hundreds of metres (Burrows, 1994) indicates that to get a better idea of the behaviour of different individual blackbirds, I would either need to be able to individually identify them (e.g. through bird bands), or have the models spaced further apart. On the other hand, Raukawa geckos often show strong site fidelity to very small home ranges (Whitaker, 1982; Green, 2001; Lettink, 2007). For a long-lived species (van Winkel et al., 2018) that utilises a small area, perhaps there is a greater need for cryptic colouration to avoid detection by avian predators.

Other photos captured birds blocking the models, where the bird was standing between the camera and the model and bending down towards it, but because of the camera angle and bird's position, it could not be seen whether or where they were pecking the model or just looking at it. Three species were captured on camera blocking the model: Blackbirds, Song Thrushes and Greenfinches (*Carduelis chloris*). In the case of Greenfinches, these are not known lizard predators, and may have been seeking invertebrates attracted to the models

(Florence-Bennett, 2020), which they commonly eat in addition to their main food source of seeds (Angus, 2013).

Native birds did not interact with the models on camera during my experiments, but they may under different circumstances, or camera settings. Based on reported encounter rates, Miramar Peninsula is dominated by introduced species of birds (Ray & McArthur, 2018), so perhaps this result is in line with a reduced local abundance of native birds compared with introduced species.

There were also 441 pictures of mice, which is more than the number of photographs captured of birds (364). These photographs showed mice, a known lizard predator, spent a lot of time crawling over and eating clay from the models. Mice were not found in the same photos as birds, and while mainly seen in photos captured during the night, were also seen in daytime photographs. Conversely, most photos of birds were captured during the day. As mice are known to also predate on eggs and chicks (Cuthbert & Hilton, 2004; Dilley et al., 2015; Moors, 2008), they may also affect the local native bird populations, especially given that many of their own predators are being controlled/eradicated on Miramar peninsula, and much of the vegetation is low to the ground making any nests there easier to access. Future research could look into interactions between mice and birds, and also into whether there was any pattern to the location of biting and scraping marks left by mice on the models. This could provide some insight into whether brighter or more contrasted tails impact predation by mice.

Due to the nature of the set-up, where for human privacy reasons a series of three photos one second apart after a movement was sensed by the camera was used instead of video to capture attacks, few (38) photographs of birds pecking models were captured. This is likely because the bird moves quickly to peck and is only in contact with the model very briefly during a peck movement. In addition, birds frequently stood between the camera and the model, thereby blocking the view of the model. As such, the chance of capturing the bird in the optimum position for photography during the split second in which the bird is in contact with the model is very low. Future research should consider placing several cameras at different angles for each model, and using video to attempt to better capture pecking sequences. Alternatively, a camera could be fixed directly above the models, if this did not deter the birds.

One factor influencing the number of photographs captured was vegetation movement and wind. Due to the high levels of wind in the area (WCC & Eagle Technologies, 2012/2017), and the low height and stem circumference of available vegetation for affixing the cameras, the

cameras frequently moved in the wind, meaning that the model lizard was not always in the frame of the photographs captured. Future studies could attach the cameras to fixed locations, e.g. by attaching them to warratahs or otherwise anchored tripods, to minimise movement of the cameras, and to better capture the lizard models in each frame.

3.4.2 Peck marks on lizard models

Though there was weak evidence that there might be more pecks to the head in contrasted than bright treatments, the number of pecks observed to the head were similar between the control and the treatments (Table 3.3, fig 3.11), suggesting having a brighter or contrasted tail did not result in extra pecks to the head, when compared with the control. There was also no evidence of a brighter or more contrasted tail resulting in extra pecks to the body for bright-tailed treatments, and only weak evidence of such a cost for contrasted-tailed treatments. While there was very strong evidence for greater levels of area-adjusted pecks in both the limbs and the tails of bright and contrasted-tailed models, it is likely that in a living gecko the limbs would be more difficult for an avian predator to peck. This is because the gecko is likely to attempt to take action to prevent their limbs from being pecked, and to move their tail in a way that attracts the predator's attention. Movement of the tail, as I have observed both species of gecko to do, is likely to further increase the likelihood of the tail being pecked. This is both through the movement being distracting, and through making it more difficult for the bird to reach the limbs.

While attacking the limbs might make it harder for the gecko to run away, it seems likely that the limbs would be a more difficult target to attack, being the smallest body part. It would be interesting to determine whether the other body parts are more difficult to grip for the beak of the bird, and whether other birds follow the same technique as the blackbirds and thrushes in this study. It would also be interesting to investigate whether birds continued to follow this technique if the lizard models were animated to behave like real lizards. In addition, it would be interesting to set up trail cameras to capture video footage of the birds interacting with the models from multiple angles, with a greater sample size of models and using more biodiverse sites to gauge the behaviour of other species of birds.

Given that a greater number of bright- and contrasted-tailed models were pecked than plain-tailed ones (Bright-tailed 29/30 (97%), Contrasted-tailed 30/30 (100%), Plain-tailed control 24/30 (80%)), it would not be advantageous to have a brighter or more contrasted tail continuously, as it may make the gecko more conspicuous. Greater conspicuousness in lizards is associated with decreased survival against avian predators (Husak et al., 2006; Marshall et al., 2015). This is also shown by the increased number of total pecks in the Raukawa gecko

models with brighter (only weak statistical evidence of an effect) and more contrasted tails (very strong evidence).

However, being able to change colour in the tail, perhaps through increasing brightness but particularly through increasing contrast, when already detected could be advantageous as it directs the bird's attention to the tail and makes this (disposable) area more likely to be pecked. The gecko then has a greater chance of escape by dropping its tail once the bird has pecked it. The tail continues to thrash about for some time afterwards, thereby potentially increasing the time the bird pays attention to the tail. Living geckos also wave their tails when under threat (pers. obs.), thereby potentially increasing the attention drawn to their tails, when compared with a stationary clay model. Thus, future research could also look into the added effect of movement, using robotic models.

A factor worth considering for future research is whether the size is important to signalling. While SVLs of up to 82 mm have been reported in Raukawa geckos (New Zealand Herpetological Society, 2007-2017), coastal individuals tend to be smaller than those from inland habitats and the largest Raukawa gecko recorded previously at this site was 72 mm (van Winkel et al. 2018; Herbert 2020). The models used in this chapter had an SVL of 68mm (the largest Raukawa gecko used for Chapter 2), and it may be that different results would be seen for models of a different size.

Visually oriented predators such as birds can impose strong selection pressure on lizards (Ruxton et al., 2018; Brandley et al., 2014). For example, on some islands where birds are the primary lizard predators, cryptic brown tails have evolved (Kuriyama et al., 2016). In that case, a brown camouflaged phenotype is more advantageous, as the visual acuity of the bird may allow it to both distinguish the tail from the body and detect the lizard more readily with the blue tail that can be found in areas with a different suite of predators (Kuriyama et al., 2016). Likewise, there are no lizards with blue tails in New Zealand, a land where lizards evolved with birds and reptiles as their primary predators. When tails are more conspicuous, they are more likely to be attacked by birds. This can be seen in captive falcons, which are equally likely to attack red- or brown-tailed lizard models, but attack the red-tailed ones more quickly, and are more likely to attack their tails (Fresnillo et al., 2015), as well as in blue or green coloured lizard tails with other species of birds (Castill, 1999, Hawlena et al., 2006, Watson et al., 2012, Bateman et al., 2014). In this way, a more conspicuous tail does present an effective decoy. However, continuously conspicuous tails also present a potential risk to the owner of the tail (e.g. Husak et al., 2006; Marshall et al., 2015; Kuriyama et al., 2016). A better approach could be to only make the tail

conspicuous when in imminent danger of attack. The most effective way of doing that, based on these experiments, is to increase conspicuousness through increased contrast. Future research could investigate whether, when tails are simultaneously both brighter and more contrasted, there is an additional protective effect. However, increased brightness on its own did not provide a protective effect as measured in area-adjusted pecks to each bodypart.

Chapter 4 - Discussion

4.1 Introduction

The colour of prey species as seen by predators affects both its detectability and its risk of being predated, particularly for predators such as birds that rely predominantly on vision for detecting prey items (Husak et al., 2006; Baling et al., 2016; Baling, 2017). Background colour has a strong influence on the ability of birds to discriminate the colours against them, e.g. for chickens (*Gallus domesticus*) to discriminate colours such as orange or green presented on orange or green backgrounds (Olsson et al., 2020). As a result, when an animal's colouration varies across its body, some body parts may be easier for predators to detect than others. Many lizards can autotomise their tails as an attempt to evade predation and conspicuously coloured tails that contrast with cryptic body colouration can be found in a variety of species that are subject to avian predation (Arnold, 1984; Cooper & Vitt, 1985; Vitt & Cooper, 1986; Hawlena et al., 2006; Kuriyama et al., 2016). In diurnal species, conspicuous tails tend to be brightly coloured, while in nocturnal species conspicuousness tends to be a result of contrasting bands (Hawlena et al., 2006). This results in a greater likelihood that avian predators will attack their tails ahead of other body parts, giving the lizard a chance to autotomise their tails and escape (Castilla et al., 1999; Ruxton et al., 2018). However, continuously having brightly coloured tails may expose otherwise cryptic individuals to increased risk of predation (Hawlena et al., 2006; Kuriyama et al., 2016). Drawing attention to the tail only once spotted by a predator, as opposed to drawing attention to oneself all the time, has clear potential advantages.

New Zealand lizards co-evolved with birds and reptiles as their predators (Worthy & Holdaway, 2002; King 2019). A common adaptation frequently used against avian predators used by many lizard species in New Zealand and overseas is autotomy - the ability to self-amputate their tails when under threat (Hare & Miller, 2010). That this strategy is effective can be seen in stomach content analyses of lizard predators, where sometimes only the tails are found (Lea & Gray, 1935; McKinney & Ballinger, 1966; Wiseman et al., 2019), and to some extent in the existence of surviving lizards who are missing all or part of their tails. There is evidence in at least one species of New Zealand lizard, the McCann's skink (*Oligosoma maccanni*), that they do not autotomise their tails in response to conspecifics pulling or biting their tails (J. Kelly, 2021). This is likely because it would not be advantageous to lose one's tail (used, amongst other things, to store fat and escape predators) to a conspecific who may be a competitor, but is not a predator.

Autotomy is thought to be used less by the more arboreal species than by the more terrestrial species, likely because the tail is used for gripping onto branches and its loss is a greater cost for arboreal species (Vitt et al., 1977). In windy areas, such as our study area, this cost is likely to be exacerbated. This is because when the wind moves the vegetation upon which the gecko is found, the tail may assist in maintaining the gecko's position and reduce the likelihood of a fall. The cost of losing one's tail can be significant, e.g. in *Naultinus gemmeus* it can take 1.5 years to regrow (Knox, 2014). However while there are costs to losing one's tail (see chapter 1), the cost of death resulting from a predation event is greater.

4.1.1 What was the knowledge gap addressed?

Little is known and understood about colour change in New Zealand geckos and what triggers a New Zealand gecko to change colour. When I retrieved ngāhere geckos from artificial retreats, they changed from black and orange to pale green and grey across their entire body. The reason for this colour change is not known in the literature, but may be related to increased levels of light or stress, or they may change colour to match background colouration. Upon retrieving Raukawa geckos from pitfall traps or onduline artificial cover objects, their tails became brighter and more highly contrasted. Both Raukawa and ngāhere geckos are able to autotomise their tails, however ngāhere geckos are more arboreal in nature and thus might less readily autotomise their tails. From my own observations of the individual ngāhere geckos I captured, fewer (3/30) had regrown tails or tail tips than of the Raukawa geckos (7/31) I captured for this study. However it may be that this is due to differing predation pressure, rather than differing habitat use or ecological niche. A larger sample size using multiple sites could investigate this further. As Raukawa geckos from my study site are mainly terrestrial, I hypothesised that the increased brightness and contrast I observed on the tails was an anti-avian predator defence, which would increase the likelihood of birds pecking the tail in a predation event. This combination of colour change and autotomy could be highly effective as an anti-predator defence against birds, the main predators that New Zealand geckos have co-evolved with the longest. Tail specific colour change in response to a predation threat likely increases the efficacy of the distracting tail strategy used by lizards to escape predation events, and has not previously been described in the global literature.

4.1.2 Research aims and questions

In Chapter 2 of this thesis, I aimed to determine (1) whether Raukawa geckos and ngāhere geckos changed colour in response to visual and auditory simulations of avian predator presence, and (2) whether the colouration of the body and tail regions differed in response to simulated predator presence.

In Chapter 3, I aimed to determine (1) whether wild birds would preferentially peck the tails of clay lizard models with bright or contrasted tails versus those of models with plain tails, and (2) whether a model with a relatively brighter or more contrasted tail would attract more pecks overall than a plain-tailed model.

