Life in the city: the influence of the urban environment on behaviour and spatial distributions in North Island kākā

(Nestor meridionalis septentrionalis)

By

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Abstract

Urban environments are increasing in size and influence across the landscape of the world. As cities increase in number, size, and population, the influence that these modified anthropogenic spaces and the humans dwelling within them have on wildlife is becoming increasingly intense. More frequent interactions between humans and wildlife have driven species to either adapt, tolerate, or avoid urban spaces entirely. While the impacts of urban life on avifauna have been well studied globally, little is known about the response of the endemic forest-dwelling birds of New Zealand to the novel challenges presented by cities. Furthermore, the majority of existing studies have focused on northern hemisphere passerine species. The naive endemic avifauna of New Zealand, including the many threatened psittacine (parrot) species, have been subject to limited study regarding habituation and response to urban landscapes. Understanding how wildlife responds to urban environments, and the factors that drive differences in behaviour and space use, is essential to managing urban populations and planning future reintroductions of wildlife into cities.

North Island kākā (*Nestor meridionalis septentrionalis*) were reintroduced to Wellington City in 2002, with the release of six individuals into Zealandia ecosanctuary. Kākā are a deeply endemic, threatened forest-dwelling parrot species The population has since grown and expanded across many suburbs of the city, increasing the frequency of interaction between kākā and both the urban environment, and people. This thesis investigates the influence of the urban environment and human presence on the spatial distribution, behaviour, and risk perception of kākā in the Wellington and the Kāpiti Coast Regions of New Zealand. The findings of this thesis show that human presence and the urban environment did not directly influence the distribution or behaviour of kākā. Time of day strongly influenced investment in vigilance and foraging behaviour, and land cover type strongly affected investment in foraging and preening behaviour. Urban land cover was not

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significant in explaining differences in behaviour. Time of day was the most significant explanatory factor for the relative abundances of kākā observed. The distribution of kākā throughout the landscape was also strongly influenced by the presence of Zealandia, with far greater densities and relative abundances of kākā within the sanctuary compared to the urban reserves of Wellington city. Overall, findings in this study suggest that kākā behaviour and distributions are much more strongly influenced by resource availability than by human presence and the urban environment directly. Further research should be conducted to investigate the risk perception and behavioural flexibility of urban kākā. This is especially important for the ongoing management of Wellington's kākā population, and to better inform future urban reintroduction efforts.

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(Miller, 2011)

Chapter One: General Introduction

1.1 Urbanisation in a Global Context

The environments of urban spaces are often hostile for many species, featuring high levels of disturbance and climatic extremes (Rumble et al., 2019). Much of modern urbanisation is considered urban sprawl, wherein extensive areas of land are taken for urban use, with detrimental environmental impacts (Nuissl & Siedentop, 2021). Urbanisation causes one of the most dramatic and permanent shifts in anthropogenic landscapes, characterised by dramatic changes in land use type, typically across large expanses of land (Walker et al., 2008). Although cities have the capacity to support diverse natural communities (Aronson et al., 2014), as well as threatened species (Ives et al., 2016), they also tend to host high levels of diversity of non-native species as a consequence of human introduction (Kowarik, 1990; Porter et al., 2001). While land cover is dictated by land use, the biodiversity and abundance of flora and fauna within a fragment is dictated by the length of time that it has been maintained within the surrounding matrix (Vinton, 2008). In addition to urbanisation causing fragmentation and loss of natural habitats, it is important to note that this change of habitats and opening of new niches occurs over a short period of time (Major & Parsons, 2010). Consequently, many species are unable to evolve and adapt to the alterations in resource availability and vegetation structure (Major & Parsons, 2010), causing high rates of decline in wildlife, and local extinctions of various fauna species globally, including avian assemblages (Blair & Johnson, 2008; Czech et al., 2000; Marzluff, 2001; McKinney, 2002).

Alterations in abiotic and biotic factors resulting from urbanisation drive changes in environmental conditions, resource availability, predation, competition, and introductions of non-native species (Amiot et al., 2021). Urbanisation causes major biodiversity loss, especially when urbanisation is intensive (McKinney, 2002, 2006; McDonnell & Hahs, 2008; Shochat et al., 2010; Aronson et al., 2014), as well as native species declines and forest fragmentation, a dynamic process in which areas of continuous forest are divided up into smaller isolated patches (Liu et al., 2019). Over time, as originally non-urban land is transformed, continued fragmentation and deforestation occur, reducing and eliminating forest patches, further isolating remaining patches (Zipperer et al., 1990). As remnant patches are often small and located within a highly disturbed matrix, they are always open to invasion by non-native species (Rebele, 1995). As such, the capacity of these patches to sustain native species is compromised (McKinney, 2002). Fragmentation of habitats through urbanisation accelerates habitat loss, thus habitat fragmentation and habitat loss are inherently linked and occur concurrently (Fahrig, 1999; McComb, 1999). Along the gradient from rural to urban centre, there are changes in abiotic conditions in remaining patches of habitat driven by increased precipitation, temperatures, and nitrogen deposition (Gilbert, 1994; Grimm et al., 2008; Pickett et al., 2011). As a result, habitat quality, species richness and composition, and functional diversity is impacted (Concepcion et al., 2015; McKinney, 2002; Sukopp, 1998), subsequently influencing ecosystem function (Chapin III et al., 1997). Regardless, urban areas can host high levels of species richness (Godefroid & Koedam, 2007), even exceeding that of the surrounding rural areas (Kuhn et al., 2004; Sukopp, 1998).

While the species loss in urban landscapes may have an element of random chance to it, there is strong evidence supporting the notion that most of this loss is associated with species with low tolerances to urbanisation (Sol et al., 2014). Urbanisation tolerance occurs in species possessing certain biological traits that enable resource exploitation and risk avoidance in such urban habitats (Bonier et al., 2007; Croci et al., 2008; Evans et al., 2011; Kark et al., 2007; Maklakov et al., 2011; Møller, 2009). Some species are able to thrive within urban landscapes through the exploitation of novel niches, tolerance of disturbance, and even development of relationships with humans (Rumble et al., 2019). Many other

species, however, are unable to adapt, driving a net extinction debt within cities (Hahs et al., 2009). As such, biodiversity loss associated with urbanisation is reflective of the limited number of species capable of adapting and tolerating the anthropogenically driven environmental alterations (Sih et al., 2011). While urban communities as a whole are influenced by the biodiversity in the adjacent landscapes, certain species are consistently classified as either urban exploiters or avoiders across regions and the globe (Møller et al., 2012; Sol et al., 2014). This indicates that different species vary in their tolerance to urbanisation. Furthermore, variation in tolerance between species can be predicted based on their life histories and resource use habits (Sol et al., 2014).

Within urban spaces, interactions between people and nature are widespread (Fuller & Irvine, 2010). Human disturbance is considered any anthropogenic activity that causes short or long-term stress and fitness responses in wildlife (Coetzee & Chown, 2016). Such disturbance activities can include natural resource extraction, transport, construction, and recreation (Coetzee & Chown, 2016). Human disturbance can alter species' behaviour and physiology through generating costs associated with perceived risk (Blumstein et al., 2005; Coetzee & Chown, 2016; Frid & Dill, 2002), ultimately resulting in declines in both abundance and fitness (Barron et al., 2010; Ruhlen et al., 2003; Saraux et al., 2011; Stankowich, 2008). A study examining a population of snowy plovers (*Charadrius nivosus*) in California, USA, found that rates of chick loss were heightened during periods of increased human use of the beach wherein the plovers nested (Ruhlen et al., 2003). It was hypothesised that human presence may have induced reduced investment in foraging and brooding, and more time spent vigilant, causing chicks to be subjected to reduced brooding and potentially greater exposure to predators and weather conditions (Ruhlen et al., 2003).

The human desire for green spaces in close proximity to living spaces has arguably been critical in moderating the extent of the impacts of urbanisation on nature (Fuller &

Irvine, 2010). The retention of green areas as large parks and patches of undeveloped wooded remnants within cities has allowed some ecological integrity to be maintained (Fuller & Irvine, 2010). When urbanisation leads to inadequate green space retention, local extinctions can occur, especially of habitat specialists requiring large patches of habitat and the interior areas of habitat patches (Chase & Walsh, 2006; McKinney, 2002; Pickett et al., 2001). While green spaces do moderate some negative impacts of urbanisation, their use and management has a significant influence on biodiversity value (Fuller & Irvine, 2010). Within green spaces used for human activity, the health of the biodiversity within the space is subject to the intensity and frequency of human activity (Fuller & Irvine, 2010), as well as the diversity and quality of vegetation within the patch (Fuller & Irvine, 2010; Sandström et al., 2006). While the remaining habitat remnants in urbanised areas can harbour biodiversity, they often also serve as spaces for human recreation (Markovchick-Nicholls et al., 2008). These two purposes are often conflicting, especially where human activity impacts wildlife negatively, especially where fragments are small (Markovchick-Nicholls et al., 2008). With increasing frequency of outdoor recreation (Cordell, 2008; Cordell et al., 2008; Flather & Cordell, 1995) comes associated disturbance to wildlife, which has been implicated as a primary cause of threatened and endangered species declines in the United States (Czech et al., 2000). These disruptions can influence breeding success and survival rates of wildlife, resulting in cascading effects on ecosystems (Fuller & Irvine, 2010). One study by Blair (1996) found that Shannon diversity (Shannon & Weaver, 1963), bird density, and the number of species peaked where there are intermediate levels of urbanisation. This is known as the intermediate disturbance hypothesis, and in urban environments it has been suggested that urban green spaces represent areas of intermediate disturbance (Blair & Launer, 1997; McKinney, 2002).

Much of the anticipated growth of the global human population is expected to occur in urban areas (United Nations. Population Division of the Department of Economic and Social Affairs, 2004). As of 2007, over 80% of the population of New Zealand, Australia, and North America was urbanised (Gaston, 2010). As the world continues to urbanise, it has been predicted that 66% of the global human population will live in urban areas by 2050 (Reynolds et al., 2019). Urbanisation and suburbanisation result in markedly homogenous outcomes worldwide (Blair & Johnson, 2008). As cities are built to fulfil the needs of one single species - humans, the landscape consequently reflects the needs, desires, and constraints of humans (McKinney, 2006). As cities around the globe tend to have similar conditions and exert similar selective pressures on biota on a global scale, they tend to be inhabited by the same urban-adapted species (Blair & Johnson, 2008). Consequently, cities become homogenised, with lower overall biodiversity and decreased environmental variation (Shochat et al., 2006).

1.1.1 Impacts of Urbanisation on Wild Birds

With the increased human population size across cities and towns around the world has come the concept of the 'urban bird', which describes bird species that possess traits that allow for tolerance and adaptation to the urban environment, such as generalist diet and habitat requirements (Evans et al., 2011; Reynolds et al., 2019). While such urban birds are adapted to, and thrive in urban environments, the process of urbanisation greatly affects most birds through the irreversible conversion of natural and semi-natural areas into highly developed paved areas and buildings, with small gardens and parks interspersed throughout (Forman, 2014; Shanahan et al., 2014). Urbanisation has been found to have three general effects on avian wildlife; change in species composition, decreased species diversity, and increased species abundance (Blair, 1996). Urban landscapes pose many challenges to urban birds (Marzluf, 2017), including novel predators, habitats, food sources, climatic conditions, and stressors such as noise, light, and air pollution (Marzluf, 2017; Reynolds, 2019).