4.2 Overview of findings by chapter

4.2.1 Chapter 2: Colour change in New Zealand geckos (Diplodactylidae) after simulations of avian predators

Based on the outcomes of a Principal Coordinates Analysis, four variables were considered as potential measurements of a skin colour change response to predator presence: brightness, contrast, hue, and saturation. While variation was observed, there was little evidence that skin brightness, hue, or saturation of Raukawa geckos or ngāhere geckos changed in response to visual or auditory simulations of predator presence. There was weak evidence that contrast increased across the whole body of ngāhere geckos after visual simulations of moreporks. While there was weak evidence of an increase in skin contrast across the whole body of Raukawa geckos after visual simulation of a nocturnal predator (morepork) flying overhead, a difference of greater significance was observed in response to the 'settling period'. While it may be that the settling period was too brief for geckos to adjust to the experimental conditions, it cannot be excluded that these results might be more suggestive of a non-response to the predator simulations. It may also be that the colour change only occurs at a later stage of the predation sequence, e.g. at the pursuit or capture stage, rather than at the approach stage.

Evaluation of model parsimony using Akaike's Information Criterion corrected for small sample size (AIC_c) suggested that distinguishing between the colour of the body and tail was unimportant for most trials on ngāhere geckos. The exception was for saturation in the trials of auditory stimuli. That is, the observed variation in colour appeared to be consistent across the body and tail for this species, an outcome that reflects the whole-of-body colour change previously observed in animals during capture and handling by researchers. In comparison, the AIC_c values of models constructed for Raukawa geckos suggested that distinguishing between the body and tail was important for explaining the observed variation in brightness and saturation. This partially tallies with my previous observations of colour change in the tails of Raukawa geckos being handled by researchers.

4.2.3 Chapter 3: Could rapid colour change by geckos be an effective defence against avian predators?

In Chapter 3, I found that across the entire model, clay models of Raukawa geckos with contrasted or brighter tails were pecked more frequently than uniformly-coloured (i.e 'plain-tailed') models. While this effect was only statistically significant in the contrasted-tailed models, there was also weak evidence of a difference between bright-tailed and plain-tailed models. In addition, a greater number of the contrasted and bright-tailed models received pecks than plain-tailed models. These results suggested that plain-tailed models attracted substantially less attention from wild birds than contrasted-tailed models, and may also have attracted less attention than bright-tailed models.

A greater number of pecks (standardised by dorsal surface area) were directed at the tails of contrasted- and bright-tailed models compared with the tails of plain-tailed models. This effect was statistically significant in the comparison between contrasted- and plain-tailed models and there was weak evidence of a difference between bright- and plain-tailed models. The number of pecks to the body and head were similar across all three treatment types, indicating that a brighter or more contrasted tail did not result in extra pecks to these body parts. However, the limbs of contrasted-tailed models were also subject to more pecks than the limbs of both bright-tailed and plain-tailed models.

While not useful for observing the interactions of wild birds with the clay models, the camera trap data suggested that the bird species leaving peck marks on the models were predominantly blackbirds and thrushes (family Turdidae). These birds are both exotic species that do not have a long co-evolutionary history with New Zealand-endemic geckos, and it is unlikely that their behaviour toward the models would provide a useful surrogate for native passerines. This is because only two native passerines are known to predate on lizards: the New Zealand pipit (*Anthus novaeseelandiae*) and the fernbird (*Poodytes punctatus*) (Florence-Bennett, 2020). The ecology and foraging strategy of these birds differs from that of blackbirds and thrushes, with both native species spending more time on the ground than the introduced blackbirds and thrushes (Beauchamp, 2022; Miskelly, 2022). This means that they would be less likely to detect lizards from a distance, as they do not fly as frequently as blackbirds and thrushes do. Blackbird and thrush behaviour towards the models may however be a useful surrogate if there are species of native birds that exhibit a similar foraging strategy.

This evidence supports the idea that caudal colour change after detection by an avian predator could be advantageous for geckos. It appears that a lizard with a permanently more contrasted and, to a lesser extent, brighter tail would draw more attention from blackbirds and thrushes. However, once detected, lizards with a more contrasted or brighter tail appear to attract more pecks to their tail

than a uniformly coloured lizard. It therefore seems plausible that rapid caudal colour change coupled with tail autotomy could be complementary strategies for evading avian predation.

4.3 Discussion

4.3.1 Using colour and tail autotomy to avoid predation: evolutionary trade-offs for New Zealand geckos

Nocturnal vs diurnal predators. Was there a differential response?

Previous studies have already shown that the suite of predators affects animal colouration and defensive strategies (Stuart-Fox et al., 2006; Kuriyama et al., 2020). It is also known that conspicuousness affects antipredatory behaviour (Cabido et al., 2009; Martín et al., 2009). Chapter 2 showed weak evidence that Raukawa geckos may have more contrasted tails after morepork flyovers. This would be consistent with Hawlena (2006), who stated that nocturnal species of lizards tended to have contrasted tails while diurnal ones tended to have brightly coloured tails, though for those lizards the colour was not as a result of rapid colour change, but a morphological adaptation relating to their activity period. Daytime field observations showed both increased brightness and contrast in Raukawa gecko tails, and while these results were not able to be replicated using the BACI approach in the laboratory setting, such a pattern might be detectable using a different approach with longer gaps between treatments. Kingfishers are mainly diurnal, while moreporks are mainly nocturnal. Raukawa geckos are mainly nocturnal, but will also both sun bask and cryptically bask during the day. If further experiments were to find a difference in response between nocturnal and diurnal predators, it could be that rapid colour change would allow them to achieve the best of both worlds, with brighter tails for avoiding predation by diurnal predators, and more contrasted tails for avoiding predation by nocturnal predators. Combining the ability to remain camouflaged when not under threat, and only adding brightness or contrast to the tail when under immediate threat, could provide the gecko with three complementary defences against avian predators.

This is particularly necessary for a species such as the Raukawa gecko that lives in a more open habitat with greater distance visibility and greater ease of gaining an overview for predators. Contrast this with the ngāhere gecko who lives in a forested habitat with poorer visibility, where visual performance of predators is limited both through reduced light levels (Boström et al., 2016) and through vegetation blocking long distance vision from above and from within the habitat. Habitat is an important consideration when considering the ability to and need for camouflage and colour change (Baling, 2016). The greater 3-dimensionality of the forest habitat, along with increased levels of structure may offer the ngāhere gecko more

opportunities for escape. When threatened by a predator, the ngāhere gecko may just drop to another part of the habitat and 'disappear' using colour change. This would mean the predator would need to renew its search for the gecko if it wanted to continue to pursue it, increasing the cost of attempted predation for the predator, and reducing the relative reward of continuing the pursuit. With habitat and colour change as advantages against predators, perhaps there is less need for autotomy in the ngāhere gecko.

Another factor affecting the need for camouflage and antipredator defences is the behavioural niche of the species. For example, at Turakirae Head, in the Wellington region of New Zealand, 92% of Raukawa geckos were found within 5m of previous sightings during an 8-year monitoring study, and only 0.4% of animals moved further than 20m (Whitaker, 1982). Strong site fidelity in Raukawa geckos may mean that camouflage and antipredator defences are particularly important. This is because the longer a predator looks in the direction of a cryptic prey item, the more likely that prey item is to be detected (Martìn et al., 2009). If a long-living prey item is restricted to using only a small area of habitat, that may increase the chances of being detected within that small area over its lifespan. For a Raukawa gecko, this lifespan may be more than twenty years in the wild (Bannock et al., 1999). To some extent Raukawa geckos compensate for this behaviourally, but if they are detected by a predator, they need a means of escape. If the predator attacks the tail, they have a chance of survival using autotomy. Increasing conspicuousness to the tail through colour change, increases the likelihood that an avian predator will attack the tail. It is likely that this is used in combination with other strategies, such as tail waving, which is often seen in Raukawa geckos either when captured by a human, or prior to autotomy (pers. obs.).
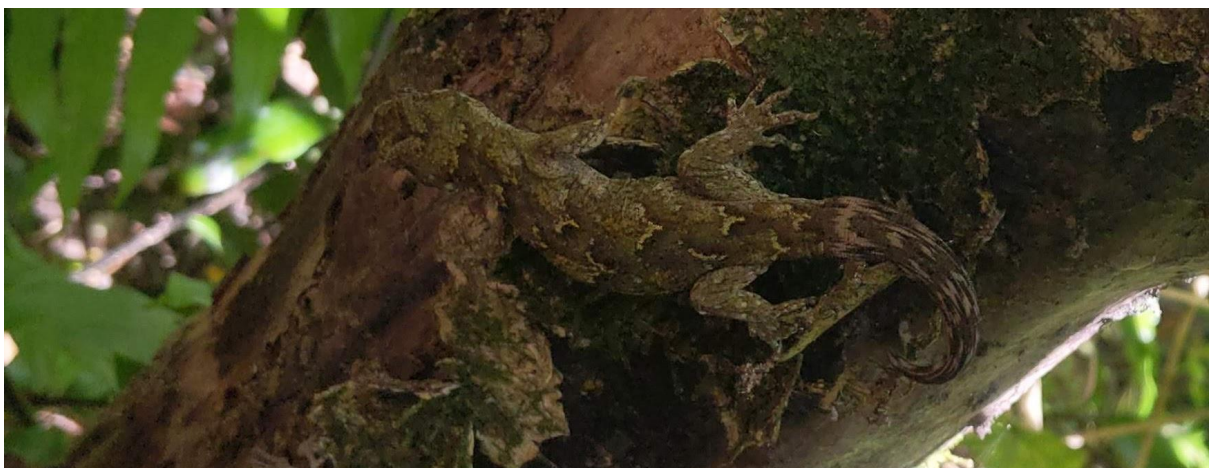
Figure 4.1 Close-up of ngāhere gecko (with regrown tail) against dead tree with peeling papery bark.

Figure 4.2 Close-up of ngāhere gecko on tree with rough bark.

Figure 4.3 Close-up of ngāhere gecko on forest floor amongst leaf litter.

Ngāhere geckos, on the other hand, are slow cruise foragers (Bauer, 2007). This means that they will spend some time moving from place to place, though they appear to stop when observed (Dennis Keall, pers. comm.). Movement increases risk of detection by predators such as birds (Cronin et al., 2014). However, ngāhere geckos are able to achieve excellent camouflage against a variety of different coloured backgrounds in the forest (pers. obs., figs 4.1-4.3, for further photographs see appendix 4.1). In addition, the greater arboreality of this species, and the high wind rating of Wellington means that it is likely to rely more on its prehensile tail for stability when moving through its habitat than a terrestrial species would. This means that the cost of tail loss for this species is likely higher than for the more terrestrial Raukawa gecko. This combination of circumstances means that the ngāhere gecko has more options before needing to resort to autotomy as a last line of defence.

4.3.2 Responses of birds to model prey colour differences

For avian predators, it is in their best interest to immediately kill or disable their prey, so that it has no further chance to escape (Florence-Bennett, 2020). Countering this is the lizard's interest to escape, and distraction using an autotomising tail is used by many species. In fleeing McCann's skinks (*Oligosoma mccannii*) photographed at 1/200 second, the head moved so rapidly that the head was blurred as a result of the speed of the movement (J. Kelly, 2021). The body was blurred to a lesser extent, while the tail was still sharply in focus, and the hind feet had not yet moved (J. Kelly, 2021). This behaviour would give a predator a greater chance of capturing the tail than the other body parts, due to the speed of movement alone. While the morphology and behaviour of skinks and geckos differ substantially, one overseas study found no substantial differences in the mechanics of locomotion of the western banded gecko (*Coleonyx variegatus*) and the western skink (*Eumeces skiltonianus*) (Farley & Ko, 1997). Skinks of the Wellington region are faster to move than geckos, but it would be interesting to determine whether Raukawa geckos and ngāhere geckos also follow the same pattern of movement as the McCann's skink, as this would add to the effect produced by the brighter or more contrasted tail once a Raukawa gecko decides to flee. Though movement may increase the likelihood of an initial detection (McClean et al., 2010; Cronin et al., 2014), a rapidly moving target is also more difficult to capture. 1/200 of a second is equivalent to 200Hz, which is faster than any bird tested so far can see without the image beginning to blur (Potier et al., 2020).

If Raukawa geckos follow the same sequencing of movement when beginning to flee as the McCann's skinks, this may also help to explain when birds might peck the limbs of stationary clay models. If the limbs and the tail are the last part of the body to move, and the bird has an understanding or previous memory of an autotomy experience, perhaps the bird has learned that pecking this area is more likely to successfully result in capturing the lizard.

Birds are thought to build a search image of prey items in their brain that they use to detect prey (Florence-Bennett, 2020). Some animals counter this with colour polymorphisms, while others have differential adult and juvenile life stages, and others still use colour change as a mechanism to impair the search efficiency of the avian predator (Poulton, 1884; Hawlena, 2006; Karpestam et al., 2014, 2016). In most diurnal lizards, only the juvenile's tail is brightly coloured, the lifestage in which those lizards have riskier behaviours (Hawlena et al., 2006). However, this also puts them at greater risk of being spotted (Arnold, 1984; Bateman et al., 2014; Fresnillo et al., 2015). Colour change could allow the Raukawa gecko greater flexibility to increase visibility in the tail when the gecko is at risk. It may be that the colour change process itself will also increase attention to the tail, i.e. the fact that the tail rapidly differs in appearance to that seen only moments before.

The vision of birds varies even between closely related species, with vision finely attuned to the niche and behaviour of the species, the challenges of their environment and how they use their senses to meet their needs (Martin, 2014; Potier et al., 2016; Martin, 2017a). Interestingly, it is thought that differences in visual abilities and adaptations are often reflected more in the anatomy and ecology of the species than in its phylogeny (Potier, 2020). Interspecific variation in foraging behaviour and tactics relating to scanning, prey detection, or capture are reflected in the visual abilities of birds (Martin, 2009; O'Rourke et al., 2010a; Fernández-Juricic, 2012; Potier et al., 2016). Subtle differences in tuning (i.e. being well adapted for one task), though, can have important implications for information gathering for a variety of purposes and can affect the behavioural ecology of the bird in other areas (Martin, 2017a).

However, there are some generalisations that can be applied (Martin, 2017a). Colour vision allows birds to better extract fine spatial details of the surrounding environment through differences in hue (wavelength), rather than relying on differences in intensity (which is highly correlated with brightness) (Martin, 2017a). These colours assist birds in behaviours such as foraging and sexual selection (Lind & Kelber, 2009). Some birds appear to show some colour preferences, e.g. Nectarivorous and frugivorous tend to feed on red and yellow fruits and flowers, while insectivorous birds prefer green over yellow caterpillars, but find them more difficult to detect (Kelly et al., 2010; Hernández-Agüero, 2020). However, it may be that contrast with the surrounding environment also increases the interest of birds in feeding or exploratory behaviour. For example in birds that predate lizards, birds were more likely to peck blue coloured parts on models (Watson et al., 2012). When the tail was the bodypart that was brightly coloured, birds were more likely to attack green-tailed models than brown-tailed models, more likely to attack the tails of blue-tailed models and the head and body of plain-tailed

models, attacked red-tailed models more rapidly than brown-tailed models and were more likely to attack the tails of red models, and plain brown tails tended to evolve on islands where birds are the primary lizard predator (Castilla, 1999, Bateman et al., 2014; Fresnillo et al., 2015; Kuriyama et al., 2016). Many predatory birds have high visual acuity, and thus on such islands a brown camouflaged phenotype is more advantageous to reduce avian detection probability (Kuriyama et al., 2016).

A further consideration is a bird's coordination of its body with its visual abilities. The accuracy of positioning and timing the arrival of the bodyparts used for foraging, the bill and the feet, utilises inputs for the optic flow-field in the binocular area surrounding the bill (Martin, 2017). Notwithstanding interspecific variation, inputs from close to the bird utilise vision that has relatively low spatial resolution, while predatory and prey detection relies on inputs detected from further away and utilise retinal regions with higher spatial resolution (Martin, 2014; Martin, 2017). This means that once the bird is close to the prey, it may be more difficult for it to focus well. This would add to the efficacy for Raukawa geckos of making the tail brighter or more highly contrasted, and to the efficacy for ngāhere geckos of dropping to another level within the forest and disappearing using camouflage. While there may be a trade-off between rapid vision and high visual acuity, with rapid vision perhaps the more common type in birds, ambient light levels place the ultimate limits on vision (Boström et al., 2016). Variation in the natural environment affects colour and perception through air clarity, which is affected by particulate matter and water vapour, and the proximity of a water body or vegetation such as a canopy can also affect the light environment through changes in light reflection and spectral distribution (Martin, 2017a).

4.4 Study limitations and future research directions

While I was not able to induce the dramatic colour changes observed in the wild in a laboratory setting, it is possible that in these geckos either a) colour change may not be a response to a threat of predation, or b) the frequency and quantum of colour change these geckos can achieve following previous colour changes are limited. Colour change provides opportunities for flexibility in behaviour and habitat use, but may be costly (Rodgers et al., 2013; Alfakih et al., 2022). While treatment was randomised in the colour change study, it may be worth investigating whether geckos are limited in either the frequency or quantum of colour change they can or do achieve after previously having changed colour. It would be possible to analyse this from the data I have collected, and this could be a subject of future research. Further research could also investigate, and perhaps quantify, the nature of any cost of colour change in New Zealand geckos.

While attempts were made to limit stress to the geckos through the study design, and the geckos were observed for signs of visible stress such as deep breathing or fainting, it is possible that the geckos were still stressed despite not showing these obvious symptoms. Stress influences colour, and if the geckos were still stressed, it may have affected the outcomes of this study.

I had no information on how long it takes geckos to recover or return to any baseline colouration (if this exists) from simulations of predators. Baseline colouration is also likely to vary based on environmental conditions. If recovery took more than the five minutes I gave them between treatments, this may have affected the before treatment comparison, and possibly also the after treatment comparison. When designing the experiment, I decided not to include taking blood samples to measure corticosteroid hormone levels in the design, as to avoid adding stress to the geckos and potentially affecting experimental outcomes.

The gecko experiments took place under controlled laboratory conditions in a glass aquarium. This is very different from the conditions experienced by geckos in the wild, and under natural light spectra. How the geckos would behave in the wild is still unknown and would be difficult to test. I initially designed the experiment to also have a field component, however this proved difficult due to geckos escaping in the field. Geckos are also difficult to detect, and adding transmitters or similar would increase their detection probability by both humans and birds. In addition, the backpack transmitters used in most studies will make it more difficult for geckos to fit into tight spaces, thereby further exposing them to predation. Pit tags are not very suitable for use in geckos due to the nature of their skin (N. Nelson, pers. comm.). Future research could measure the light spectra in the field, and attempt to mimic them and field conditions within a laboratory setting. Alternatively, as tracking technologies improve, other in situ options may become available over time.

The effects of circadian rhythm were not measured, but are known to affect lizard colouration, e.g. in Bearded dragons (*Pogona vitticeps*) (Fan et al., 2014). The effects of season were also not possible to measure due to the small number of lizards sampled. Future research could look into these areas, if a sufficient sample size could be achieved. This is more likely to be possible for Raukawa geckos.

The next steps would be to analyse the full data set and determine whether any further patterns become apparent, consider co-variates such as light levels, temperature, and humidity, and analyse the experimental data for other factors, e.g. light, temperature, colour of the background, and timescale. Anecdotal evidence suggests that for one species of New Zealand gecko, humidity may be a factor related to colour change (Chukwuka, pers. comm.). Another consideration could be to further increase the sample size and consider whether there is an influence of sex, reproductive status, or age, though availability of geckos may be a limiting factor. Females are likely to be under different pressures than males due to the additional

burden of long pregnancies, which result in reproductive female geckos of several NZ species maintaining higher body temperatures than other adults (Rock et al., 2000; Knox, 2014; Cree & Hare, 2016; Bertoia et al.,2021), and may increase their risk of predation through additional basking needs and lower mobility (Husak, 2006; Knox, 2014). In addition, it would be interesting to compare the individual colour patches on the body, and the dorsal and ventral surfaces, as the geckos are not uniformly coloured across the dorsal surface, and the ventral surface exhibits countershading.

Another area to investigate when considering the visual capabilities of avian and reptilian predators is the potential role of UV in colour change. The visual acuities and spectral sensitivities of birds are different to those of humans. Future work could analyse the visual acuity and spectral sensitivities of kingfishers and moreporks, and determine whether they are Violet or UV-sensitive. No UV camera was available for this research, and I elected not to use a spectrometer due to the instrument requiring close proximity to the gecko's skin. Placing a spectrometer close to the skin of the gecko would likely have disturbed them and affected experimental results. Future research could use a UV camera if one was available. In addition, biofluorescence could be considered, by shining a UV torch on the geckos and measuring whether there is a fluorescent response. A further area to consider is the ambient spectra of light available in the habitat and how these affect the vision and visual acuity of avian predators. Ngāhere geckos live in forested environments with dappled light and reduced light levels compared to the bright, relatively open coastal environment of the Raukawa geckos in this study. While a forested area provides a relatively low light environment, coastal areas can be intensely bright, especially as light is also reflected from the surface of the sea. Both of these are challenging visual environments for avian predators, but for differing reasons. Further, it would be interesting to investigate whether the avian predator species simulated in the experiments respond differently to the blackbirds and thrushes that interacted with the lizard models. This could be of particular interest given that the Raukawa geckos responded differentially to the morepork and kingfisher models, and that their tail colour responses to the nocturnal and diurnal predator respectively are consistent with the tail types often seen in nocturnal and diurnal species of lizards respectively.

Future research could also investigate whether there are colour responses of geckos to larger reptiles that might predate them, or to mammalian predators. While reptile and avian visual systems are often tetrachromatic, with high acuity, mammalian visual systems are usually di- or sometimes trichromatic, with lower acuity (Jacobs, 2018; Bowmaker, 1998). Mammalian predators are also blind to UV (Bowmaker, 1998), while the vision of some lizards (Pianka & Vitt, 2003) and many birds is known to encompass UV wavelengths (Dawson, 2006). Given that mammalian predators have different visual spectral sensitivities compared with birds and they

also rely on smell to a greater extent than avian predators (Osorio & Vorobyev, 2008), this may affect the ability of geckos to camouflage against these predators, and the use of such camouflage, against a predator who may 'sniff them out' anyway. Recent coexistence with predatory mammals seems to have induced a shift among lizards from antipredator freeze behaviour towards greater activity (Monks et al., 2019), which may reflect the ineffectiveness of a freeze response to predators that rely on smell and have a different visual spectrum to birds and reptiles. As a result, birds and reptiles tend to rely more on their visual acuity for hunting, while mammals rely more on scent. There is some evidence that lizards change their behaviour over time when exposed to different predators e.g. differing colour change responses to different predators, reduction in freeze response when mammals are introduced; and when exposed to varying predation pressure (Cooper et al., 2004; Hoare, 2006; Stuart-Fox et al., 2008; Pafilis et al., 2009; Semegen, 2018; Monks et al., 2019; Schwarz et al., 2020; BeVier et al., 2021; Whiting et al., 2022). Future research could measure predation pressure, and compare different populations of each species under varying predation pressure to investigate whether these have an impact on colour change responses.

The birds that responded to the gecko models on camera were blackbirds and thrushes. No native birds were photographed interacting with the models, so the responses of native birds remain unknown. Future studies could utilise areas that contain more native birds and Raukawa geckos, e.g. Matiu-Somes Island. While captive studies could be more efficient, the behaviour of captive birds may differ from those of wild birds.

A living gecko moves its tail, especially when under threat of predation, or when about to autotomise its tail. Tail waving was observed both during the chapter 2 experiments and in the field. This behaviour may affect the responses of birds. Future research could use robotic tails to mimic this behaviour. Experiments could be performed looking at whether the movement and colour interact to affect pecking behaviour of the birds. A cross-designed factorial experimental design could be used.

Trail camera photographs from one camera per model were not an effective method for capturing pecking action due to both the rapidness of the action and birds frequently standing between the camera and the model. Future studies could better capture the pecking action using video and multiple cameras from different positions. While the clay models provided considerable information through peck marks, improvements in camera data could answer the biologically relevant question of where the birds pecked first. If a gecko was first killed with a peck to the head, it would not be relevant if the bird later pecked the tail more often.

4.5 Conclusions

This thesis has provided evidence of a potential mechanism for the field observations of increased brightness and contrast in the tails of Raukawa geckos to be used as an effective anti-predator defence against birds. However, while variation in colour was seen, laboratory experiments were unable to show a clear colour change response to simulations of avian predators. This may be the result of insufficient time between experiments, limitations to the frequency, quantum, and magnitude of colour change geckos can achieve, or it may be that the field observations of colour change were the result of another trigger such as changes in light, temperature, or stress levels. Nonetheless, this thesis provides the first experimental data on colour change in New Zealand geckos, and demonstrates some of the variation in colour expressed by New Zealand geckos through colour change.

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Appendix 2A - Trees on which ngāhere geckos were found, and invertebrates found under covers

Trees on which ngāhere geckos were found

I mainly captured the ngāhere geckos under foam covers on the trunks of mature trees such as *Pseudopanax arboreus*, *Knightia excelsa*, *Myrsine australis*, *Pittosporum eugenioides*, *Hedycarya arborea*, *Pittosporum tenuifolium*, *Melicytus ramiflorus*, frequently with climbers such as *Blechnum filiforme*, *Metrosideros perforata*, and *Microsorum pustulatum*.

List of invertebrates found under ngāhere gecko covers:

Spiders (e.g. *Cycloctenus* spp., *Cambridgea* spp.), velvet worms (*Peripatoides* spp.), leaf vein slugs including gherkin slugs (*Arthoracophorus papillatus*), millipedes including *Siphonophorida*, Wētā including Wellington tree wētā (*Hemideina crassidens*) and various cave wētā (e.g. *Neonetus* spp., *Hemiandrus* spp.), land planarians (e.g. *Australopacifica* spp.).