Large cities tend to be more similar to other cities than to the adjacent habitats, and as such the typical urban bird biomass is non-native to its region (Vinton, 2008). Such birds, classified as urban exploiters, are adapted to exploit anthropogenic food resources and shelter, and reach peak densities in developed sites (Blair, 1996; McKinney, 2006). Species that are more sensitive to human disturbance tend to be less abundant in more modified sites (Vinton, 2008). Such species are typically natives, whose abundance is dependent on the extent of native vegetation presence (Blair, 1996). Urbanisation results in either elimination or fragmentation of native vegetation, consequently altering the abundance and distribution of the wildlife species that are dependent upon it for habitat (Davis et al., 2013). A study in Australia found that at least 83% of the surveyed land birds were dependent to some extent on native vegetation (Davis et al., 2013). In order to retain avian diversity in urban landscapes, management should aim to conserve the integrity of the remaining remnant native vegetation (Davis et al., 2013).

A study by Major & Parsons (2010) investigated changes in the avian assemblages of Sydney in the context of urbanisation, wherein they compared the pre-1900 and 1998-99 bird communities. A major difference they found was a significant increase in body size, with a larger proportion of the recent bird community comprising larger species, thought to be a result of both a relative decline in smaller species such as small insectivores, and a relative increase in larger species such as parrots. In spite of an overall decline in species diversity, some bird species possess adaptations for survival in urban landscapes, such as behavioural flexibility and a generalist diet (Evans et al., 2011) and have become widespread globally (Antos et al., 2006; Case, 1996; Emlen, 1974; Major & Parsons, 2010). Some native bird species are capable of transitioning into urban areas by capitalising on small habitat fragments that resemble natural ones, and exploiting novel food resources (Major & Parsons, 2010). Other native species, typically smaller species with more limited habitat requirements, can occur frequently in remnant habitats in the urban matrix, but infrequently within more intensely urban areas (Blair, 1996; Jokimaki & Suhonen, 1993; Parsons et al., 2003). Such species tend to be vulnerable to slow extinction as fragmentation increases, and the impacts of stochastic forces accumulate on small, isolated populations (Crooks et al., 2001). The conditions of urban landscapes can also drive phenotypic changes through predation pressure. As urban areas accommodate the proliferation of non-native predatory species (Amiot et al., 2021), increased predation pressure in urban environments can drive morphological adaptations (Gosler et al., 1995; Swaddle & Lockwood, 1998), or exert selection pressure on birds based on the physical traits related to predator escape performance (Amiot et al., 2021; Møller et al., 2009, 2013; van den Hout et al., 2010). A study by Massaro et al. (2008) investigating the response of the New Zealand endemic korimako (Anthornis melanura) to predation risk from introduced mammalian predators found that incubating bout length increased with increased predation risk for female korimako, effectively reducing activity at the nest during incubation (Massaro et al., 2008). The number of feeding visits per hour also decreased as nest predation risk increased, suggesting some island bird species, including New Zealand endemics, can respond adaptively to increased novel predation risk (Massaro et al., 2008).

Studies have shown a link between behavioural boldness and dispersal, in which bolder species that were more likely to take risks, also exhibit a great tendency to disperse (Rehage & Sih, 2004). Species that thrive in urban landscapes are often more generalist feeders with broader dietary requirements, which enables species to capitalise on the abundant novel food sources present in cities (Kark et al., 2007). Bird species that have broad diets have been found to outcompete specialist species when inhabiting urban environments (Kark et al., 2007). In urban environments, bird species with highly specific dietary needs become limited (Kark et al., 2007), as natural food sources become less abundant and

fragmented as urbanisation increases (Alberti et al., 2008). The capacity to utilise novel food sources allow species to exploit new niches within the urban landscape and capitalise on the highly available anthropogenic food sources present (Alberti, 2008). Species with highly diverse diets prior to urban colonisation are more easily able to adapt to exploit anthropogenic food sources (Charles & Linklater, 2013b).

While human disturbance may be perceived as subtle compared to more destructive forms of disturbance such as deforestation, it often still has less obvious cumulative impacts (Price, 2008). The perceived predation risk posed by humans to wildlife causes redirection of time and energy investment from fitness-enhancing behaviours such as feeding and reproduction, to vigilance and escape responses (Price, 2008). As birds have a tendency to overestimate the risk posed by humans, they are more likely to habituate to a limited extent to repeated harmless human disturbance than they are to lose fear towards humans altogether (Price, 2008). The effects of human recreation are often considered to be potential biodiversity threats, through the restriction of access to resources that would otherwise be utilised by animals (Gill, 2007). As access to areas with wildlife is a major means of increasing the public value of these areas, and thus creates pressure to conserve them, it is critical to determine when human presence poses a threat to conservation, and when it does not (Gill, 2007). The primary impact of human presence on wildlife is the restriction of access to resources such as food and nesting sites, or through altering the perceived or actual quality of such resources (Gill, 2007; Liley, 1999; Tombre et al., 2005). Human presence can directly restrict access, whereas attraction of predators to humans, or reduction of prey abundance can lower site quality (Gill, 2007). Some argue that the birds perceive and react to humans on foot in the same manner as they would to natural predators, through the display of antipredator responses (Frid & Dill, 2002; Blumstein et al., 2003). Such antipredator responses involve various physiological processes and behaviours to prepare the animal for

fight and/or flight (Sapolsky et al., 2000), including an increase in HPA (hypothalamicpituitary-adrenal) axis activity, known as the stress response (Price, 2008).

In response to human presence, birds should alter their behaviour adaptively in order to maximise the trade-off of costs and benefits, by responding to certain disturbances in particular manners (Cooper & Frederick, 2007). In theory, when resource quality is high and human disturbance risk is low, birds should display reluctance in leaving their foraging and breeding grounds (Frid & Dill, 2002; Cooper & Frederick, 2007). Conversely, a bird can be expected to avoid a localised human disturbance when resources are abundantly available nearby or are evenly distributed throughout the bird's home range (Ydenberg & Dill, 1986). If a situation is perceived as being especially risky, an individual should avoid humans at the cost of fitness-enhancing activities (Blumstein et al., 2005; Frid & Dill, 2002). As such, risk levels must be constantly monitored and evaluated, rather than immediately fleeing, in order to avoid the unnecessary energetic and time cost of fleeing and losing access to foraging and breeding areas (Price, 2008). At the same time, however, continuous intense monitoring can hinder investment into fitness-enhancing activities (Blumstein, 2003). Thus, birds should exhibit greater vigilance when the perceived risk of predation or significant disturbance is high (Geist et al., 2005; Price, 2008). Vigilance reduces the chance of birds experiencing injury or death at the cost of investment in other critical activities (Frid & Dill, 2002). As such, the choice to flee from humans is based on an evaluation of the costs and benefits of escaping, as opposed to the risk of being detected and harmed (Cooper & Frederick, 2007; Ydenberg & Dill, 1986). The distance at which a bird flees, known variously as flight initiation distance (FID), instance flush, or approach distance, is considered to reflect the degree of tolerance towards humans (Price, 2008). As with other responses to human presence, FID will vary in relation to a bird's assessment of risk (Blumstein, 2003; Blumstein et al., 2003; Ydenberg & Dill, 1986).

1.1.2 Impacts of Urbanisation on New Zealand's Avifauna

The history of the introduction of predators into New Zealand is now fairly well known (Tennyson & Martinson, 2006; Towns & Daugherty, 1994). With the arrival of Polynesian people in about 1280 came kiore (*Rattus exulans*) (Wilmshurst et al., 2008), and kurī (*Canis familiaris*) (Tennyson & Martinson, 2006). From 1769 onwards, the remaining mammalian predator species arrived with Europeans (Towns et al., 2011). Since the arrival of humans in New Zealand, there has been catastrophic species diversity decline within mainland ecosystems, including the extinction of at least 40% of frog and avian species, and range restrictions in many others (Towns & Daugherty, 1994). These declines and extinctions can be linked to human occupation, and predation by introduced mammalian species (Towns & Daugherty, 1994).

The number of species of mammalian predators released onto the mainland island of New Zealand is the highest of any archipelago (Towns et al., 1997). Globally, the most widespread predator species on islands are mice (*Mus musculus*), cats (*Felis catus*), ship rats (*Rattus rattus*), kiore, and Norway rats (*Rattus norvegicus*) (Atkinson, 1989). While most of the predators introduced to New Zealand don't necessarily modify the habitat, they often can eliminate certain species, whilst simultaneously altering the environment directly or indirectly (Atkinson, 1989). In New Zealand, the introduction of cats has resulted in significant population declines in native forest bird species (Innes et al., 2010), the destruction of seabird colonies, and the extinction of Stephens Island wren (*Traversia lyalli*) (Galbreath & Brown, 2004), and rats have affected bird, lizard, and invertebrate populations (Towns et al., 1997). The later introduction of mustelid species was especially devastating, as the remaining native fauna were already depleted from cats and rats (King, 1984). The introduction of these species, alongside harvesting by humans, had widespread devastating

impacts, such as the extirpation of almost all burrowing seabird species from the main islands (Taylor, 2000).

Since the arrival of humans, New Zealand has undergone significant deforestation and native forest fragmentation (Park, 1999). The forest bird communities of New Zealand have been irreparably altered over the past 150 years, with the extinction of at least six endemic forest bird species since 1870, and the restriction of five further species to offshore islands (Miskelly, 2018). Furthermore, many of the endemic species that do remain have been confined to limited areas of remote forest (Miskelly, 2018). Along with the introduction of various exotic various bird species, this has led to the bird communities in forest remnants within and around cities being represented by a few widespread native species such as tauhou/silvereye (Zosterops lateralis), pīwakawaka/fantail (Rhipidura fuliginosa), and tūī (Prosthemadera novaeseelandiae) and a wide variety of introduced bird species (Miskelly, 2018). Furthermore, urbanisation and agricultural intensification have driven fragmentation and habitat loss in New Zealand, resulting in much of the nation's native biodiversity becoming threatened, as native vegetation dependent species struggle to tolerate modified environments (Battles et al., 2013; Marzluff & Ewing, 2008; Standish et al., 2012; Yu et al., 2012; Zipperer et al., 2012). Natural habitat fragments that remain are often incapable of supporting biodiversity at the same levels as prior to urbanisation, resulting in continued loss of species unable to survive in the 'patch' (OliverSmith, 2015; Saunders et al., 1991).

Today, New Zealand is a highly urbanised nation, with over 85% of its population dwelling in urban centres (United Nations, 2018). Within cities, the single largest green space is often private gardens (Gaston et al., 2005; Mathieu et al., 2007), but there is significant variation between cities in terms of presence of native vegetation, trees, and structural complexity (DeGraaf & Wentworth, 1986; Kirkpatrick et al., 2007). Residential gardens have been shown to host high levels of biodiversity (Gaston et al., 2005). Beyond

gardens, native vegetation fragments possess the potential to support high levels of avifauna diversity and abundance (Crooks et al., 2004; Donnelly & Marzluff, 2004), and potentially serve as population source areas for surrounding suburbs (van Heezik et al., 2008). While urban areas often host significant species diversity, high numbers of non-native species can mask low levels of native diversity (van Heezik et al., 2008). A study conducted in Dunedin, New Zealand found that almost half of the 39 species recorded throughout the city were non-native, with four species, of which three were exotic, comprising 45% of birds counted (van Heezik et al., 2008). It was also found that while native and exotic species richness had little variation between habitats, the abundance and number of bush-dependent natives did vary, with significantly fewer in commercial, industrial, and residential areas than in bush fragments (van Heezik et al., 2008).