Appendix 2B - Plants and invertebrates found in Raukawa habitat

Plant species found in Raukawa habitat:

Shrubs
Coprosma repens
C. propinqua
Lupinus arboreus
Malva arborea
Melicytus crassifolius
Myoporum laetum
Phormium cookianum
P. tenax
Pimelea prostrata
Plagianthus divaricatus
Pseudopanax lessonii
Olearia solandri
Ozothamnus leptophyllus

Grasses such as
Ammophila arenaria
Bromus diandrus
Dactylis glomerata
Ehrharta erecta
Holcus lanatus
Lagurus ovatus
Lolium perenne
Poa cita

Vines such as
Calystegia soldanella
Muehlenbeckia complexa
Tetragonia spp.

Herbs such as
Apium prostratum
Atriplex prostrata
Cakile maritima
Plantago coronopus
Raphanus raphanistrum
Senecio lautus
S. elegans
Silene uniflora
S. gallica
Sonchus oleraceus

and various trifoliate legumes (*Melilotus indicus* etc.).

Invertebrates included spiders (e.g. *Salticidae, Steatoda capensis, Porrhothele antipodiana),* ground beetles (e.g. *Lebiinae*), rove beetles (*Staphylinidae*), burrowing bugs (*Cydnidae*), darkling beetles (*Tenebrionidae*), soldier flies (*Stratiomyidae*), Snails (e.g *Oxychilus*, *Cornu*), *Lepidoptera,* flies (e.g. *Sarcophagidae*), woodlice (*Armadillidiidae*), earwigs (*Dermaptera*), and Seed bugs (e.g. *Dieuches notatus*).

Appendix 2C - Principal Components Analyses
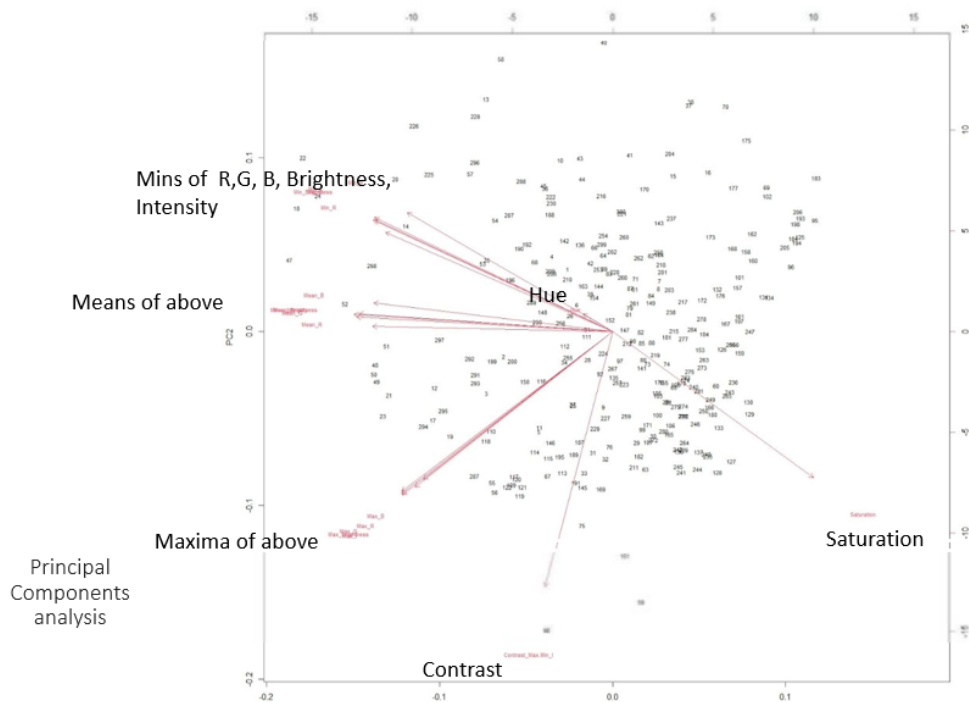
Fig.C2.1 Principal Components Analysis for colour components in photos of ngāhere geckos.

Principal component 1 (PC1) explains 64.23% of the variance, meaning that almost two-thirds of the information in the data set can be encapsulated in just that principal component. Principal component 2 (PC2) explains 21.26% of the variance, so if the position of a sample is known relative to PC1 and PC2, this position can be used to give an indication of where it stands in relation to other samples, as PC1 and PC2 alone can explain 85% of the variance of where it stands in relation to other samples.
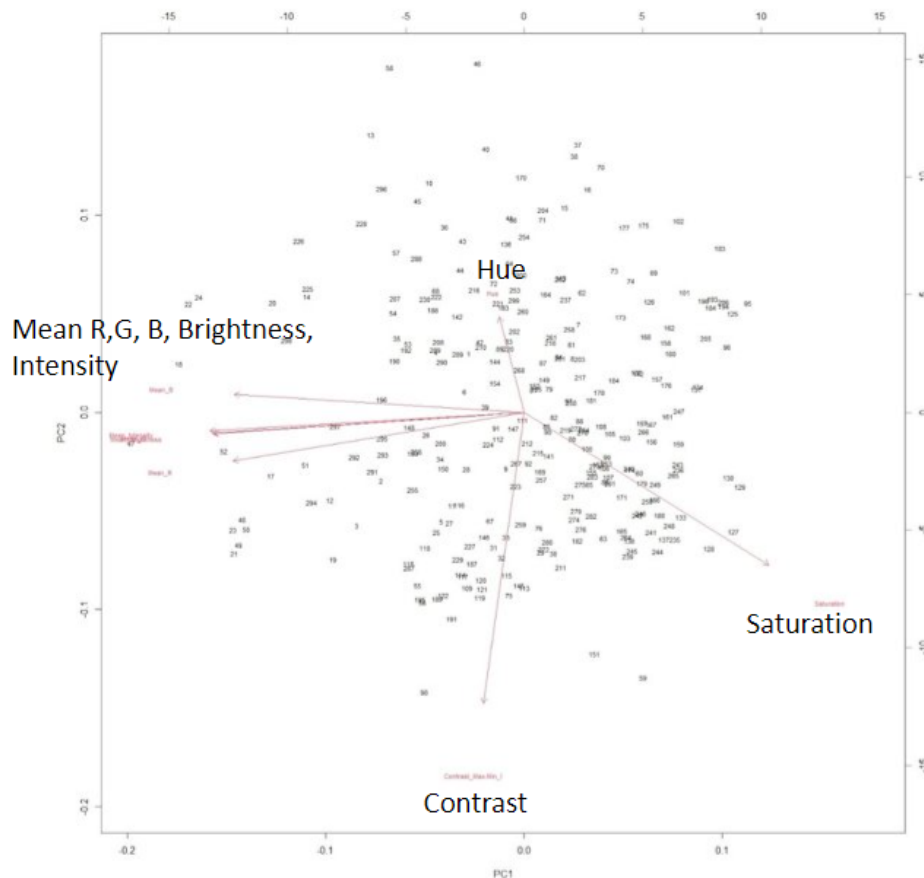
Fig.C2.2 Principal Components analysis for colour components in photos of ngāhere geckos after removing components that did not contribute much to the result.

These analyses show that:
1) The responses of (mean) R, G, B, Brightness, and Intensity are similar across all geckos.
2) The responses of Hue and Saturation are not grouped with any responses.
3) Hue does not contribute much to either PC1 or PC2, however it does contribute considerably to PC3 (87.93%), so I also investigated this factor.

As such, I focussed on Brightness (as a single variable showing similar responses to (mean) R, G, B, and Intensity), as well as Hue, Saturation, and Contrast which were not grouped with other responses.
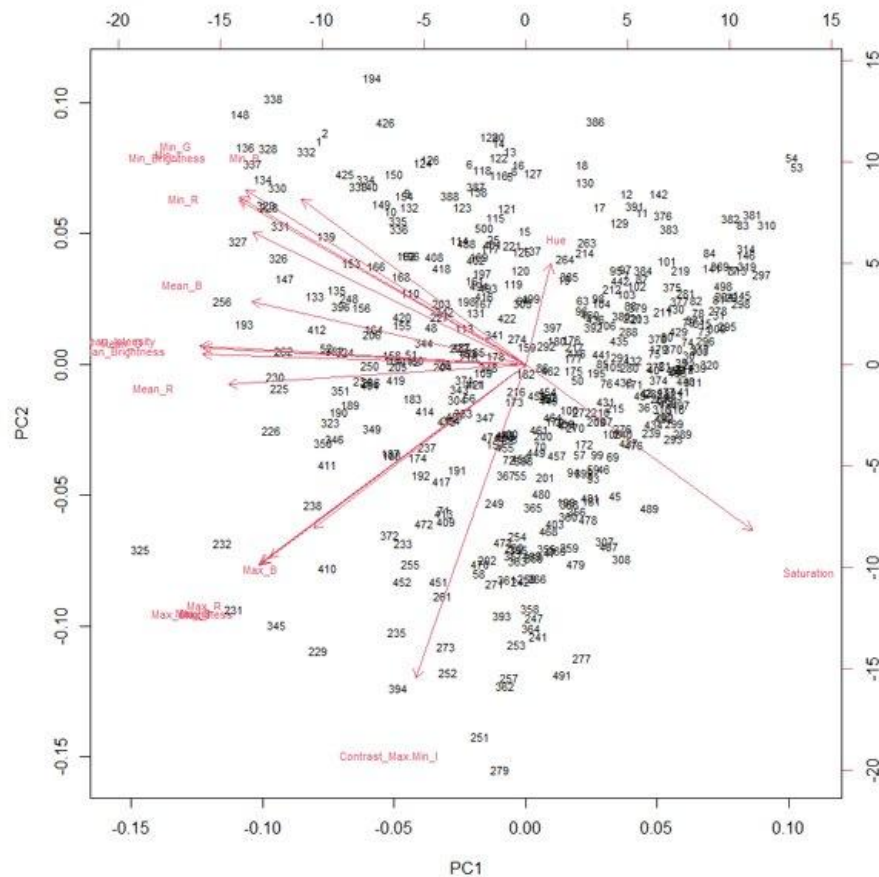
Fig. C2.3 Principal Components Analysis for colour components in photos of Raukawa geckos.

Principal component 1 (PC1) explains 60.05% of the variance, meaning that more than half of the information in the data set can be encapsulated in just that principal component. Principal component 2 (PC2) explains 22.38% of the variance, so if the position of a sample is known relative to PC1 and PC2, this can give an indication of where it stands in relation to the other samples, as PC1 and PC2 alone can explain 82% of the variance.
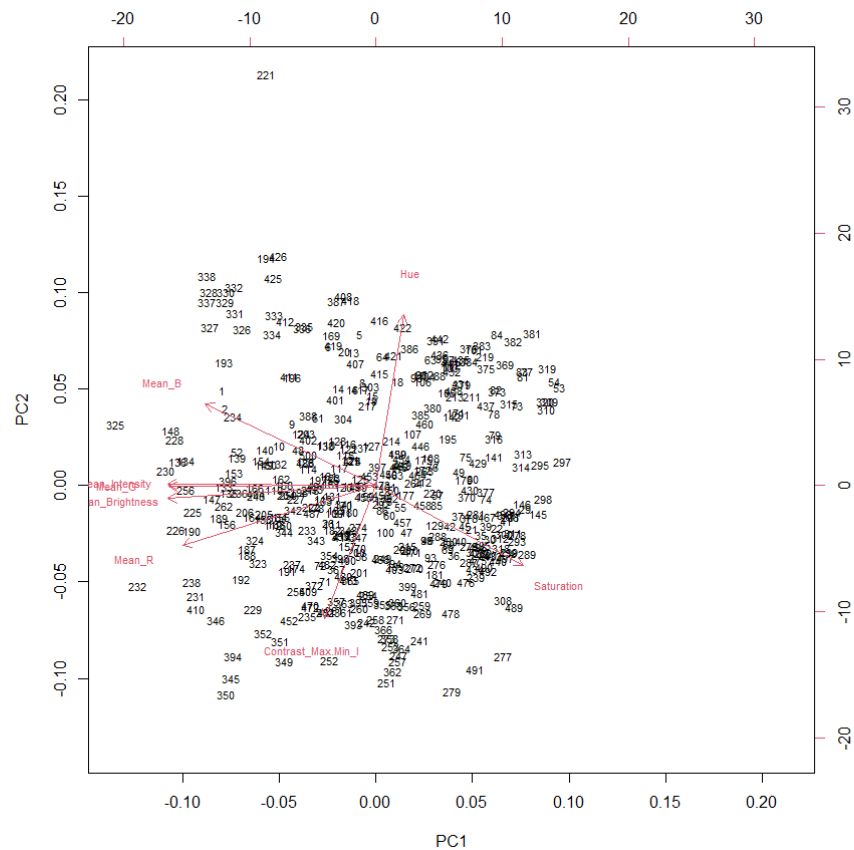
Fig C2.4 Principal Components analysis for colour components in photos of Raukawa geckos after removing components that did not contribute much to the result.

These analyses show that:
4) The responses of (mean) R, G, B, Brightness, and Intensity are similar across all geckos.
5) The responses of Hue and Saturation are not grouped with any responses.
6) Hue does not contribute much to PC1, however it does contribute to PC2 (67.64%) and PC3 (51.98%), so I also investigated this factor.

As such, I focussed on Brightness (as a single variable showing similar responses to (mean) R, G, B, and Intensity), as well as Hue, Saturation, and Contrast which were not grouped with other responses.

Appendix 2D - LMM model summary outputs and predicted mean tables comparing body and tail before and after treatments for more complex models (where supported)

Ngāhere gecko - visual simulations

Table 2.2a Estimates of the effect sizes of fixed factors from a LMM for the effect of visual simulations on the brightness of 15 ngāhere geckos. The model formula was Mean Brightness~ Treatment*BA+(1|Individual). The levels for the fixed factor *Treatment* were *Butterfly* (non-predator), *Fantail* (non-predator), *Kingfisher* (predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *BA* were *Before* simulation and *After* simulation. SE = standard error. *t* values (on 1 degree of freedom) that have a corresponding *p*-value of < 0.05 are indicated in bold.

Fixed factor	Estimate	SE(Estimate)	t
Butterfly (Intercept)	65.34	6.27	**10.43**
Fantail	9.05	5.19	1.74
Kingfisher	12.96	5.19	1.74
Morepork	-0.055	5.19	-0.01
Settling Period	1.27	5.19	0.24
After	7.73	5.19	1.49
Fantail × After	-12.52	7.34	-1.70
Kingfisher × After	-16.27	7.34	**-2.22**
Morepork × After	-6.58	7.34	-0.90
Settling Period × After	-9.59	7.34	-1.31

Table 2.3b Estimates of the effect sizes of fixed factors from a LMM for the effect of visual simulations on the contrast of 15 ngāhere geckos. The model formula was Contrast ~ Treatment*BA+(1|Individual). The levels for the fixed factor *Treatment* were *Butterfly* (non-predator), *Fantail* (non-predator), *Kingfisher* (predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *BA* were *Before* simulation and *After* simulation. SE = standard error. *t* values (on 1 degree of freedom) that have a corresponding *p*-value of < 0.05 are indicated in bold.

Fixed factor	Estimate	SE(Estimate)	t
Butterfly (Intercept)	149.90	6.72	**22.31**
Fantail	7.40	7.94	0.93
Kingfisher	-0.23	7.94	-0.029
Morepork	-15.70	7.94	-1.98
Settling Period	-6.53	7.94	-0.82
After	-4.93	7.94	-0.62
Fantail × After	-0.033	11.24	-0.003
Kingfisher × After	8.10	11.24	0.72
Morepork × After	18.63	11.24	1.66
Settling Period × After	3.63	11.24	0.32

Table 2.4b Estimates of the effect sizes of fixed factors from a LMM for the effect of visual simulations on the saturation of 15 ngāhere geckos. The model formula was Saturation ~ Treatment*BA+(1|Individual). The levels for the fixed factor *Treatment* were *Butterfly* (non-predator), *Fantail* (non-predator), *Kingfisher* (predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *BA* were *Before* simulation and *After* simulation. SE = standard error. *t* values (on 1 degree of freedom) that have a corresponding *p*-value of < 0.05 are indicated in bold.

Fixed factor	Estimate	SE(Estimate)	t
Butterfly (Intercept)	236.225	4.423	**53.405**
Fantail	-4.332	3.507	-1.235
Kingfisher	-8.483	3.507	**-2.419**
Morepork	-1.258	3.507	-0.359
Settling Period	-3.426	3.507	-0.977
After	-4.769	3.507	-1.360
Fantail × After	5.769	4.959	1.163
Kingfisher × After	10.479	4.959	**2.113**
Morepork × After	1.272	4.959	0.256
Settling Period × After	5.324	4.959	1.074

Table 2.5b Estimates of the effect sizes of fixed factors from a LMM for the effect of visual simulations on the hue of 15 ngāhere geckos. The model formula was Hue ~ Treatment*BA+(1|Individual). The levels for the fixed factor *Treatment* were *Butterfly* (non-predator), *Fantail* (non-predator), *Kingfisher* (predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *BA* were *Before* simulation and *After* simulation. SE = standard error. *t* values (on 1 degree of freedom) that have a corresponding *p*-value of < 0.05 are indicated in bold.

Fixed factor	Estimate	SE(Estimate)	t
Butterfly (Intercept)	53.73	11.19	**4.80**
Fantail	33.87	13.15	**2.58**
Kingfisher	23.36	13.15	1.78
Morepork	7.22	13.15	0.55
Settling Period	13.62	13.15	1.04
After	34.82	13.15	**2.65**
Fantail × After	-55.65	18.52	**-3.01**
Kingfisher × After	-51.09	18.52	**-2.76**
Morepork × After	-36.63	18.52	-1.98
Settling Period × After	-24.56	18.52	-1.33

Ngāhere gecko - auditory simulations

Table 2.7b Estimates of the effect sizes of fixed factors from a LMM for the effect of auditory simulations on the brightness of 15 ngāhere geckos. The model formula was Mean Brightness~ Treatment*BA+(1|Individual). The levels for the fixed factor *Treatment* were *Fantail* (non-predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *BA* were *Before* simulation and *After* simulation. SE = standard error. *t* values (on 1 degree of freedom) that have a corresponding *p*-value of < 0.05 are indicated in bold.

Fixed factor	Estimate	SE(Estimate)	t
Fantail (Intercept)	59.822	6.010	**9.953**
Morepork	7.119	5.097	1.397
Settling Period	6.796	5.097	1.333
After	6.546	5.097	1.284
Morepork × After	-8.367	7.209	-1.161
Settling Period × After	-8.403	7.209	-1.166

Table 2.8b Estimates of the effect sizes of fixed factors from a LMM for the effect of auditory simulations on the contrast of 15 ngāhere geckos. The model formula was Contrast~ Treatment*BA+(1|Individual). The levels for the fixed factor *Treatment* were *Fantail* (non-predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *BA* were *Before* simulation and *After* simulation. SE = standard error. *t* values (on 1 degree of freedom) that have a corresponding *p*-value of < 0.05 are indicated in bold.

Fixed factor	Estimate	SE(Estimate)	t
Fantail (Intercept)	142.100	7.155	**19.861**
Morepork	6.933	8.443	0.821
Settling Period	1.267	8.443	0.150
After	8.200	8.443	0.971
Morepork × After	-17.400	11.940	-1.457
Settling Period × After	-9.500	11.940	-0.796

Table 2.9b Predicted mean saturation of ngāhere geckos before and after each auditory simulation treatment from the model Saturation ~ Treatment*Bodypart*BA+(1|Individual). Figures in brackets are the standard error of the predicted means, while figures in square brackets are the 95% Confidence Intervals. P-values are generated from pairwise comparisons of *Before* and *After* values for Body and Tail after each treatment. P-values of less than 0.01 are indicated with an **. *p*-values were calculated on 154 degrees of freedom.

Treatment	Body	Tail	**t**	p
Fantail Before	240.27 (± 4.55) [231.28, 249.25]	230.09 (± 4.55) [221.10, 239.07]	2.2208	0.0278*
Fantail After	239.89 (± 4.55) [230.90, 248.87]	231.69 (± 4.55) [222.71, 240.68]	1.7871	0.0759'
Morepork Before	234.65 (± 4.55) [225.66, 243.63]	228.98 (± 4.55) [219.99, 237.96]	1.2366	0.2181
Morepork After	241.16 (± 4.55) [232.18, 250.15]	234.09 (± 4.55) [225.11, 243.07]	1.5435	0.1248
Settling period Before	235.56 (± 4.55) [226.58, 244.55]	230.04 (± 4.55) [221.05, 239.02]	1.2055	0.2299
Settling period After	234.99 (± 4.55) [226.01, 243.97]	231.72 (± 4.55) [222.74, 240.70]	0.7134	0.4767

Table 2.9c Estimates of the effect sizes of fixed factors from a LMM for the effect of auditory simulations on the saturation of 15 ngāhere geckos. The model formula was Saturation~Treatment*Bodypart*BA +(1|Individual). The levels for the fixed factor *Treatment* were *Fantail* (non-predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *Body Part* were *Body* and *Tail*, and levels for the fixed factor *BA* were *Before* simulation and *After* simulation. SE = standard error. *t* values (on 1 degree of freedom) that have a corresponding *p*-value of < 0.05 are indicated in bold.

Fixed factor	Estimate	SE(Estimate)	t
Fantail (Intercept)	240.266	4.548	**52.835**
Morepork	-5.620	4.583	-1.226
Settling Period	-4.704	4.583	-1.026
Tail	-10.178	4.583	**-2.221**
After	-0.380	4.583	-0.083
Morepork x Tail	4.511	6.482	0.696
Settling period x Tail	4.654	6.482	0.718
Morepork × After	6.899	6.482	1.064
Settling Period × After	-0.193	6.482	-0.030
Tail x After	1.987	6.482	0.307
Morepork x Tail x After	-3.394	9.167	-0.370
Settling period x Tail x After	0.268	9.167	0.029

Table 2.10b Estimates of the effect sizes of fixed factors from a LMM for the effect of auditory simulations on the hue of 15 ngāhere geckos. The model formula was Hue ~ Treatment*BA+(1|Individual). The levels for the fixed factor *Treatment* were *Fantail* (non-predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *Body Part* were *Body* and *Tail*, and levels for the fixed factor *BA* were *Before* simulation and *After* simulation. SE = standard error. *t* values (on 1 degree of freedom) that have a corresponding *p*-value of < 0.05 are indicated in bold.

Fixed factor	Estimate	SE(Estimate)	t
Fantail (Intercept)	58.354	12.217	**4.776**
Morepork	8.143	14.124	0.577
Settling Period	8.999	14.124	0.637
After	7.512	14.124	0.532
Morepork × After	-0.181	19.975	-0.009
Settling Period × After	2.748	19.975	0.138

Raukawa geckos - visual simulations

Table 2.12b Estimates of the effect sizes of fixed factors from a LMM for the effect of visual simulations on the brightness of 20 Raukawa geckos. The model formula was Mean Brightness~Treatment*Bodypart*BA+(1|Individual). The levels for the fixed factor *Treatment* were *Butterfly* (non-predator), *Fantail* (non-predator), *Kingfisher* (predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *Body Part* were *Body* and *Tail*, and levels for the fixed factor *BA* were *Before* simulation and *After* simulation. SE = standard error. *t* values (on 1 degree of freedom) that have a corresponding *p*-value of < 0.05 are indicated in bold.

Fixed factor	Estimate	SE(Estimate)	t
Butterfly (Intercept) x Body	50.08	6.45	**7.77**
Fantail x Body	4.92	5.46	0.90
Kingfisher x Body	4.82	5.46	0.88
Morepork x Body	-2.52	5.46	-0.46
Settling Period x Body	4.97	5.40	0.92
Tail	9.55	5.46	1.75
After	-0.31	5.46	-0.057
Fantail x Tail	-2.98	7.72	-0.39
Kingfisher x Tail	1.53	7.72	0.20
Morepork x Tail	-0.13	7.72	-0.02
Settling period x Tail	-0.17	7.63	-0.22
Fantail x After	-8.16	7.72	-1.06
Kingfisher x After	-0.13	7.72	-0.02
Morepork × After	7.82	7.72	1.01
Settling Period x After	2.89	7.63	0.38
Tail x After	-2.07	7.72	-0.27
Fantail x Tail x After	2.37	10.92	0.22
Kingfisher x Tail x After	1.61	10.92	0.15
Morepork x Tail x After	0.55	10.92	0.05
Settling Period × Tail x After	4.34	10.79	0.40

Table 2.12.c Predicted mean brightness of Raukawa geckos comparing the body and tail before and after each visual simulation treatment from the model Mean Brightness ~ Treatment*Bodypart*BA+(1|Individual). Figures in brackets are the standard error of the predicted means, while figures in square brackets are the 95% Confidence Intervals. P-values are generated from pairwise comparisons of *Before* and *After* values for each bodypart and each treatment. P-values of less than 0.01 are indicated with an **. Least significant difference and *p*-values were calculated on 365 degrees of freedom.