In order to bolster native species populations, many predator-proof fences have been erected throughout New Zealand on the basis of extensive research (Day & MacGibbon, 2007), in tandem with multi-species eradication programmes that are world-leading in regard to the number of vertebrate species eradicated (Innes & Saunders 2011; Speedy et al., 2007). Exclusion fences have consistently proven highly effective in managing pest species, with the exception of mice (*Mus musculus*) (Innes et al., 2012). While fenced sanctuaries are more pest-resistant than pest-proof, they are capable of maintaining significantly lower abundances of pest species than unfenced areas (Innes et al., 2012). Sanctuaries such as Zealandia, in Wellington, have allowed for the spillover of reintroduced bird species into nearby reserves and residential areas as the population increases, resulting in the proliferation of native species throughout the surrounding area (Brockie & Duncan, 2012). The dispersal of endemic bird species beyond the fence of Zealandia, known as the halo effect, has been well documented at several fenced sanctuaries across New Zealand (Smuts-Kennedy & Parker, 2013; McArthur et al., 2017; Tanentzap & Lloyd, 2017). All bird species that have been

successfully translocated to Zealandia have significantly higher survival rates and breeding success within the sanctuary than outside (Miskelly, 2018). Five of the species translocated to Zealandia, however, have successfully bred in unfenced reserves nearby to Zealandia, including kākā (Miskelly, 2018). To support populations of native birds throughout Wellington, there are both nearby halo reserves and the 'Predator Free Wellington' project, each aiming to reduce introduced predator numbers (Miskelly, 2018). As Zealandia is located nearby to the heart of Wellington City, the spillover of native species has introduced them to an urbanised environment, where challenges and opportunities are abundant.

Wellington is the third largest urban centre in New Zealand, with a population of just over 200,000 people (Statistics New Zealand, 2018). Today, less than five percent of the original lowland forest remains (Gabites, 1993). This five percent of remnant forest, however, is an important source of native seeds, and as a habitat for native wildlife (OliverSmith, 2015). Through natural regeneration of vegetation, many adjacent areas of remnant native vegetation cover, such as abandoned hillsides and gullies have been reclaimed by forest cover (DOC, 1996; Gabites, 1993; Park, 1999), providing further habitat and seed source for future recruitment. Additionally, the WCC began native regeneration planting projects throughout Wellington city in the 1990s, in order to both reclaim exotic tree sites, and conserve and restore nature (OliverSmith, 2015). Management of urban areas to increase avian biodiversity is complex (Vinton, 2008). It requires land use planning designed to continue meeting the needs of a human settlement, while simultaneously conserving habitat for birds (Vinton, 2008). In order to manage the sustainability and environmental integrity of urban spaces, urban areas must be treated as part of biodiversity management plans (Vinton, 2008). Within Wellington, since 2001 the translocations of rare species into a predator-proof fenced sanctuary where mammalian predators are eliminated or highly controlled (Zealandia), has allowed for the recolonisation of the city by native forest bird species (Miskelly et al., 2005).

Extensive pest animal management alongside ongoing restoration efforts being undertaken by the Department of Conservation, the Wellington City Council, the Greater Wellington Regional Council, and Karori Wildlife Sanctuary Trust have allowed for the continued successful establishment of rare bird species throughout Wellington City (Vinton, 2008).

New Zealand is interesting as a context to investigate the responses of birds to the novel environmental conditions created through urbanisation, especially considering the relative recency of the introduction of mammalian predators (Amiot et al., 2021). The naive native avian fauna of New Zealand are especially susceptible to predation by introduced mammalian species, due to a lack of evolutionary adaptation (Woolley, 2020). As the urban landscape of the city of Wellington has changed, so too has the species richness of the avian population (Vinton, 2008). The less developed, greener spaces support greater species richness than the highly modified central business district (Vinton, 2008). Vinton (2008) found that the abundance of certain species varied across different landscapes. A select few species, such as house sparrows (Passer domesticus) and starlings (Sturnus vulgaris) were abundant and widespread across the city, while others such as tuī, tauhou, and blackbird (Turdus merula) were less abundant but similarly widespread. The majority of species, however, were rare and occupied constricted areas. Avian site occupancy can be indicative of species tolerance to disturbance, and their capacity to utilise smaller habitat fragments (Vinton, 2008). Most species that were limited in their occupancy of sites, but still present, were specialists in both food and habitat requirements, such as kākā (Nestor meridionalis septentrionalis), which require dense forest, and available mature or decaying trees for nesting (Vinton, 2008). More generalist species with broader habitat ranges were more commonly found in the more urbanised landscape types (Vinton, 2008). While the loss of mature forest, alongside intense hunting, resulted in large declines in birdlife in the urban reserves of Wellington, recent years records have shown increasing bird numbers, likely

benefitting from the rigorous possum control and development of Zealandia (Wellington City Council, 2007).

1.2 Focal Species: North Island kākā (Nestor meridionalis septentrionalis)

The North Island kākā (*Nestor meridionalis septentrionalis*) is a threatened forest-dwelling parrot endemic to New Zealand (Moorhouse et al., 2003; Oliver, 1974; Robertson, 1996; Wilson et al., 1998). Kākā were previously abundant throughout New Zealand, though rapid declines began being noticed in some areas as early as 1885, and by 1930 their distributions were localised (O'Donnell & Rasch, 1991). Numbers in some local populations remained high, though others suffered major declines as late as the 1960s, such as in Northland (O'Donnell & Rasch, 1991). Kākā became largely absent from the North Island with the exception of two areas - Pureora and Whirinaki (O'Donnell & Rasch, 1991). Extensive forest clearance resulting in habitat loss severely limited their distribution (Moorhouse et al., 2003), as kākā are dependent on large tracts of forest for their survival (O'Donnell & Rasch, 1991). Much of the original habitat of kākā has been destroyed or degraded through extensive deforestation (Oliver, 1974), and introduced predators and competitors have only compounded their population decline (Moorhouse, 1997; O'Donnell & Rasch, 1991; Oliver, 1974).

The loss of large tracts of lowland forest and the degradation of the remaining forest from introduced browsing mammals all contributed to the decline in kākā numbers (Moorhouse et al., 2003; Wilson et al., 1998). Predation by stoats and possums is considered the primary cause of continued population decline of kākā (Greene et al., 2004). As kākā nest in deep holes and thus have limited ability to escape nest predators, as well as long nesting periods and conspicuous nests, they are vulnerable over long periods of time (O'Donnell & Rasch, 1991). Kākā are also vulnerable to competition from mammalian browser species such as brushtail possums (*Trichosurus vulpecula*) which feed on similar foods and can induce dieback in the preferred habitats of kākā (O'Donnell & Dilks, 1986; O'Donnell & Rasch, 1991). Intensive pest management over extended periods of time has been proven to substantially reduce possum and stoat populations and has provided great benefits to kākā populations (Greene et al., 2004). Predator management efforts are in place to combat these declines, with kākā at managed sites having significantly greater numbers of individuals surviving to sexual maturity (Moorhouse et al., 2003). Nesting success at managed sites has been found to be far greater than at unmanaged sites, and predation on adult females far lower at managed sites (Moorhouse et al., 2003).

There has been limited research regarding how reintroducing kākā to an urban environment has impacted their behaviour and distribution, with existing studies in an urban context having primarily investigated their sap-feeding behaviour, and impacts on people (Charles, 2012; Charles & Linklater, 2014; Durand et al., 2013; Linklater et al., 2018). Strikingly, there are no current estimates of the kākā population size in Wellington. Previous estimates vary from 180-250 individuals (Charles & Linklater, 2013a; Recio et al., 2016) to 350-400 individuals (Leopelt et al., 2016). However, the kākā range in Wellington appears to be continuing to extend, and they are now commonly sighted in city suburbs (Gouws, 2020). A 2017 study (McArthur et al., 2017) has also shown that encounter rates of people with kākā in Wellington City increased significantly between 2011 and 2016. Kākā also possess many of the features found in urban adapter species, such as a generalist diet, medium size, behavioural flexibility, and large relative brain size. As such, they are an ideal species for exploring how endangered endemic forest species may cope with reintroduction to urbanised areas.

1.3 Thesis Objectives and Structure

The overarching aim of this study is to quantify the behaviour and spatial distribution of wild kākā in response to the novel conditions and pressures presented by the urban landscape. To achieve these objectives, I conducted observations of kākā across different locations in the Greater Wellington and Kāpiti Coast Regions of New Zealand, including urban reserves throughout Wellington, Zealandia sanctuary, and Kāpiti Island. Having a deeper understanding of how urbanisation affects kākā behaviour and distributions is important. It can help inform decisions made by city planners regarding future land use change and urban expansion, as well as assist conservation management efforts through an understanding of habitat preferences and their tolerance of human disturbance. Furthermore, this work can contribute to future studies to better understand how urban conservation can best be directed for the management of endangered species worldwide.

In Chapter Two of this study, I investigate variation in the relative abundance of kākā across Wellington, specifically in response to habitat type and human presence, and provide estimates of kākā density across Wellington, including differences in density within and outside of Zealandia. In Chapter Three of this study, I explore the influence of human presence and land cover on kākā investment in a suite of various behaviours; and investigate how kākā risk perception in response to humans varies with land cover type and human presence. In Chapter Four, I consider broadly how inhabiting an urban landscape has affected kākā behaviour, and their responses to, and tolerance of variably urbanised spaces. Furthermore, I reflect on how their responses can inform ongoing management of kākā across New Zealand, as well as implications for endangered species management worldwide.

Chapter 2: Exploring Spatial Distribution Patterns of North Island Kākā (*Nestor meridionalis septentrionalis*) Across Predatorfree Sanctuaries and Urban Reserves.

2.0 Abstract

The growing influence of humans and urban landscapes is affecting the distribution and abundance of wildlife worldwide. While the influence of human presence and urban environments on the abundance and density of birds has been studied, there is limited research on how such factors impact a forest-dwelling species reintroduced into an urban setting. I investigated the relative abundance and density of North Island kākā (*Nestor meridionalis septentrionalis*) at a mainland sanctuary, island sanctuary, and urban reserves across the Greater Wellington and Kāpiti Coast Regions in New Zealand from March to November, 2021. I found kākā abundance is not significantly influenced by human presence or land cover vegetation type. The most influential factor determining relative abundance was the time of day, with far more detections in the morning and afternoon than midday. The population density of kākā was found to be greater in the sanctuary environment of Zealandia than the urban reserves. Overall, results indicate that a sanctuary habitat with consistent resource availability is the most significant driver of kākā landscape use.

2.1 Introduction

As urbanisation increases globally, so too do novel selection pressures upon species in urban landscapes (Fernandez-Juricic & Telleria, 2000; Reijnen et al., 1997). These pressures include increased human presence, novel habitat types, and altered resource availability (Møller, 2008). In response to these challenges, species must either adjust to the new conditions or avoid urbanised spaces entirely (Lowry et al., 2013). Adjustment requires urban-dwelling species to be highly adaptable (Lowry et al., 2013), particularly in response to the increasing impacts of human interactions with wildlife (Hamer & McDonnell, 2010). Accordingly, species in urban landscapes may show altered behaviours, as compared to their rural counterparts (Traut & Hostetler, 2003). To manage the impacts of urbanisation, conservation in urban anthropogenic landscapes is becoming an increasingly common conservation management strategy (Turo & Gardiner, 2020). Within the urban conservation framework, there is the opportunity for the reintroduction of species into urban areas. However, reintroducing extirpated species into urban areas poses various challenges, especially when species that are adapted for unmodified environments, such as pristine forest, are introduced into urban landscapes, where they may either avoid, tolerate, or adapt to their new environment (Conole & Kirkpatrick, 2011). As urban conservation management becomes increasingly widespread, it is important to understand how threatened reintroduced species cope with urban environments.