Treatment	Body	Tail	t	p
Butterfly Before	50.08 (± 6.45) [37.40, 62.75]	59.62 (± 6.45) [46.95, 72.30]	-1.7484	0.0812`
Butterfly After	49.77 (± 6.45) [37.09, 62.44]	57.24 (± 6.45) [44.56, 69.91]	-1.3686	0.1720
Fantail Before	54.99 (± 6.45) [42.32, 67.67]	61.56 (± 6.45) [48.88, 74.23]	-1.2025	0.2300
Fantail After	46.52 (± 6.45) [33.85, 59.20]	53.40 (± 6.45) [40.70, 66.06]	-1.2259	0.2100
Kingfisher Before	54.90 (± 6.45) [42.22, 67.58]	65.98 (± 6.45) [53.30, 78.65]	-2.0288	0.0432*
Kingfisher After	54.46 (± 6.45) [41.79, 67.14]	65.07 (± 6.45) [52.40, 77.75]	-1.9434	0.0527`
Morepork Before	47.55 (± 6.45) [34.88, 60.23]	56.97 (± 6.45) [44.29, 69.65]	-1.7248	0.0854`
Morepork After	55.06 (± 6.45) [42.39, 67.73]	62.95 (± 6.45) [50.28, 75.63]	-1.4456	0.1491
Settling period Before	55.04 (± 6.39) [42.47, 67.61]	62.90 (± 6.39) [50.33, 75.47]	-1.4755	0.1409
Settling period After	57.63 (± 6.39) [45.05, 70.20]	67.76 (± 6.39) [55.19, 80.33]	-1.9015	0.0580`

Table 2.13b. Estimates of the effect sizes of fixed factors from a LMM for the effect of visual simulations on the contrast of 20 Raukawa geckos. The model formula was Contrast ~ Treatment*BA+(1|Individual). The levels for the fixed factor *Treatment* were *Butterfly* (non-predator), *Fantail* (non-predator), *Kingfisher* (predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *BA* were *Before* simulation and *After* simulation. SE = standard error. *t* values (on 1 degree of freedom) that have a corresponding *p*-value of < 0.05 are indicated in bold.

Fixed factor	Estimate	SE(Estimate)	t
Butterfly (Intercept)	95.55	6.91	**13.84**
Fantail	-1.60	6.35	-0.25
Kingfisher	4.73	6.35	0.75
Morepork	4.50	6.35	0.71
Settling Period	2.44	6.28	0.39
After	6.60	6.35	1.04
Fantail × After	-8.58	8.97	-0.96
Kingfisher × After	2.45	8.97	0.27
Morepork × After	4.35	8.97	0.49
Settling Period × After	6.11	8.87	0.69

Table 2.14b Estimates of the effect sizes of fixed factors from a LMM for the effect of visual simulations on the saturation of 20 Raukawa geckos. The model formula was Saturation ~ Treatment*Bodypart*BA+(1|Individual). The levels for the fixed factor *Treatment* were *Butterfly* (non-predator), *Fantail* (non-predator), *Kingfisher* (predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *Body Part* were *Body* and *Tail*, and levels for the fixed factor *BA* were *Before* simulation and *After* simulation. SE = standard error. *t* values (on 1 degree of freedom) that have a corresponding *p*-value of < 0.05 are indicated in bold.

Fixed factor	Estimate	SE(Estimate)	t
Butterfly (Intercept) x Body	240.01	4.78	**50.22**
Fantail x Body	-3.33	4.33	-0.77
Kingfisher x Body	1.92	4.33	0.44
Morepork x Body	2.03	4.33	0.47
Settling Period x Body	-9.48	4.28	**-2.21**
Tail	-8.08	4.33	-1.87
After	3.33	4.33	0.77
Fantail x Tail	2.36	6.13	0.39
Kingfisher x Tail	0.50	6.13	0.08
Morepork x Tail	3.23	6.13	0.53
Settling period x Tail	1.93	6.06	0.32
Fantail x After	2.58	6.13	0.42
Kingfisher x After	-2.83	6.13	-0.46
Morepork × After	-3.38	6.13	-0.55
Settling Period x After	3.026	6.06	0.54
Tail x After	4.28	6.13	0.70
Fantail x Tail x After	-2.99	8.67	-0.35
Kingfisher x Tail x After	-7.91	8.67	-0.91
Morepork x Tail x After	-4.95	8.67	-0.57
Settling Period × Tail x After	-3.76	8.56	-0.44

Table 2.14c Predicted mean saturation of Raukawa geckos comparing the body and tail before and after each visual simulation treatment from the model Saturation ~ Treatment*Bodypart*BA+(1|Individual). Figures in brackets are the standard error of the predicted means, while figures in square brackets are the 95% Confidence Intervals. P-values are generated from pairwise comparisons of *Before* and *After* values for each bodypart and each treatment. P-values of less than 0.01 are indicated with an **. Least significant difference and *p*-values were calculated on 365 degrees of freedom.

Treatment	Body	Tail	t	p
Butterfly Before	240.01 (± 4.78) [230.61, 249.41]	231.93 (± 4.78) [222.53, 241.33]	1.8652	0.0630'
Butterfly After	243.34 (± 4.78) [233.95, 252.74]	239.54 (± 4.78) [230.14, 248.93]	0.8784	0.3803
Fantail Before	236.68 (± 4.78) [227.28, 246.08]	230.96 (± 4.78) [221.56, 240.36]	1.3197	0.1877
Fantail After	242.59 (± 4.78) [233.19, 251.99]	238.16 (± 4.78) [228.76, 247.56]	1.0226	0.3072
Kingfisher Before	241.93 (± 4.78) [232.54, 251.33]	234.35 (± 4.78) [224.96, 243.75]	1.7490	0.0811'
Kingfisher After	242.43 (± 4.78) [233.03, 251.83]	231.21 (± 4.78) [221.82, 240.61]	2.5887	0.0100**
Morepork Before	242.04 (± 4.78) [232.64, 251.44]	237.19 (± 4.78) [227.79, 246.59]	1.1198	0.2635
Morepork After	241.99 (± 4.78) [232.59, 251.39]	236.47 (± 4.78) [227.07, 245.86]	1.2751	0.2031
Settling period Before	230.53 (± 4.73) [221.22, 239.84]	224.37 (± 4.73) [215.06, 233.68]	1.4557	0.1463
Settling period After	237.12 (± 4.73) [227.82, 246.43]	231.49 (± 4.73) [222.18, 240.80]	1.3329	0.1834

Table 2.15b Estimates of the effect sizes of fixed factors from a LMM for the effect of visual simulations on the hue of 20 Raukawa geckos. The model formula was Hue ~ Treatment*BA+(1|Individual). The levels for the fixed factor *Treatment* were *Butterfly* (non-predator), *Fantail* (non-predator), *Kingfisher* (predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *BA* were *Before* simulation and *After* simulation. SE = standard error. *t* values (on 1 degree of freedom) that have a corresponding *p*-value of < 0.05 are indicated in bold.

Fixed factor	Estimate	SE(Estimate)	t
Butterfly (Intercept)	101.38	12.74	**7.96**
Fantail	10.08	10.53	0.96
Kingfisher	-7.42	10.53	-0.70
Morepork	-6.82	10.53	-0.65
Settling Period	-32.08	10.41	**-3.08**
After	1.16	10.53	0.11
Fantail × After	-21.26	14.89	-1.43
Kingfisher × After	-13.60	14.89	-0.91
Morepork × After	-4.88	14.89	-0.33
Settling Period × After	-11.14	14.71	-0.76

Table 2.17b Estimates of the effect sizes of fixed factors from a LMM for the effect of auditory simulations on the brightness of 20 Raukawa geckos. The model formula was Mean Brightness~ Treatment*Bodypart*BA+(1|Individual). The levels for the fixed factor *Treatment* were *North Island Fantail* (non-predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *Body Part* were *Body* and *Tail*, and levels for the fixed factor *BA* were *Before* simulation and *After* simulation. SE = standard error. *t* values (on 1 degree of freedom) that have a corresponding *p*-value of < 0.05 are indicated in bold.

Fixed factor	Estimate	SE(Estimate)	t
Fantail (Intercept)	51.88	5.99	**8.67**
Morepork	8.85	5.40	1.64
Settling Period	3.04	5.34	0.57
Tail	9.31	5.40	1.72
After	-1.01	5.40	-0.19
Morepork x Tail	-1.90	7.64	-0.25
Settling period x Tail	-1.45	7.55	-0.19
Morepork × After	-4.01	7.64	-0.53
Settling Period x After	3.69	7.51	0.49
Tail x After	0.47	7.64	0.06
Morepork x Tail x After	-0.83	10.81	-0.08
Settling Period × Tail x After	2.12	10.62	0.20

Table 2.17c Predicted mean brightness of Raukawa geckos comparing the body and tail before and after each visual simulation treatment from the model Mean Brightness ~ Treatment*Bodypart*BA+(1|Individual). Figures in brackets are the standard error of the predicted means, while figures in square brackets are the 95% Confidence Intervals. P-values are generated from pairwise comparisons of *Before* and *After* values for each bodypart and each treatment. P-values of less than 0.01 are indicated with an **. Least significant difference and *p*-values were calculated on 215 degrees of freedom.

Treatment	Body	Tail	**t**	p
Fantail Before	51.88 (± 5.99) [40.08, 63.68]	61.19 (± 5.99) [49.39, 72.99]	-1.7221	0.0865'
Fantail After	50.86 (± 5.99) [39.06, 62.66]	60.64 (± 5.99) [48.84, 72.44]	-1.8083	0.0720'
Morepork Before	60.73 (± 5.99) [48.93, 72.53]	68.14 (± 5.99) [56.34, 79.94]	-1.3708	0.1719
Morepork After	55.71 (± 5.99) [43.91, 67.51]	62.75 (± 5.99) [50.95, 74.56]	-1.3039	0.1937
Settling period Before	54.92 (± 5.93) [43.23, 66.61]	62.78 (± 5.93) [51.09, 74.07]	-1.4904	0.1376
Settling period After	57.60 (± 5.88) [46.01, 69.19]	68.04 (± 5.88) [56.45, 79.63]	-2.0272	0.0439*

Table 2.18b Estimates of the effect sizes of fixed factors from a LMM for the effect of auditory simulations on the contrast of 20 Raukawa geckos. The model formula was Contrast ~ Treatment*BA+(1|Individual). The levels for the fixed factor *Treatment* were *North Island Fantail* (non-predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *BA* were *Before* simulation and *After* simulation. SE = standard error. *t* values (on 1 degree of freedom) that have a corresponding *p*-value of < 0.05 are indicated in bold.

Fixed factor	Estimate	SE(Estimate)	t
Fantail (Intercept)	98.00	7.05	**13.90**
Morepork	11.00	5.89	1.87
Settling Period	-1.19	5.83	-0.20
After	-1.78	5.89	-0.30
Morepork × After	-6.80	8.33	-0.82
Settling Period × After	14.50	8.19	1.77

Table 2.19b Estimates of the effect sizes of fixed factors from a LMM for the effect of auditory simulations on the saturation of 20 Raukawa geckos. The model formula was Saturation~Treatment*Bodypart*BA +(1|Individual). The levels for the fixed factor *Treatment* were *North Island Fantail* (non-predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *Body Part* were *Body* and *Tail*, and levels for the fixed factor *BA* were *Before* simulation and *After* simulation. SE = standard error. *t* values (on 1 degree of freedom) that have a corresponding *p*-value of < 0.05 are indicated in bold.

Fixed factor	Estimate	SE(Estimate)	t
Fantail (Intercept)	240.21	5.11	**47.00**
Morepork	-5.89	3.88	-1.52
Settling Period	-9.80	3.84	**-2.56**
Tail	-8.92	3.88	**-2.30**
After	-1.13	3.88	-0.29
Morepork x Tail	2.41	5.49	0.44
Settling period x Tail	2.77	5.42	0.51
Morepork × After	2.63	5.49	0.48
Settling Period x After	6.54	5.40	1.21
Tail x After	0.79	5.49	0.14
Morepork x Tail x After	1.01	7.76	0.13
Settling Period × Tail x After	-0.21	7.63	-0.03

Table 2.19c Predicted mean saturation of Raukawa geckos comparing the body and tail before and after each auditory simulation treatment from the model Saturation ~ Treatment*Bodypart*BA+(1|Individual). Figures in brackets are the standard error of the predicted means, while figures in square brackets are the 95% Confidence Intervals. P-values are generated from pairwise comparisons of *Before* and *After* values for each bodypart and each treatment. P-values of less than 0.01 are indicated with an **. Least significant difference and *p*-values were calculated on 215 degrees of freedom.

Treatment	Body	Tail	**t**	p
Fantail Before	240.21 (± 5.11) [230.14, 250.29]	231.29 (± 5.11) [221.22, 241.36]	2.2987	0.0225*
Fantail After	239.09 (± 5.11) [229.01, 249.16]	230.95 (± 5.11) [220.88, 241.03]	2.0948	0.0374*
Morepork Before	234.33 (± 5.11) [224.26, 244.40]	227.81 (± 5.11) [217.74, 237.89]	1.6783	0.0947'
Morepork After	235.83 (± 5.11) [225.75, 245.90]	231.11 (± 5.11) [221.04, 241.18]	1.2149	0.2257
Settling period Before	230.41 (± 5.08) [220.40, 240.42]	224.25 (± 5.08) [214.25, 234.26]	1.6252	0.1056
Settling period After	235.82 (± 5.05) [225.88, 245.77]	230.25 (± 5.05) [220.30, 240.20]	1.5064	0.1334

Table 2.20b Estimates of the effect sizes of fixed factors from a LMM for the effect of auditory simulations on the hue of 20 Raukawa geckos. The model formula was Hue ~ Treatment*BA+(1|Individual). The levels for the fixed factor *Treatment* were *North Island Fantail* (non-predator), *Morepork* (predator), and *Settling Period* (no simulation). Levels for the fixed factor *BA* were *Before* simulation and *After* simulation. SE = standard error. *t* values (on 1 degree of freedom) that have a corresponding *p*-value of < 0.05 are indicated in bold.