Tolerance of urban environments tends to vary greatly between species, with mediumsized generalist species with broader dietary requirements typically coping more effectively than specialist species in response to habitat changes and loss (Evans et al., 2011). Such generalist species can capitalise on the abundant novel food sources present in cities (Kark et al., 2007), and exploit novel niches (Alberti, 2008). Species with broader diets have been found to outcompete specialist species in urban environments (Kark et al., 2007). For example, it has been found that the relative abundance and spatial distributions of urban tolerant birds have a positive association with areas of higher urban intensity, as opposed to urban avoiders which are associated with areas of lower urban intensity (Conole & Kirkpatrick, 2011). Previous studies have also shown a correlation between behavioural boldness and dispersal, wherein bolder species that are more likely to take risks also exhibit a

greater tendency to disperse out of their initial range (Dingemanse et al., 2003; Rehage & Sih, 2004), and are more successful as urban colonisers (Lowry et al., 2011; Myers & Hyman, 2016). For a species to be suitable for reintroduction to urban spaces, they must be able to tolerate or adapt to the challenges presented by urban landscapes. Species that can overcome such challenges and thrive in urban spaces tend to be able to exploit anthropogenic resources, such as artificial nesting sites, and processed foods, and subsequently adapt to urban living (Stofberg et al., 2019).

Globally, the transformation of natural habitats into agricultural and urbanised areas has diminished the available habitat for birds and consequently resulted in global bird population declines (Gaston et al., 2003; Hostetler & Knowles-Yanez, 2003; Shochat et al., 2010). Cities often incorporate remnant fragments of the original habitats of the area (Suhonen & Jokimäki, 1988), as well as presenting novel habitats (Pautasso, 2007). Species presence in patches of similar habitats is thought to be driven by several factors, including patch size, patch age, isolation from other patches, and the extent of the surrounding urbanisation (Soulé et al., 1988). It has been suggested that as vegetation within urban areas increases, so too should bird abundance (Savard et al., 2000), however, the vegetation cover type is influential for the bird communities (Beissinger & Osborne, 1982). Forest adapted species have been shown to be constrained when travelling through fragmented landscapes and deforested areas (Bélisle et al., 2001). The habitat suitability of urban green spaces such as parks can be further reduced by the impacts of human disturbance on such landscapes (Fernández-Juricic, 2004). Accordingly, correlations have been found between increased human visitation and decreased animal foraging, breeding, and roosting in wooded parks (Fernández-Juricic, 2004). The fragmentation and replacement of native vegetation through human disturbance, land cover change (Lowry et al., 2011; Sol et al., 2013), and mammalian predation (Sorace, 2002; Loss et al., 2013), all create novel challenges for urban-dwelling

species (Stofberg et al., 2019). As such, the reintroduction of wildlife to urban areas is limited by the extensive influence of human presence on urban green and forested spaces.

To address the various effects that humans have on the environment, and consequently wildlife in urban areas, city administrators are increasingly accounting for biodiversity in their decision making, to increase the richness of nature in urban areas (ODPM, 2005; Wellington City Council, 2015). More recently, cities have been employing the restoration of remnant indigenous vegetation patches, with some urban restoration projects involving the control or removal of invasive plants and animals, replanting, and occasionally reintroductions of indigenous species (Woolley, 2020). Such ecological restoration projects have been shown to have significant effects on a city's biodiversity. Accordingly, Zealandia ecosanctuary in Wellington, New Zealand, has brought great increases in the biodiversity of the city's avifauna (Brockie & Duncan, 2012). Zealandia is a 225-hectare 'mainland island' ecosanctuary surrounded by a predator-proof fence, located within Karori Reservoir Valley, 3 km from Wellington's highly urbanised city centre (Miskelly, 2018). The predator-proof fence was erected around the sanctuary in 1999, and a pest eradication campaign was undertaken to create a predator-free wildlife sanctuary (Miskelly, 2018; Starbridge, 2009). Prior to the erection of the fence, various revegetation projects were already underway and today Zealandia is covered by a mix of exotic and native hardwood forest in various stages of succession (Blick et al., 2008; Miskelly, 2018). The establishment of the fence allowed the eradication of fourteen mammalian pest species (Hicks, 2004) and was followed by the reintroduction of vulnerable endemic species, such as little spotted kiwi (Apteryx owenii), whitehead (Mohoua albicilla), and kākā (Miskelly, 2018). By 2002, the sanctuary was open to the public and it remains an ongoing restoration project under intensive management (Hicks, 2004). Urban ecosanctuaries also create conditions for the spill-over of reintroduced bird species to occur into nearby reserves and

residential areas (Brockie & Duncan, 2012). In Wellington, the loss of mature forest, alongside intense hunting historically, resulted in large declines in birdlife in the region (Wellington City Council, 2007). However, spill-over from Zealandia has markedly increased the prevalence of vulnerable endemic bird species in the city's urban reserves (Wellington City Council, 2013).

The kākā, an endangered endemic forest-dwelling parrot, was one of the species reintroduced to Zealandia, with the release of six captive-reared individuals in 2002 (Charles & Linklater, 2013a). Subsequent supplementary releases and successful breeding have allowed Wellington's kākā population to extend beyond the boundaries of the sanctuary across most city suburbs (Linklater et al., 2018), becoming the only known urban breeding kākā population (Charles & Linklater, 2014). Kākā possess many of the features found in urban adapter species, such as a generalist diet, behavioural flexibility, and large relative brain size (Loepelt et al., 2016). As such, they are an ideal species for exploring how endangered endemic forest species may cope with reintroduction to urbanised areas.

International research on the reintroduction of birds to urban areas is relatively limited (van Heezik & Seddon, 2018). Furthermore, there has been little research regarding how reintroducing kākā to an urban environment has impacted their behaviour and distribution, with existing studies in an urban context having primarily investigated their sap-feeding behaviour, and impact on people (Charles, 2012; Charles & Linklater, 2014; Cote et al., 2013; Linklater et al., 2018). Strikingly, there are no current estimates of the kākā population size in Wellington. Previous estimates vary from 180-250 individuals (Charles & Linklater, 2013a; Recio et al., 2016) to 350-400 individuals (Loepelt et al., 2016). However, the kākā range in Wellington appears to be continuing to extend, and they are now commonly sighted in city suburbs (Gouws, 2020). A 2017 study (McArthur et al., 2017) has also shown that encounter rates of people with kākā in Wellington City increased significantly between 2011

and 2016. As an endangered endemic species that has only recently been reintroduced to the urban environment, in which interaction with humans and a heavily modified environment occur regularly, it is critical to understand what impact these interactions may have. By understanding how kākā distributions and densities respond to urban landscapes, we can determine preferred sites and land cover types, as well as features of the urban landscape that may deter kākā foraging or nesting behaviour. Areas that have lower and greater relative abundances of kākā can be compared to find the differences between the habitats that may be attracting or deterring kākā. This may help with future reintroductions or efforts to improve the habitability of urban spaces for kākā, for example by releasing and anchoring kākā populations in favourable habitats surrounded by suitable vegetation and removing or distancing features of the landscape that act as deterrents. As such, this study intends to provide knowledge to inform and assist with future research and management of wild kākā populations in urban areas.

The first aim of this chapter was to examine how habitat availability and human presence influence the relative abundance of kākā across the Greater Wellington and Kāpiti Coast Regions. To measure the relative abundance of kākā, I used five-minute bird counts (5MBCs). In New Zealand, 5MBCs have been the standard method for counts of forest birds since the 1970s (Hartley, 2012). Given the large history of 5MBCs, and the ease of replication of the method, results from 5MBCs are easily comparable to both past and future studies (Hartley, 2012). The second aim of this chapter was to provide some of the first density estimates for kākā in the Wellington region. To estimate the density of kākā across Wellington, I used point transect distance sampling. Spatial point process models have a long history in ecology (Farr et al., 2021), and point transect sampling is one of the two most widely used methods of distance sampling (Fewster et al., 2009). Distance sampling allows for the estimation of animal density given a sample of distances to detected individuals

(Buckland et al., 2015), and is less effort-intensive, and more operatively simple than other methods such as capture-mark-recapture (Corlatti et al., 2017). Kākā have been shown to prefer establishing home ranges within native forest patches and urban areas nearest Zealandia (Recio et al., 2016). Within the Wellington region, I predicted that kākā abundance and density would be greatest within Zealandia. At study sites beyond Zealandia in Wellington city, I expected abundance and density would be greatest at parks nearest Zealandia, due to the spill-over effect. I also expected abundance and density to be greatest in areas of indigenous forest, followed by exotic forest, indigenous scrub, exotic scrub, and least in areas of exotic grassland. Finally, I predicted that kākā abundances would decrease with increased human presence across all sites.
2.2 Methodology

2.2.1 Study sites

Observations of kākā were conducted at multiple sites throughout the Greater Wellington and Kāpiti Coast Regions of New Zealand. These included Zealandia Ecosanctuary, as well as reserves across Wellington city and Kāpiti Island. Sites were selected that represented varying degrees of urbanisation, human presence, and habitat types. The Wellington urban reserves all form part of Wellington's 'Town Belt' and included Waimapihi Polhill Reserve, Mount Victoria, the Wellington Botanic Garden, and Otari-Wilton's Bush. These reserves share a total area of 256 ha (Wellington City Council, 2017). Currently, native forest comprises 22.5% of the Town Belt (Rastandeh et al., 2018), with most of the native vegetation in early stages of regeneration, consisting primarily of native forest, with some native scrub and



Figure 2.1. Map of study sites throughout Greater Wellington Region

mixed shrubland (Wellington City Council, 2013). Endemic faunal diversity has been reduced throughout the Town Belt due to habitat loss and fragmentation, as well as food supply declines through reductions in native plant diversity, predation, and pest competition (Wellington City Council, 2013). Pest mammals are the focus of ongoing control, including a possum-control programme run jointly by Wellington City Council and Greater Wellington Regional Council and intensive mustelids trapping by community groups (Wellington City Council, 2013).

Kāpiti Island is a predator-free offshore island sanctuary located approximately 5 km from the Kāpiti Coast, north of Wellington, comprising 1965-ha of regenerating native forest and shrubland (Gollin et al., 2020). As an undeveloped area with very low human presence, Kāpiti Island offers a unique environment for comparison with other sites such as Zealandia and urban reserves, which have far greater human presence and are in much more urbanised areas. The island has an extensive history of human settlement, having been occupied by Māori for centuries, resulting in the introduction of kiore (Rattus exulans) and impacts on vegetation (Maclean, 1999). Following the arrival of Europeans, most of the vegetation on the island was cleared for farming, and the island was inhabited by brushtail possums (Trichosurus vulpecula), Norway rats (Rattus norvegicus), and cats (Felis catus), as well as introduced browsing mammals such as goats (Capra hircus) and sheep (Ovis aries) (Sinclair et al., 2005). Efforts to eradicate exotic mammals on the island began in 1913 (Hicks, 2004), and were completed in 1996 when an aerial brodifacoum operation successfully removed the remaining kiore and Norway rats (Empson & Miskelly, 1999). The current vegetation on Kāpiti Island is primarily regenerating native forest and shrubland, with an abundance of kohekohe (Dysoxylum spectabile), whauwhaupaku (Pseudopanax arboreus), and tawa (Beilschmiedia tawa), with some areas of flat grasslands and flax (Gollin et al., 2021). The removal of browsing mammals from Kāpiti both encouraged re-vegetation, and increased the resources available for other species, by increasing flowering and thus nectar supply (Veitch & Bell, 1990; Towns et al., 1997).