Fixed factor	Estimate	SE(Estimate)	t
Fantail (Intercept)	89.92	11.74	**7.15**
Morepork	0.09	11.38	0.01
Settling Period	-12.11	11.26	-1.08
After	-26.85	11.38	**2.36**
Morepork × After	-25.98	16.09	-1.62
Settling Period × After	-38.30	15.82	**-2.42**

Appendix 3A Camera settings used

Some settings were only able to be specified in one model. If not specified below, the default settings were used.

Camera model	Reconyx Hyperfire H.0 Covert IR	Bushnell Aggressor	Bushnell Trophy
Resolution (used highest available for the camera)	3.1 MP	14 MP	Highest available
Setting	Default (Normal/Trail)	Full screen	
Number of photos per trigger	3	3	3
		Low	
Interval	1 second	1 second	1 second
Sensor level	Motion sensor -on, high	Auto	
Execute		On	
NV Shutter		Medium	
Delay between triggers	None		
Battery type (as per user instructions)	Reusable NiMH	Alkaline AA	Alkaline AA
Night mode	Balanced		

Appendix 3B Details of photos captured by trail cameras.

Categories		Overall result
	Number of trail cam photos	12558
	Number of photos containing birds	364
	Number of bird species	9
Photos of birds potentially interacting with model (182)	Bird pecking model	38
	Bird looking at model	40
	Bird blocking model	103
	Bird vocalising while perched on model	1
Photos of birds not interacting with model (182)	Bird flying away	5
	Bird walking past	56
	Bird perched nearby	30
	Bird looking at camera	25
	Bird standing nearby	25
	Bird feeding nearby	29
	Bird walking away from model	12
Photos of mice	Number of photos with mice	441

Appendix 3C Birds recorded by trail cameras and seen in situ.

Y = Yes, WMP = Wahine Memorial Park, TB = Tarakena Bay, RR = Rangitatau Reserve * = native species.

Common name	Scientific name	N photos (% of total n bird photos)	Recorded by Trail camera pictures and site	Seen in situ during field work
Blackbird	*Turdus merula merula*	331 (74%)	WMP, TB, RR	Y
Chaffinch	*Fringilla coelebs*	14 (3.1%)	TB, RR	Y
Dunnock	*Prunella modularis*	13 (2.9%)	TB, RR	Y
House Sparrow	*Passer domesticus*	2 (0.4%)	RR	Y
Red Billed Gull*	*Chroicocephalus novaehollandiae scopulinus*	0		Y
Silvereye*	*Zosterops lateralis*	3 (0.7%_	RR	Y
Southern Black-Backed Gull*	*Larus dominicanus dominicanus*	2 (0.4%)	WMP	Y
Starling	*Sturnus vulagris*	0		Y
Variable Oystercatcher*	*Haematopus unicolor*	0		Y
White fronted tern*	*Sterna striata*	0		Y
Little Blue Penguin*	*Eudyptula minor*	15 (3.4%)	WMP, RR	
Greenfinch	*Chloris chloris*	30 (6.7%)	WMP, TB, RR	Y
Song Thrush	*Turdus philomelos*	36 (8.1%)	WMP, TB, RR	Y

Appendix 3D Bird species recorded at the sites by various sources

Bird species recorded at the sites by various sources. Y = Yes, WMP = Wahine Memorial Park, TB = Tarakena Bay, RR = Rangitatau Reserve, * = native species, [1] = lizard predator

Bird Species	Recorded by Florence-Bennett (2020)	Recorded by Inaturalistnz (2021) and site	Recorded by Trail camera pictures and site	Seen in situ during field work
Blackbird[1]	Y		WMP, TB, RR	Y
Chaffinch	Y		TB, RR	Y
Dunnock	Y		TB, RR	Y
Goldfinch	Y			
House Sparrow	Y		RR	Y
Little Shag*	Y	WMP, TB		
Little Black Shag*	Y			
Pied Shag*	Y	RR, TB		
Red Billed Gull*[1]	Y	RR, TB, WMP		Y
Silvereye*	Y		RR	Y
Southern Black-Backed Gull*[1]	Y	RR, TB	WMP	Y
Starling[1]	Y			Y
Tui*[1]	Y			
Variable Oystercatcher*	Y	RR, TB		Y
Welcome Swallow*	Y			
White fronted tern*	Y			Y
Grey duck x Mallard		RR, TB		
Little Blue Penguin*		TB	WMP, RR	
Black Shag*		RR, TB		
Greenfinch			WMP, TB, RR	Y
Black Swan*		WMP		
Song Thrush			WMP, TB, RR	Y

Appendix 3E Peck data without area adjustment

Distribution of pecks on the body by treatment

The number of pecks observed to the head, body, and limb were similar between treatments (fig E3.1), suggesting brighter and contrasted tails did not result in extra pecks to other body parts.
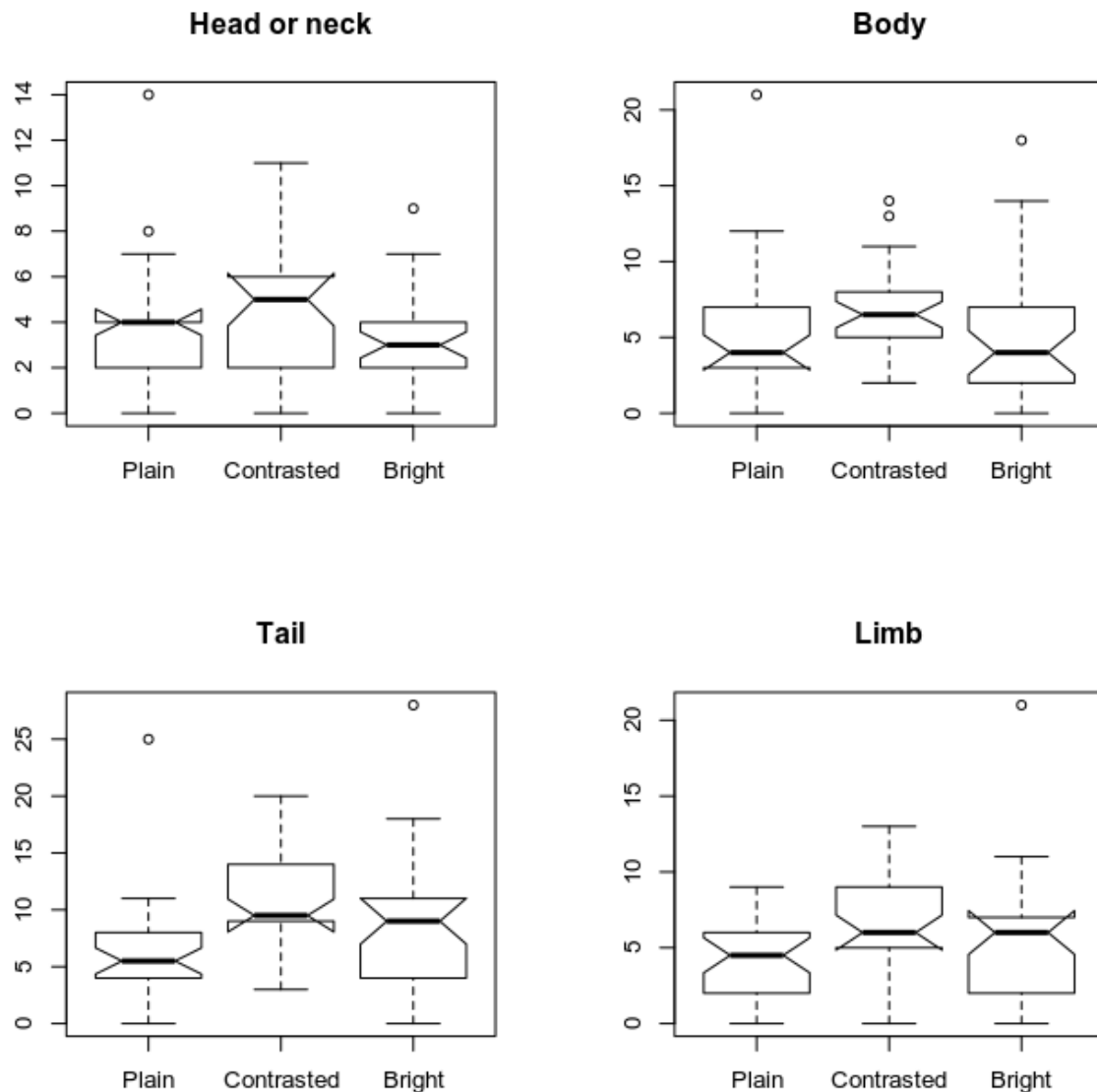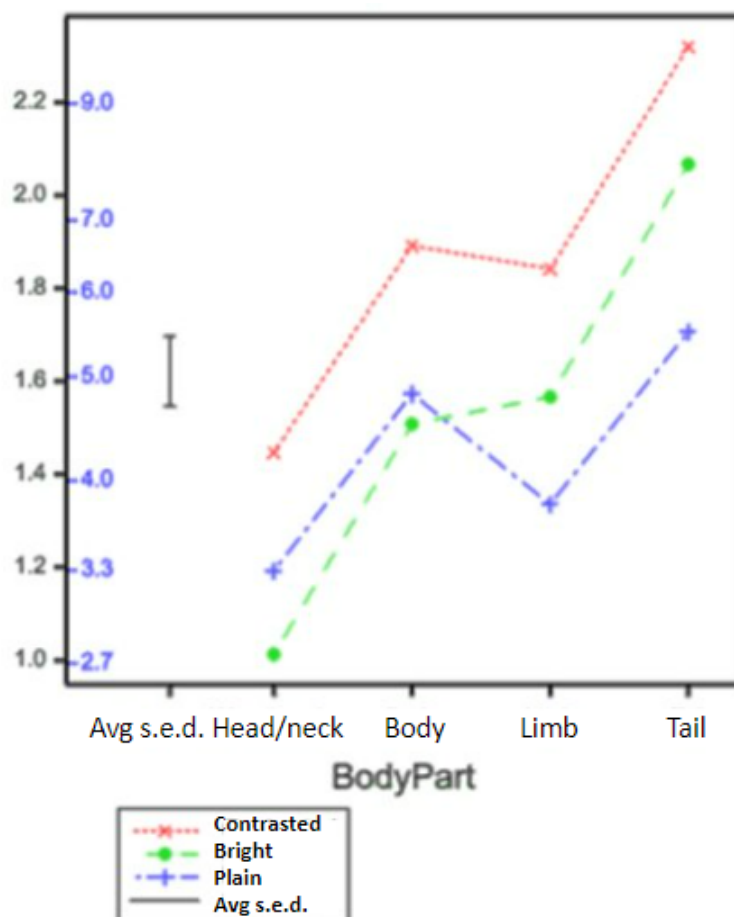

Figure E3.1 Number of pecks to each body part for each treatment. The notched area approximates the 95% confidence interval of the median. If the notches of two plots do not overlap, this is considered strong statistical evidence that the medians differ. The dark line represents the median, the box indicates the interquartile range and the whiskers extend to either 1.5x the interquartile range, or if this is more than the range of the data, then to the extremes of the data instead. The circles represent points outside 1.5x the interquartile range (rdocumentation.org, 2021)

The y-axis shows the number of pecks, while the x-axis shows the colour of the tail when compared with the rest of the body (the treatment). Plain indicates the tail is the same colour as the rest of the body (the control), contrasted indicates greater contrast in the tail than in the rest of the body, and

bright indicates a brighter tail than the rest of the body. The notched boxplot above shows that for the tail region, when the tail was more contrasted or brighter than the rest of the body, more pecks were observed on the tail area than when the tail was the same colour as the rest of the body.

Geometric mean pecks for each body part for different treatments

There was strong statistical evidence of an interaction between body part and treatment (p-value <0.001). That is, the differences in geometric mean number of pecks between body parts is impacted by treatment (fig. E3.2). For all body parts, the contrasted tail treatment has the highest geometric mean number of pecks. The interaction arises because for the head/neck and body, the geometric mean for the plain-tailed treatment is higher than for the bright-tailed treatment, whereas for the limb and the tail, the converse is true.

Figure E3.2 Geometric mean pecks for each body part for the different treatments with average standard error of differences using the 'predictmeans' package (Luo et al., 2020) in R (R Core Team, 2020). The y-axis is on a natural log scale, the blue numbers are the back-transformed values.