Permissions/Animal Ethics

All observations were conducted under either COVID Alert Level 1, Alert level 2, or when there were no COVID related restrictions. During COVID Alert levels 1 and 2, all fieldwork was undertaken with additional Health & Safety precautions as required by Victoria University of Wellington, Zealandia, and Kāpiti Island. This study was approved under Victoria University of Wellington Ethics Committee AEC29088, performed under the New Zealand Department of Conservation Wildlife Authority 93048-RES, with additional permissions from Zealandia's Conservation and Research Manager, Wellington City Council, and the Otari-Wilton's Bush Trust.

2.2.2 Procedure



Figure 2.2. Locations of count stations across all study sites. Count stations are shown as coloured points, categorised by land cover type (green = indigenous forest, yellow = indigenous scrub, blue = exotic forest, orange = exotic grassland, white = exotic scrub, red = urban). Study sites are encompassed by a yellow oval. Kāpiti Island (not to scale) has been superimposed over the image of Wellington.

5-Minute Bird Counts

I performed 5-minute bird counts at Waimapihi Polhill Reserve, Wellington Botanic Garden, Mt Victoria, Otari-Wilton's Bush, Zealandia, and Kāpiti Island (Fig. 2) over a 9-month period from March to November of 2021. At each location, bird count stations were established prior to commencing data collection to avoid biasing of results by selecting specific habitat types while in the field. Each count station was a minimum distance of 200m apart. The station locations were chosen to have the greatest number of count stations possible at a location, spread most evenly over the areas, with a balance of edge and central stations within each site. All count stations were on the main tracks of each site, due to limited permit access and the risks associated with off-track work. In total there were 4 count stations in Waimapihi Polhill Reserve, 9 in Mt Victoria, 7 in Wellington Botanic Garden, 15 in Otari-Wilton's Bush, 31 in Zealandia, and 13 on Kāpiti Island.

Ten 5MBCs were undertaken at each count station except Kāpiti Island, at which seven 5MBCs were performed at each count station due to access and weather limitations. A total of 751 5MBCs were performed across the 79 count stations. All 5MBCs were conducted during daylight hours, between 9 AM and 6 PM. Counts were performed only on fine days or days with light precipitation, to ensure consistency of conditions, and to prevent biasing of results due to lower visibility and greater difficulty hearing calls on days of heavy rain. A maximum of one count per station was conducted per day. I assumed my presence would have minimal impact on kākā, as my count stations at all locations were on main tracks where visitors regularly walk and are able to observe the birds from short distances, thus acclimating the birds to human presence.

To conduct a 5MBC I stood at a station and counted all kākā heard and seen over a 5minute period. No detections of other species were recorded. At each station, I waited 30

seconds after arriving to minimise disturbance, then undertook a systematic scan for 5 minutes total. During the scan, I noted all kākā seen or heard within an estimated 200m from my location including flyovers, as well as noting whether kākā were heard only, were heard before being seen, were only seen, or were seen before they were heard. Estimates of whether a kākā was within 200m of my location were conducted through bird-counts during study piloting, wherein I would measure the distance from myself to kākā using a rangefinder, thus becoming familiar with the appearance and vocalisations of kākā at distances less and greater than 200m. The counts were recorded using a Samsung Tablet, with the results categorised by whether the bird was detected by sound or sight, and the distance from myself to the bird at the moment of detection. Where possible, I avoided counting the same bird twice within and between counts on the same day. Whenever kākā calls were heard from different directions, I assumed the birds to be unique unless confirmed otherwise, such as by witnessing an individual move from one spot to another. All counts were conducted by me, with those on Kāpiti Island conducted with the assistance of a field assistant.

For each 5-minute bird count, I also measured various other factors that could affect the distribution and conspicuousness of kākā. Data for weather factors, including precipitation, wind speed, and cloud cover, was obtained from World Weather Online (World Weather Online, 2021). Canopy height was measured at each count station using a Bushnell rangefinder, by measuring the distance from my eye at standing, to the highest point of the canopy directly overhead. As a proxy for human presence, for the duration of each 5-minute bird count, I also counted all people either seen or heard within an estimated 100-metre radius of myself.

Point Transect Distance Sampling

In conjunction with each 5MBC, I also performed point transect distance sampling (see Fig. 2) over a 9-month period from March to November of 2021. Point transect distance sampling was therefore carried out 737 times across the 79 count stations. Distance sampling was performed during daylight hours, between 9 AM and 6 PM and directly followed each 5MBC. During the preceding 5MBC, I became familiar with the kākā activity and locations in the immediate area. Immediately following the 5MBC, I took a snapshot count of all visible kākā around me. I then measured the distance from myself to the kākā using a laser rangefinder. These measurements were taken from my location to the nearest tree trunk or branch to the kākā at my eye level. When visible, I also recorded whether a kākā was banded, and the band combination (if applicable). Only kākā visible at the end of each 5MBC were included in the sampling. For each distance sample conducted, I used the same environmental data as recorded from the 5MBC carried out immediately prior. This included precipitation, wind speed, cloud cover, and canopy height, as well as the human presence count.

2.2.3 Statistical Analyses

Five-Minute Bird Counts

Analyses of count data were conducted in RStudio version 1.4.1717 (Integrated Development for R. RStudio, Inc., Boston, MA, http://www.rstudio.com/). For all tests, the alpha level was 0.05. Initially, data reformatting was conducted to make the data more suitable for modelling how the relative abundance of kākā was influenced by factors including human presence and land cover. Land cover classes were ranked from 1 - 6, with 1 expected to be the most preferred habitat, and 6 expected to be the least preferred habitat. Urban areas were defined using the New Zealand Land Cover Database (LINZ, 2020), with all "Urban parkland/open space", "Built-up area (settlement)", "Transport infrastructure" and "Surface mine or dump" polygons (henceforth "Urban"), considered urban zones. All areas of land within these polygons were categorised as urban land cover. Of the 26 land cover categories defined in the land cover database, the categories present in and around the study sites were recategorised into six broader classes, ranked as follows: 1) Indigenous Forest; 2) Exotic Forest; 3) Indigenous Scrub; 4) Exotic Scrub; 5) Exotic Grassland, and 6) Urban, with 1 expected to be the most preferred by kākā, given their ecology, and 6 the least. Areas classified as water were disregarded in the analysis. The number of people present during each count was categorised into bins of 0, 1, 2, 3, 4, and 5+, due to a few samples having very high numbers of people present (max = 68), but relatively few overall having greater than 5. Time of day was reformatted to hours after sunrise, rounded to the nearest hour. Due to few observations at 2 and 11 hours after sunrise, these categories were combined with the nearest value (2 hours with 3 hours, 11 hours with 10 hours). To examine whether land cover type, number of people present, or any other factor could predict the relative abundance of kākā across sites, I used a generalised linear mixed-effect model (GLMER) with day and count station ID as random factors. The response variable was the number of kākā counted during a 5MBC, and fixed factors were land cover type (categorical with six variables: indigenous forest, exotic forest, indigenous scrubland, exotic scrubland, exotic grassland, and urban), number of people present (categorical as 1, 2, 3, 4, or 5+), time of day (categorical as hours after sunrise from 3-11), canopy cover (measured as a percentage, included as a numeric integer), precipitation (as a numeric integer), cloud cover (measured as a percentage, included as a numeric integer), and wind speed (as a numeric integer). While it would have been preferable for all factors to be continuous where possible, including number of people and land cover type, this was not possible due to the model experiencing convergence errors when these factors were run as numeric.

Various generalised linear mixed-effects models were run, with different independent variables and random effects structures trialled to find a model that could run successfully with many parameters included. Models were initially run with maximum complexity, including all parameters possible (count, count station location, predator control, date, hours after sunrise, number of people, canopy cover, wind speed, precipitation, cloud cover, land cover type, and distance from nearest urban area) but the maximally complex models were unsuccessful due to failure of the model to converge entirely, caused by a non-positive Hessian matrix. This can occur if a model is over-parameterised, where random effect terms are estimated to be perfectly correlated, or when random-effect variance is estimated at zero. Thus, I ran further models with fewer parameters, with the most complex parameters or those directly correlating with others being removed first (Bolker et al., 2009). These models either failed to converge or violated assumptions of normality, even with removal of parameters. The final iteration of the model only converged when predator control, canopy height, and distance from nearest urban area were removed. I attempted to then use this modal as a global model from which to generate a model set by running all possible combinations of predictors, however, this resulted in significant convergence issues and thus was not possible. The residuals in this model did not violate assumptions, including normality. Consequently, a generalised linear mixed-effects model (GLMER) with a Poisson distribution, with number of birds counted as the dependent variable factors was created using lme4 package in R. Land cover type, number of people present, canopy cover, wind speed, precipitation, and cloud cover were included as fixed factors. Date and count station were included as random effects. To address final convergence issues in this GLMM, the bobyqa optimiser was employed, and the number of function evaluations increased to 200,000. Model fit checks were then evaluated. The model did not have overdispersion (p =

0.63). Residuals were plotted against expected outputs; some minor but acceptable deviation was found.

An ANOVA table was generated using Type III Wald chi-square tests to check for statistical significance among factors in this final model. Where the ANOVA suggested significant differences among categories, post-hoc Tukey tests (corrected for multiple contrasts) were used to compare across categories.

The model was used to plot graphs as dot plots using the ggplot package in R to show the effect of land cover type, number of people present, and hours after sunrise on kākā counts. Variables not shown in each plot were held at their mean value.

Point Transect Distance Sampling

The distance data was modelled using the conventional distance sampling analysis engine (CDS) in DISTANCE 7.2 (Thomas et al., 2010). This allowed the detection probability to be estimated as a function of the distance from the transect point. Density was estimated at global and stratum levels, while encounter rate was estimated at the stratum level. The detection function was estimated using global level estimates. Pooled estimates of density were constructed from area-weighted stratum estimates. The global detection function pooled all data to maximise sample size, allowing density to be estimated for each survey location, operating under the assumption that the detection curve is constant over time and location.

I used 30 manually generated equidistant distance intervals of 2 m, from 0 - 60 m, to effectively truncate the outlying data. This truncation was done as there were six samples from Waimapihi Polhill Reserve measuring 100 - 150 m, all from the same sampling event, with all other samples measuring below 60 m. The data was analysed as individuals rather than clusters. I fitted five alternative detection models: the uniform key function with a

simple polynomial or cosine adjustment term, the half-normal key function with a hermite polynomial or cosine adjustment term, and the hazard-rate key function with a simple polynomial adjustment term. I then selected the density estimates and standard errors based on the model with the lowest AIC (Akaike Information Criterion), after checking the chisquare goodness of fit outcome, and visually checking the distance histogram to ensure the model had an adequate fit to the data.

All models except the half-normal cosine model ran with warnings. The hazard-rate simply polynomial and uniform cosine models warned of parameters being constrained to obtain monotonicity, though this is typically not considered an issue, and commonly arises from small datasets (L. Thomas, personal communication, January 19, 2011). The half-normal hermite polynomial model ran with very high parameter correlation warnings. The uniform simple polynomial model ran with parameters being constrained to obtain monotonicity, and convergence failure. The hazard-rate simple polynomial model was selected, taking into consideration the above warnings, as well as this model having the lowest Delta AIC (0.00), and a non-significant goodness of fit test (*p*-value = 0.13; chi-squared value = 35.43, df= 27), and its data aligned with the detection curve most closely upon visual inspection. All other models had significant chi-square goodness of fit values (*p* <0.05) indicating significant variation of the data from the detection curve for all other models

2.3 Results

2.3.1 Five-minute bird counts

A combined total of 3755 minutes were spent conducting 5-minute bird counts across all study sites from March to November, 2021. A total of 751 unique counts were completed

across 79 count stations. A total of 1086 kākā were detected over the counts. Of the 751 counts, kākā were detected during 346 counts (46.07%), and were detected at 68 of 79 count stations (86.08%). Kākā were detected at least once at all study sites and across all sites the number of birds counted during each 5-minute bird count ranged from 0 to 11 (median 0), with a mean number of birds per count of 1.45 (SE = 0.08). An average of 1.87 (SE = 0.18) people were present during each bird count. The average 5-minute bird count was taken 6 hours and 50 minutes after sunrise. The average weather conditions were 22.7 km/h wind speed (SE = 0.54), 0.23 mm precipitation (SE = 0.05), 43.70% cloud cover (SE = 1.32). The average canopy cover was 57.79% (SE = 1.16).

From Table 2.1, we can see that Zealandia had the greatest average abundance of kākā (2.67, SE = 0.13) relative to the other sites, closely followed by halo reserve Waimapihi Polhill Reserve (1.925, SE = 0.35). Mt Victoria had by far the fewest, with an average of 0.14 kākā observed per count (SE = 0.06).

Table 2.1. Average number of kākā counted, average number of people present during sampling, and average distance from nearest area of urban land cover, at each study site.

	Waimapihi		Botanic	Otari-Wilton's			
	Polhill Reserve	Mt Victoria	Garden	Bush	Zealandia	Kapiti Island	
Count	1.93	0.14	0.43	0.43	2.67	0.51	
People	2.35	2.74	7.06	1.24	1.07	0.53	
Distance	100.25	33.89	19.86	399	506.90		
Count SE	2.24	0.59	1.57	1.26	2.24	1.15	
Count SD	0.35	0.06	0.19	0.10	0.13	0.12	

An ANOVA Type III Sum of Squares test (Table 2.2) of the model conducted shows that the factors most strongly influencing the number of birds counted, and thus relative abundance, were the land cover type ($\chi 2 = 13.71$, df = 5, p = 0.02), and time of day ($\chi 2 =$ 38.08, df = 7, p < 0.01). Overall, there was an effect between land cover types, however, when a post-hoc *p*-value adjustment using the Tukey method for multiple pairwise comparisons between land cover types was conducted, no significance was found between land cover types, with the most significant difference being between indigenous scrub and exotic scrub (z = 2.70, p = 0.07). There were far more kākā observed within indigenous scrubland environments (rate = 0.93; 95% CI [0.58, 1.49]) than exotic scrubland (rate = 0.04; 95% CI [0.00, 0.39]).

Table 2.2. ANOVA results of type III Wald chi-square tests, showing correlation between

 kākā counts and other variables

Response to Count	χ2	Df	Pr(>χ2)
(Intercept)	1.35	1	0.25
Land cover type	13.71	5	0.02
People	10.47	1	0.06
Canopy cover	0.55	1	0.46
Hours after sunrise	38.08	7	<0.01
Wind speed	0.01	1	0.91
Precipitation	3.01	1	0.08
Cloud cover	0.07	1	0.80

A *p*-value adjustment using the Tukey method showed that upon adjusting for multiple comparisons between times of day, there were significant differences in influence on kākā counts, with significantly more kākā observed 5 hours after sunrise than there were 6 or 7 hours after sunrise (z = 3.91, p < 0.01; z = 3.33, p = 0.02). There were also significantly fewer kākā observed 6 hours after sunrise than there were 9 or 10 hours after sunrise (z = -3.70. p = 0.01; z = -5.16, p < 0.01). Furthermore, there were significantly fewer observations of kākā 7 hours after sunrise than there were 9 or 10 hours after sunrise (z = -3.23, p = 0.03; z = -4.68, p < 0.01).

The number of people present showed a trend suggesting it affected the number of birds sighted, though this was not statistically significant ($\chi 2 = 10.47$, df = 1, p = 0.06). There was also a correlation between kākā observed and precipitation, though this also was not statistically significant ($\chi 2 = 3.01$, df = 1, p = 0.08).

From Figure 2.3, a trend is shown in which the greatest expected count is at count stations with between one and two people present. At zero or three people present, similar counts are expected. Furthermore, expected counts of kākā are lowest with four or more people present.



Expected Total Count by Number of People

Figure 2.3. Expected total kākā count by number of people. Bars depict standard error.

From Figure 2.4 a trend in kākā observations is visible in which the number of kākā observed decreases at six to seven hours after sunrise. Relative kākā abundance is heightened in the mornings and evenings and is greatest at around 10 hours after sunrise.



Figure 2.4. Expected total kākā count by hours after sunrise. Bars depict standard error.

Figure 2.5 shows relative kākā abundance was lowest within areas of exotic scrub and urban land cover. Relative kākā abundance was greatest in areas of indigenous scrub and exotic grassland land cover, though the large error bars indicate this correlation is not statistically significant.



Figure 2.5. Expected total kākā count by land cover type. Land cover types are ranked as follows: 1) Indigenous Forest; 2) Exotic Forest; 3) Indigenous Scrub; 4) Exotic Scrub; 5) Exotic Grassland, and 6) Urban. Bars depict standard error.

2.3.2 Distance Sampling

A total of 751 distance samples were conducted across the Greater Wellington and Kāpiti Coast Regions from March to November, 2021. These records spanned 79 sampling sites, with 42 observations of kākā. 18 of these observations were of only one bird, while 11 of the distance samples had observations of two or more individuals. Two of the observations were made on Kāpiti Island, and were excluded from the model. This was due to the significantly lower number of distance samples on Kāpiti Island compared to Zealandia, which strongly influenced the density estimates for sanctuary habitats. The model truncated observations of sightings at over 60 metres, resulting in a total of 34 observations rather than 42. The model ran included 660 distance samples, with 34 observations. The most individuals observed in one distance sample was at Waimapihi Polhill Reserve, where six kākā were detected. The location with the greatest number of kākā observed was Zealandia, at 23, while the least was Mt Victoria, at zero (Table 2.3). Overall, there were 25 observations within sanctuary environments, including Zealandia and Kāpiti Island, and 17 in urban reserves. For the purposes of this analysis, however, Kāpiti was excluded to allow for a simpler comparison of sanctuary vs non-sanctuary, due to the large site area (19.65km²) of Kāpiti Island, and the low detection rate of 2 observations potentially biasing model outputs. The greatest number of kākā observed relative to sample size was at Waimapihi Polhill Reserve, at seven, though this was over only two unique distance samples. There appears to be a trend in which the number of kākā observed decreases with distance from Zealandia. The lack of observations in data collected from Kāpiti Island, Mt Victoria, and Otari-Wilton's bush despite adequate sampling effort (90-150 samples per site) likely reflects low densities of kākā at these locations.

Location	Samples Taken	Kākā observed
Polhill	40	7
Mt Vic	90	0
Botanic	70	8
Otari-Wilton's	150	2
Zealandia	310	23
Kapiti	91	2

Table 2.3. Number of kākā observed and total samples taken during point transect distance sampling, at each study site in the Greater Wellington and Kāpiti Coast Regions (Figure 2.1)

The global detection probability of kākā was 0.05. Figure 2.6 shows the data violates the assumption of all kākā on the point being detected (Buckland et al., 2005), as none were detected at 0 metres. No kākā were detected at fewer than 4 metres from the observer. Most records for kākā were <12m from the point, reflecting the density of vegetation and low visibility at most count stations. Within this range, there were significantly more kākā recorded at 4-6 metres from the point than any other distance. Beyond 30 metres from the point transect, very few kākā were detected. The number of individuals of kākā decreased as distance from the point transect increased, and the standard detection functions gave adequate fit to the distributions of frequency ($\chi 2 = 35.43$, df = 27, p = 0.13).



Figure 2.6. Detection probability of kākā across the Wellington Region fitted to a hazard-rate model with a simple polynomial adjustment. Data produced from Distance, using a hazard-rate model with a simple polynomial adjustment.

Within the urban sanctuary site, 310 samples were conducted, with a total of 23 observations of k $\bar{a}k\bar{a}$ recorded. The estimated density of k $\bar{a}k\bar{a}$ within the urban sanctuary site is 145.29/ per km² (CI 69.17, 305.17) (Table 2.4). The estimated total number of k $\bar{a}k\bar{a}$ within the urban sanctuary was 327 (CI 156.00, 687.00).

Table 2.4. Density and abundance estimates of kākā in a sanctuary habitat (Zealandia) in Wellington, New Zealand. Data produced from Distance, using a hazard-rate model with a simple polynomial adjustment. D denotes estimated density per square kilometre; N denotes estimated total abundance. Effort = 310 metres; Width = 60 metres, number of observations = 23.

Parameter	Point Estimate	Standard Error	Percent Coef. of Variation	95% Confidence Interval
D	145.29	56.29	38.74	69.17 305.17
N	327.00	126.69	38.74	156.00 687.00

Within Urban Reserves, 350 samples were conducted, with 11 total observations. The estimated density of kākā within urban reserves is 61.54 per km2 (CI 24.75, 153.01) (Table 2.5). The estimated total number of kākā within the urban reserves is 158.00 (CI 63.00, 392.00).

Table 2.5. Density and abundance estimates of $k\bar{a}k\bar{a}$ in an urban reserve habitat in Wellington, New Zealand. Data produced from Distance, using a hazard-rate model with a simple polynomial adjustment. D denotes estimated density per square kilometre; N denotes estimated total abundance. Effort = 350 metres; Width = 60 metres, number of observations = 11.

Parameter	Point Estimate	Standard Error	Percent Coef. of Variation	95% Confidence Interval
D	61.54	30.01	48.76	24.75 153.01
Ν	158.00	77.05	48.76	63.00 392.00

The estimated density of kākā within the sanctuary environment was over twice as great as that of the urban reserves, at 145.29 (SE = 56.29, 95% CI [69.17, 305.17]) as compared to 61.54 (SE = 30.01, 95% CI [24.75, 153.01]). The confidence intervals, however, do overlap, suggesting they could be more similar than suggested. It also is worthwhile to note that kākā observed within the urban reserves could be the same as those identified in the urban sanctuary environment, due to the large ranges of kākā, and the close proximity of the sanctuary site to some of the urban reserve sites.

2.4 Discussion

Overall, the results suggest that kākā were more abundant in Zealandia than in urban reserves. Kākā density and abundance across the Greater Wellington Region was found to be greater in sanctuary habitats than in urban reserves. The relative abundance of kākā across the Greater Wellington and Kāpiti Coast Regions is not strongly influenced by human presence. Land cover type broadly influences the relative abundance of kākā, but there is no significant difference in abundance specifically between each land cover type. The relative abundance of kākā varies with hours after sunrise, being significantly reduced at six to seven hours after sunrise, and greater in the morning and afternoon. Kākā detectability is greatest in the morning and afternoon, and lowest during midday, which is consistent with other studies that have found significant declines in bird detection between early and late morning (Blake, 1992; Lynch 1995), at which point activity continues at a reduced capacity (Robbins, 1981). Increased ambient temperatures at midday have been suggested to reduce bird activity in order for birds to conserve energy (Verbeek, 1972).