Distribution of mean number of pecks by treatment, after controlling for site and trial effects

An ANOVA for each body part, looking at whether the mean number of pecks on the selected body part differed between the treatments, after controlling for site and trial effects, gave the following results:

Table E3.2. ANOVA for each body part: mean number of pecks on selected body parts between treatments, after controlling for site and trial effects.

	Tail	Head and neck	Body	Limb	Total
Mean plain	a	a	a	a	a
Mean bright	ab	a	a	ab	ab
Mean contrasted	b	a	a	b	b
F-value	6.548	2.178	2.335	5.092	6.598
P-value	0.00229**	0.120	0.10316	0.0082**	0.00218**

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

This is discussed in further detail for each body part below:

Tail

The ANOVA showed that the mean number of pecks on the tail differed after controlling for site and trial effects (p=0.00229). From the ANOVA looking at whether the mean number of pecks on the tail differed between treatments after controlling for site and trial effects, there was statistical evidence that the means for contrasted and plain were different (p=0.0015938), weak statistical evidence that bright and plain means differ (p=0.0811453), and no evidence of a difference between bright and contrasted means (p=0.3378835) according to Tukey's HSD pairwise comparisons.

The mean for models with contrasted tails is an estimated 4.4 pecks per tail of lizard model over 3 days higher than for plain tailed models, with 95% confidence interval (CI) for the difference of 1.5 to 7.3 pecks per tail of lizard model over 3 days.

The head and neck area

For the head and neck area, there was no statistical evidence of a treatment effect (p=0.120), meaning that there was no statistical evidence of a disadvantage, in terms of pecks to the head or neck, of having a bright or contrasted tail. However, "failing to find to show the difference between

two treatment effects (i.e. p>0.05) is not the same as saying that they are the same" (Ganesh and Cave, 2018), and if we wanted to say they were the same this would change the burden of proof, and require a different approach.

A statistically significant effect of site and trial number were observed, meaning the timing and site of the model impacted the mean number of pecks to the head and neck area.

The Body

From the ANOVA looking at whether the mean number of pecks on the body differed between treatments after controlling for site and trial effects, we found no statistically significant effect of treatment on the mean number of pecks to the body (p=0.10316). While there was a statistically significant effect of site on the mean number of pecks to the body (p=0.00352), the study design planned for this by ensuring that each treatment occurred at each site, and there was no evidence for a statistically significant effect of trial (p=0.35409), so the effect of site was not important to the results.

The limbs

From the ANOVA looking at whether the mean number of pecks on the limbs differed between treatments after controlling for site and trial effects, we found highly statistically significant effects of site (p=0.000000026) and treatment (p=0.0082) on the mean number of pecks to the limbs. After controlling for site and trial effects, there was a highly statistically significant difference between the contrasted and plain tailed models (p=0.0056368) in terms of mean number of pecks to the limbs. Contrasted tailed models had on average 2.3 more pecks to the limbs over 3 days than plain tailed models, with a 95% Confidence Interval of 0.579 - 4.02 pecks difference over 3 days.

Total pecks over the entire gecko model

The ANOVA looking at whether the mean number of pecks on the whole body differed between treatments after controlling for site and trial effects found a highly significant effect of treatment (p=0.00218) on the mean number of total pecks over the entire lizard model. Plain-tailed models had on average 4.4 less total pecks than contrasted-tailed models (CI 1.5-7.3), with a highly statistically significant p-value of 0.00151. Plain-tailed models had on average 2.7 less total pecks than bright-tailed models (CI 0.2-5.6), approaching statistical significance with a p value of 0.0796. No statistically significant difference was detected between bright-tailed and contrasted-tailed models (p=0.335).
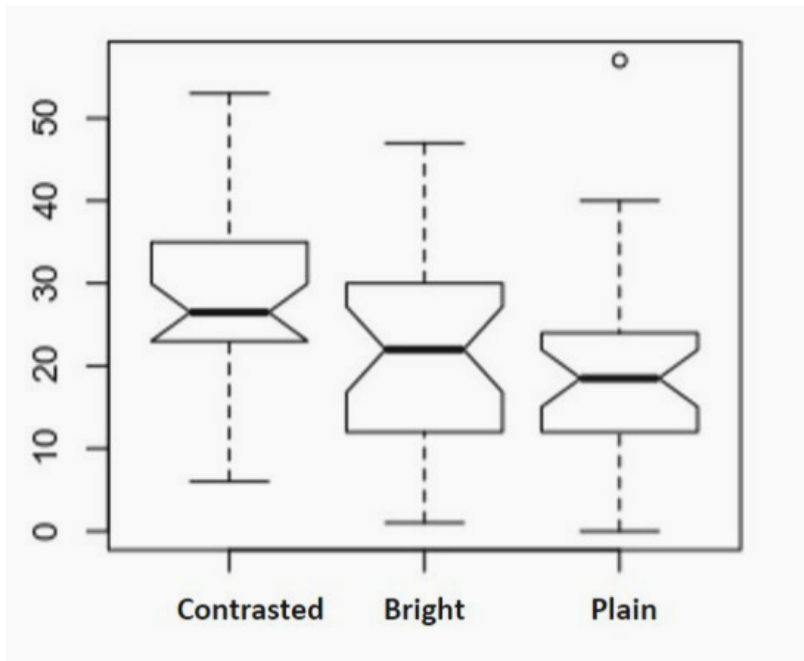
Figure E3.3 Notched plots of total pecks over the entire lizard model.

Appendix 3F Pairwise comparisons of the responses of each area- adjusted body part to each treatment by treatment

Pairwise comparisons by area - Treatments

For the models with tails the same colour as the rest of their body (**plain-tailed** (control) models), there was moderate statistical evidence of the limbs receiving more area-adjusted pecks than the body (p=0.0161) and strong statistical evidence of the limbs receiving more area-adjusted pecks than the head/neck (p= 0.0095). There was no evidence of a statistically significant difference in the number of pecks by area between the tail and other body parts (fig 3.11, table F3.1), although there is weak statistical evidence for the head receiving fewer area-adjusted pecks than the tail (p=0.0791).

Table F3.1 Pairwise comparisons of pecks by area for models with tails the same colour as the rest of their body (plain-tailed models). *p* -values are calculated on 261 degrees of freedom. Body parts that do not share a group letter, show evidence of a statistically significant difference (*p* < 0.05) in area-standardised pecks.

	Tail	Head	Body	Group
Tail				AB
Head	t = 1.7626 *p* = 0.0791'			B
Body	t = 1.5710 *p* = 0.1174	t = -0.1916 *p* = 0.8482		B
Limb	t = -0.8516 *p* = 0.3952	t = -2.6142 *p* = 0.0095**	t = -2.4226 *p* = 0.0161*	A

For models with **brighter tails** than the rest of their bodies, there was evidence of a statistical difference between the head/neck or body and the limb or the tail (p=0.0001) in number of pecks by area (fig 3.11, table F3.2). There were fewer area-adjusted pecks to the head and neck than to the limbs or the tail, and there were fewer area-adjusted pecks to the body than to the limbs or the tail. There was no evidence of a statistically significant difference between the head and the body (p=0.9243), and no evidence of a statistically significant difference between the limb and the tail (p=0.8725) in number of area-adjusted pecks.

Table F3.2 Pairwise comparisons of pecks by area for models with tails brighter than the rest of their body. *p* -values are calculated on 261 degrees of freedom. Body parts that do not share a group letter, show evidence of a statistically significant difference (*p* < 0.05) in area-standardised pecks.

	Tail	Head	Body	Group
Tail				A
Head	t = 4.3772 *p* = 0.0001***			B
Body	t = 4.4723 *p* = 0.0001***	t = 0.0951 *p* = 0.9243		B
Limb	t = -0.1606 *p* = 0.8725	t = -4.5378 *p* = 0.0001***	t = -4.6329 *p* = 0.0001***	A

Likewise, for the models with more **contrasted tails** than the rest of their bodies, there was evidence of a statistically significant difference between the head/neck or body and the limb or the tail in number of pecks by area (fig 3.11, table F3.3). Again, the head and neck received fewer area-adjusted pecks than the tail and limbs, and the body also received fewer area-adjusted pecks than the tail and limbs. There was no evidence of a statistically significant difference between the head and the body (p=0.345), and no evidence of a statistically significant difference between the limb and the tail (p=0.2693) in number of pecks by area.

Table F3.3 Pairwise comparisons of pecks by area for models with tails more contrasted than the rest of their body. *p* -values are calculated on 261 degrees of freedom. Body parts that do not share a group letter, show evidence of a statistically significant difference (*p* < 0.05) in area-standardised pecks.

	Tail	Head	Body	Group
Tail				A
Head	t = 4.6115 *p* = 0.0001***			B
Body	t = 3.6653 *p* = 0.0003***	t = -0.9461 *p* = 0.3450		B
Limb	t = -1.1069 *p* = 0.2693	t = -5.7184 *p* = 0.0001***	t = -4.7723 *p* = 0.0001***	A

These results are shown graphically below:
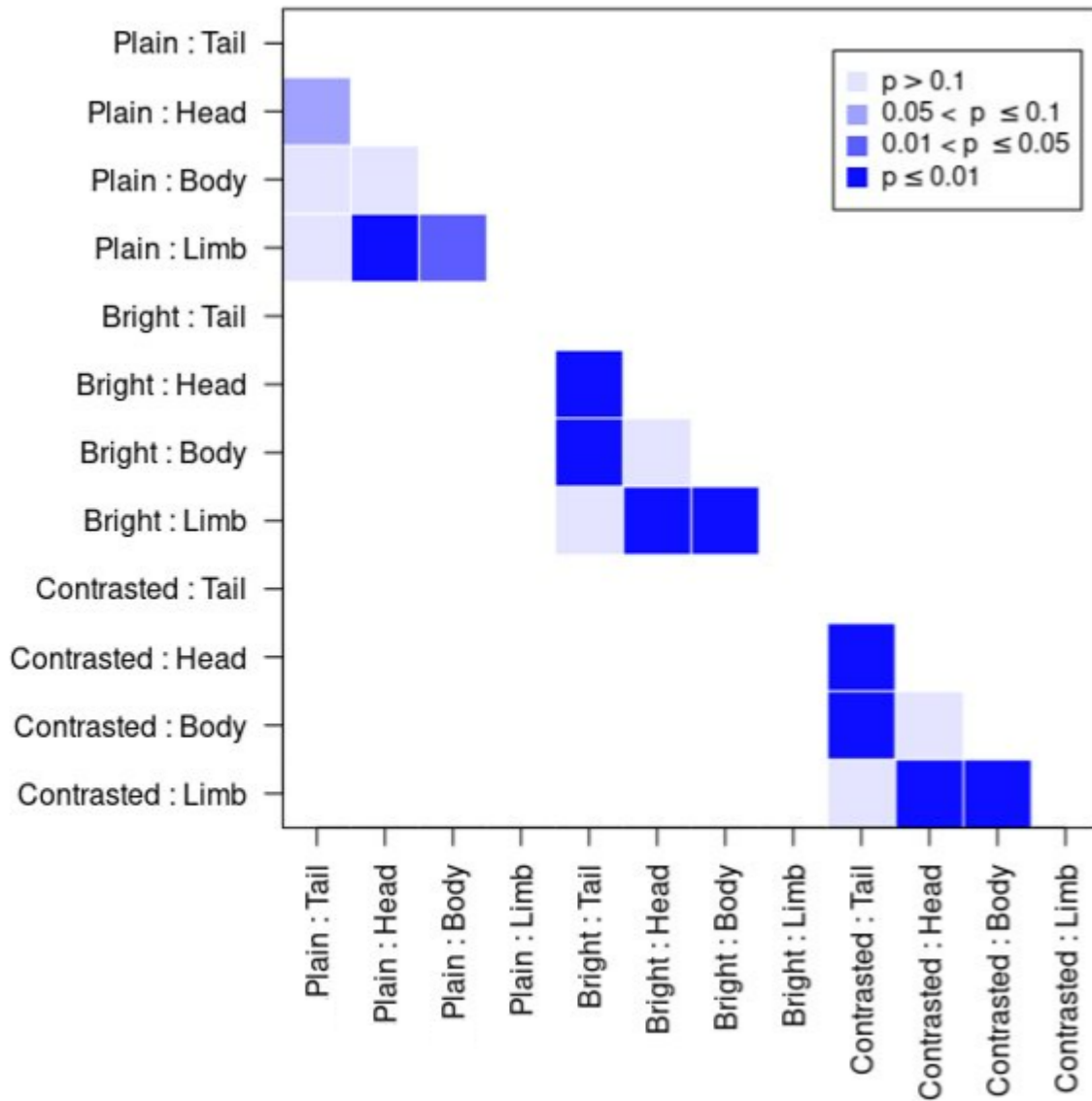
Figure F3.1. Pairwise comparisons comparing differences in pecks (adjusted for area) between body parts within a treatment.

Appendix 4.1 Additional photographs of ngāhere geckos