Surprisingly, the relative abundance of kākā was not shown to decrease with increased human presence. A study conducted by St Clair et al. (2010) found that increased exposure to humans led to habituation in a shorebird species. It is possible that kākā, similarly, have adapted to humans and do not perceive people as a predatory threat, and thus their use of the landscape is not influenced by human presence. The lack of a significant decline in relative kākā abundance in areas with greater human presence may be in part due to the influence of humans on predator species. The primary predators of k \bar{a} k \bar{a} in New Zealand are suggested to be possums (*Trichosurus vulpecula*) and stoats (*Mustela erminea*) (Moorhouse et al., 2003; Wilson et al., 1998). In residential areas within Wellington, possums have been found to be rarely present, if not absent, as compared to a high presence in forest habitats (Balls, 2019), due to intensive possum management investment (Greater Wellington Regional Council, 2007). Pest control can increase the size of bird populations, as has been shown by a study wherein counts of kākā, amongst other endemic avian species, were significantly higher in an area with intensive pest control compared to an area with lesser pest control and consistently higher numbers of possums (Smith & Westbrooke, 2004). In urban and urban-adjacent areas, we could thus expect decreased densities of possums, effectively countering the expected decrease in kākā abundance in urban areas. There is also evidence that stoats can identify the scent of male humans, and exhibit agonistic responses (Watson & King, 2021), suggesting stoats may be averse to human interaction. Thus, the potentially

lower presence in areas with greater human presence of species that predate and compete with kākā may counteract the disturbance caused by humans, resulting in an insignificant difference in kākā abundance with increasing human presence.

While high levels of human recreation, most commonly walking, have been found to decrease bird densities at points close to trails, this effect was significantly smaller at points further from trails (Bötsch et al., 2018). As the bird counts conducted were unbounded, the detection of kākā far from trails, on which the counts were undertaken, may have countered the expected impacts of pedestrian areas on kākā. Kākā are conspicuous birds due to their large size and loud vocalisations, allowing for detection at large distances. In fact, at all study sites there were more kākā detected at distances of over 200 metres as compared to less than during 5MBCs, excluding Otari-Wilton's Bush, where the difference was negligible. Alternatively, this may also indicate an avoidance of highly trafficked areas. Forest birds have been shown to avoid areas such as trails that have high levels of pedestrian use (Bötsch et al., 2018).

Existing literature suggests that kākā abundance should be expected to decrease with increased human presence, due to human-induced disturbance, vegetation alteration, and fragmentation (Bötsch et al., 2018; Campbell, 2009; Fernández-Juricic, 2000). The level of significance found in our results for the relationship between number of people and kākā abundance was still near significant following a Tukey's *p*-value adjustment. It is possible that this correction may have resulted in a type I error (Ruxton & Beauchamp, 2008), and thus the non-significance seen. Regardless, we can still infer that the results still show a trend in which kākā are less abundant in areas with more people present. The presence of people in forest environments has been shown to disturb wildlife, due to the perception of humans as potential predators (Bötsch et al., 2018; Frid & Dill, 2002). Greater levels of human presence within fragments has been shown to reduce abundances of forest birds (Fernández-Juricic,

2000). Birds in similar tree patches have also been shown to be less abundant in areas with greater, compared to lesser, human presence (Campbell, 2009). As well as the human presence being greater on trails, the construction of trails themselves can impact wildlife through habitat loss, alterations in vegetation, and fragmentation (Benninger-Truax et al., 1992; Bregman, et al., 2014; Trombulak & Frissell, 2000). Furthermore, as recreation intensity increases, bird abundances decline, and birdlife in forests used for recreation for decades was still found to be negatively affected by recreationists, indicating the effects of human disturbance are not outweighed by habituation (Bötsch et al., 2018). It has been found that in areas with greater presence of a mammalian predator, the feral cat, sensitivity to human presence is increased, and birds exhibit greater flushing distances (St Clair et al., 2010). As such, in urban spaces, where free-roaming cats are abundant (Balls, 2019; Flockhart et al., 2016), we can expect sensitivity to humans to be greater, and thus relative abundances to be lower.

The relative abundance of kākā at Mt Victoria was lower than any other location (mean = 0.14, SE = 0.59), despite exotic forest environments, which comprise the majority of Mt Victoria's land cover, not being associated with especially low abundance. This may be driven by the high levels of human disturbance in Mt Victoria, which experiences the highest intensity of use of all forested areas of the Wellington Town Belt, being used by pedestrians, dog-walkers, and mountain bikers (Wellington City Council, 2018). The unexpectedly high relative abundance of kākā in exotic grassland habitats is likely a result of both the small sample size (n=24) of observations in exotic grassland areas, and due to sixteen of the nineteen kākā observed in exotic grassland land cover types being sighted at distances of over 200 metres. All these observations were conducted at count stations on Kāpiti Island, wherein distances greater than 200 metres indicate the birds themselves were not within or over exotic grassland habitats, but more likely indigenous forest land cover.

The finding that land cover type showed no significant effect on kākā abundance is unusual, given the evidence that kākā tend to establish home ranges in native forest patches within urban landscapes (Recio et al., 2016), suggesting abundance should be greatest in indigenous forest habitats relative to other land cover types. It is therefore likely that kākā spatial distributions in Wellington are being driven more strongly by other factors. Supplementary feeder locations have been shown to strongly drive the visitation rates and group sizes of kākā in residential areas (Recio et al., 2016), and conspicuousness in Zealandia (Armstrong, 2020).

While the results indicate that $k\bar{a}k\bar{a}$ detectability is greatest in indigenous scrub, this may reflect differences in visibility between indigenous scrub environments and forested areas. The natural habitat of kākā is native forest, wherein they occupy the mid to high canopy (Recio et al., 2016), as such greater kākā abundance would be anticipated in areas of indigenous forest. As scrubland environments tend to have greater visibility and lower canopy heights than forests, visibility is greater in scrubland, and kākā present are more likely to be perched at eye level, and thus are more likely to be detected. Past studies suggest that birds will typically exhibit human avoidance behaviour, especially forest-dwelling species (Bötsch et al., 2018; Fernández-Juricic, 2000; Miller et al., 2001). Such literature tends, however, to be based on northern hemisphere species, whereas kākā are a naïve island species that did not co-evolve with humans or any mammalian predators (Maloney, 1991; Massaro et al., 2008). As such, kākā may not fit the assumption of abundance decreasing with increased human presence. Furthermore, the relatively high abundances of kākā in urban adjacent areas such as Wellington Botanic Garden, and the statistically insignificant relationship between human presence and kākā abundance suggests that kākā living in urban spaces may become accustomed to people and not associate them with the threat posed by other mammalian species.

Zealandia was found to have greater densities of kākā present than the Wellington urban reserves. Furthermore, though not statistically significant, kākā were found to be most abundant in areas of indigenous scrub and exotic grassland, and least in exotic grassland and urban areas (Fig. 6). This may be a result of the count stations in most count stations in Zealandia, and all count stations in Waimpaihi Polhill Reserve being primarily categorised as having indigenous scrub land cover. The presence of supplementary feeders, alongside nesting boxes, and an absence of mammalian predators in Zealandia have resulted in significant growth of the kākā population in Zealandia, likely driving the abundance of kākā found in habitats of indigenous scrub (Gouws, 2020; Karori Sanctuary Trust, 2013). Kākā are vulnerable to competition from introduced mammalian browsers such as possums, due to the similarity in preferred food types (O'Donnell & Rasch, 1991). As cavity nesters with long nesting periods, conspicuous nests due to the strong scent associated, and fledglings that spend time on the ground before learning to fly, kākā are also vulnerable to predation (O'Donnell & Rasch, 1991). A study by Moorhouse et al. (2003) found predation to be the primary cause of nesting failure in kākā, with stoats being the main predator and possums being implicated in egg, nestling, and nesting female predation also. The distribution of kākā throughout Wellington has been shown to be driven mostly by resource availability, especially supplementary food (Recio et al., 2016). Gouws (2020) found kākā sightings to be most common in areas nearest Zealandia, at which visitation rates and group sizes were greatest. Zealandia and Waimapihi Polhill Reserve having the greatest relative abundances of kākā indicates that the impact of Zealandia's halo is a stronger driver of kākā spatial distribution than land cover type.

Of the distance samples conducted at Kāpiti Island, very few detected any kākā. While distance sampling detection rates were very low, there were still 47 5MBC detections, of which the majority (n = 24) were birds at distances of over 200 metres, or that were heard only (n = 18). This is likely a result of a low density of kākā present on Kāpiti Island, and the terrain of the island, which features sharp cliffs, ridges, and gullies (Brown & Sherley, 2002; Cowan, 1992). The mountainous terrain made visual sightings of kākā much more difficult at Kāpiti Island as compared to other sites, such as Zealandia. It is also possible that due to the lower human presence on Kāpiti Island, the kākā present are less habituated to people, and as such are more wary than individuals with greater exposure to people (Metcalf et al., 2000), and less likely to stay in close enough proximity to be detected during distance sampling, following a 5MBC.

The number of kākā detected at Mt Victoria, Kāpiti Island, and Otari-Wilton's Bush was very low compared to that of the rest of the sites, suggesting low densities at these locations. Sampling results recorded with distances greater than 100 metres from the observer were truncated. Kākā may violate the assumption that detection probability depends on the distance from the observer as they are a highly conspicuous species, being relatively large and very vocal birds. As such they may not be appropriate for distance sampling. In future, an alternative framework may be adopted for determining the density of kākā populations, such as capture-mark-recapture. Although distance sampling is a cost-effective method of determining the density of a species, the high required effort and intensive labour required for this method, and the low number of distance sample detections as compared to 5MBC detections suggests that this method is not ideal for highly mobile species such as kākā.

The effect of predator control on kākā abundance was not able to be accounted for in this study despite attempts. Multiple attempts to incorporate predator control as a factor into the 5MBC model were unsuccessful due to the model encountering various errors and being unable to run. Predator control was attempted to be included through the following categories of sanctuary status: urban reserve, mainland sanctuary, offshore island sanctuary.

Overall, findings suggest that the relative abundance of kākā throughout the Greater Wellington and Kāpiti Coast Regions is not significantly influenced by either human presence or land cover type. Relative abundance is more likely to be driven by resource availability, and proximity to Zealandia. The population density, however, of kākā is greater within the sanctuary environment of Zealandia than amongst the urban reserves of Wellington. Limitations of this study include the inability to account for seasonal effects on kākā abundance, as all study sites were not visited proportionately throughout the year. Furthermore, the kākā abundance model was not able to include all desired parameters, including the distance from the nearest urban area, or whether the count station in question was within a sanctuary. Additionally, distance sampling was likely not an ideal means of determining kākā density, as kākā violate the assumption that detection probability is based on proximity to the observer due to their highly conspicuous nature. Finally, only 42 distance samples detected any individuals, as opposed to the recommended 60. Alternative frameworks could be employed in future to greater success, such as mark-recapture (Lettink & Armstrong, 2003).

2.5 Conclusion

Although limited, this study has produced some of the first density estimates of Wellington's kākā population, reinforcing the efficacy of Zealandia and mainland sanctuaries as a tool for reintroduction and long-term management of endangered endemic bird species. The influence of human presence and land cover type has not been found to influence kākā abundance, though this may reflect shortcomings in study design. I encourage future researchers to investigate further into the factors influencing kākā landscape use and spatial distributions is critical for a greater understanding of how conservation efforts can best be tailored to ensure the continued growth of New Zealand's urban kākā populations.

Chapter 3: Variations in Behaviour and Risk Perception of North Island Kākā (*Nestor meridionalis septentrionalis*) Across Urban Reserves and Sanctuaries

3.0 Abstract

Increasing interaction between humans and wildlife has driven species to either adapt or avoid urban spaces. The effects of human exposure on risk perception and flight initiation distances in birds are well studied but remain limited in the context of forest-dwelling species within urban landscapes. I explored the behaviour and risk perception of North Island kākā within a mainland sanctuary, island sanctuary, and urban reserves across the Greater Wellington and Kāpiti Coast Regions in New Zealand from March to November of 2021. Human presence and whether the individual was within a sanctuary did not affect the behaviours measured, though time of day influenced the time individuals spent vigilant and foraging. The vegetation land cover type was shown to influence time spent foraging and preening. Insufficient flight initiation distance data was able to be collected for meaningful conclusions to be drawn. Overall, time of day and environmental conditions were found to be the most significant factors predicting behaviour in kākā.

3.1 Introduction

Direct encounters between humans and wildlife have become increasingly frequent as habitat fragmentation and human population growth have rapidly increased (Tätte et al., 2018). For a species to successfully colonise an urban area, they must be tolerant of novel disturbances and be able to avoid chronic stress and significant disruption to essential activities (McGiffin et al., 2013). The success of establishing in urban areas is largely determined by behavioural

flexibility, with urban colonising species of birds tending to have larger relative brain sizes, and high frequencies of foraging innovation as compared to species that do not establish in urban landscapes (Sol et al., 2002). Behavioural flexibility allows urban birds to tolerate a wide variety of environmental conditions, including those found in modified landscapes, such as disturbed habitat (Bonier et al., 2007). Such flexibility also allows birds to adjust their behaviour to overcome novel causes of potential detriment, including the challenges of breeding in urban environments, and to take advantage of novel nesting sites and food sources (Bonier et al., 2007). Birds living in urban environments tend to either be urban adapters, and able to adapt to the urban habitat and utilise natural resources, or urban exploiters, which thrive in urban environments to the extent to which they become dependent on urban resources (Blair, 1996). Urban adapters and exploiters are tolerant of a wide breadth of urban conditions (Shochat et al., 2006).

Urban-dwelling species tend to exhibit different traits from those in surrounding nonurban habitats, such as in behaviour, breeding, and stress responses (Partecke et al., 2006; Sih et al., 2010; Tuomainen and Candolin, 2011). Risk perception and anti-predatory behaviour is notably different between urban and rural animals (Cavalli et al, 2018). The risk perception of some species has been linked to environmental risk perception, with individuals capable of recognising and learning when a given stimulus ceases posing a threat (Cavalli et al., 2018). Human presence presents the primary disturbance factor in urban environments, with many species perceiving it as threatening (Blumstein, 2014; Frid & Dill, 2002; Lima, 2009). To manage the trade-off between the energetic cost of a response to an approaching threat and the cost of predation, urban animals must learn to assess risk to maximise cost reduction (Cavalli et al., 2016, 2018; Frid & Dill, 2002). Habituation to humans develops through the acquisition of tolerance to human presence, and as such, the extent of tolerance is reflective of the level of opportunity to learn that humans generally are not a threat (McGiffin,

Beckman, & Johnson, 2013). As such, habituation should be expected to increase with proximate human presence, and tolerance of humans to increase along the rural to urban gradient (McGiffin, Beckman, & Johnson, 2013).

Urban-dwelling animals often consider humans to be predators (Frid & Dill, 2002). As such, risk perception and fearfulness are important to measure. Vigilance and flight initiation distance (FID) are both considered measures of fearfulness (Laundré et al., 2010; Stankowich & Blumstein, 2005; Welp et al., 2004). Reduced vigilance has been suggested to indicate increased boldness as well as increased habituation to humans (Uchida et al., 2019). A study by Tätte et al. (2019), however, suggested that vigilance and FID do not reflect fear equally; vigilant individuals escape at shorter distances, with urban birds being more vigilant and less fearful, thus having shorter FIDs. As such, greater vigilance may be associated with a less sensitive response to risk. It has been suggested that increased tolerance of humans may result in decreased time allocated to vigilance and shorter FID, as well as increased time allocated to other activities such as foraging (Ward & Low, 1997). Urban animals tend to show increased boldness, which is thought to be a coping response to human-induced environmental alterations (Uchida et al., 2019).

Increased boldness has been associated with reductions in FID in response to humans approaching (Uchida et al., 2019). FIDs and alert distances have been found to be shorter in urban areas as compared to non-urban areas, and birds from ancestral non-urban populations (García-Arroyo & MacGregor-Fors, 2020; Møller & Tryjanowski, 2014; Uchida et al., 2019). Rural bird populations also tend to have greater variance in their FIDs than urban bird populations (Møller, 2010). A study by Lin et al. (2012) suggests that bird species that have large populations and a high propensity for dispersal tend to have FIDs that decrease more significantly along the rural-urban gradient. Urban birds also tend to exhibit a less sensitive escape response to human approach than their non-urban counterparts (Davey et al., 2019; Møller et al., 2013). The variation in flight distance between rural and urban populations varies between species (Møller & Tryjanowski, 2014). A study by Møller (2010) has shown that urban populations of birds experience increasing variation in FIDs with time since urbanisation, associated with increased urban population density, suggesting that as birds become more urban adapted, they also develop behavioural flexibility. FIDs of birds in forests have been found to be shorter when the forests are more heavily frequented by people (Bötsch et al., 2018), reflecting adaptation of stress responses over exposure to risk stimuli. Not all species are able to habituate to the urban environment (Blumstein, 2014). In a study by Blumstein (2014), it was found that increased human visitation, which would be expected to habituate birds, was found to increase FIDs, reflecting sensitisation of the birds rather than habituation.

There are multiple hypotheses that attempt to explain the differences in FID between urban and non-urban individuals, and the relationship to human disturbance tolerance (Cavelli et al., 2018). One hypothesis posits habituation and associated fear reduction in response to humans through exposure over time (Blumstein, 2016; Cooke, 1980; Li et al., 2011; Rodríguez-Prieto et al., 2009; Vincze et al., 2016). Alternatively, the differential colonisation hypothesis proposes that a selection process has resulted in species that are inherently bolder and less fearful being capable of settling areas closer to humans, whereas those exhibiting more fear would settle farther (Carrete & Tella, 2010, 2011; Møller, 2010). As such, fear behaviour is considered a result of selection (Møller, 2008). Cavalli et al.'s (2018) study found that in urban and rural owls exposed to human stimuli at two different frequencies, rural owls had decreased FIDs for both treatments, whereas urban individuals only decreased their FIDs at the higher intensity treatment. At a glance, this would suggest that increased exposure to approaching humans led to habituation, yet in the light of the differential colonisation hypothesis (Carette & Tella, 2010, 2013), it is possible that individuals of behavioural types with greater tolerance are more likely to colonise areas in closer proximity to humans (Cavalli et al., 2016, 2018).

A study on flush distances in birds in urban parks found that larger species showed less tolerance for human disturbance compared to smaller ones (Fernández-Juricic et al., 2001). They also found that birds in parks with greater levels of human visitation were more tolerant of humans. Complex habitat structures also have been shown to increase the tolerance of birds to humans as there is greater available cover for hiding (Fernández-Juricic et al., 2001). Bird species diversity and movement in fragmented urban landscapes is influenced by patch and cover configuration and characteristics (Visscher et al., 2018). At a local level, however, risk perception in birds is more strongly correlated with foraging effort (Lee et al., 2005; Tsurim et al., 2008, 2010; Valcarcel & Fernández-Juricic, 2009). Availability and proximity of cover influenced bird risk perception, with birds foraging more, and thus perceiving risk as less, when closer to the nearest cover, and with greater overhead canopy coverage (Vischer et al., 2018). Some species are able to habituate to areas of high pedestrian density, as reflected by decreased response to exposure to a stimulus, whereas some species are not (García-Arroyo & MacGregor-Fors, 2020). Research regarding the relationship between vertical space use and risk perception and avoidance in urban birds is very limited; altered vertical space use could potentially be an urban behavioural adaptation that has been largely overlooked in the existing literature. Nyatanga et al. (2021) did find, however, that FID decreases as the perch height of an individual increases, potentially due to a greater field of view, and decreased perception of threat upon the approach of a human (Nyatanga et al., 2021).

Vigilance, or scanning, is a monitoring behaviour, or state of alertness, wherein relevant stimuli such as predators, food, and competition are readily detected (Beauchamp, 2015; Bednekoff & Lima, 1998; Quenette, 1990; Treves, 2000). Vigilance is considered an

anti-predator behaviour used in preventing and escaping predation (Tätte et al., 2019; Ward & Low, 1997). As such, it reflects fearfulness (Tätte et al., 2019). Birds in urban areas and areas of greater human disturbance tend to be more vigilant than rural birds, indicating that the distractions of an urban environment more significantly impact vigilance than the lower expected risk of predation (Tätte et al., 2019; Ward & Low, 1997). Greater vigilance in urban areas may also be a method of compensating for the pressure placed upon the sensory and cognitive systems of birds by excessive environmental distractions (Quinn et al., 2006). Birds exhibiting greater vigilance have been observed as detecting predators no earlier than less vigilant individuals but investing more time in risk assessment and having shorter escape distances (Tätte et al., 2019). The proportion of time spent vigilant was also not found to differ along the rural-urban gradient (McGiffin et al., 2013). Urban birds exposed to high rates of human contact that is largely harmless would need to habituate to an extent in order to function optimally, but this habituation may require a threshold of contact in order to occur (McGiffin et al., 2013).

As vegetation presence and structures change in urban landscapes, so too can the communities of avifauna present within them; studies investigating the presence and relative abundances of bird species within urban spaces have found that species that have specialist dietary and habitat requirements are typically limited in their presence to sites that host such specific resources (Vinton, 2008). Furthermore, habitat specialists that require especially large patches of natural habitat and interior spaces within habitat patches are often significantly impacted within urban spaces (Chace & Walsh, 2006; McKinney, 2002; Pickett et al., 2001), as fragmentation and patch size reduction minimise their available habitat (Battles et al., 2013; Marzluff & Ewing, 2008; Standish et al., 2012; Yu et al., 2012; Zipperer et al., 2012). As such, the highly disturbed mosaic of vegetation and land cover types within urban environments can limit the presence of some species with specific habitat requirements

(Vinton, 2008), such as forest-dwelling birds, and altered resource availability and vegetation structures likely also influence investment in foraging and vigilance behaviours.

Urban bird populations can also be negatively impacted through anthropogenic noise associated with developed urban spaces (King et al., 2012), which can interfere with vocal communication (Merrall & Evans, 2020). Increased exposure to anthropogenic noise has been shown to increase vigilance levels (Quinn et al., 2006), as well as reducing feeding rates and visitation rates to supplementary feeders (Van Donselaar et al., 2018). Birds at more urban sites, however, showed less notable reductions in feeding rates, suggesting urban populations may have habituated to noisy environments (Merrall & Evans, 2020). Human presence was also not found to influence foraging rates in birds, though it did influence vigilance and flight responses (Prestes et al., 2018); in areas of high anthropogenic noise, birds have been observed to fail to exhibit anti-predator responses when exposed to conspecific alarm calls (Grade & Sieving, 2016; Zhou et al., 2019). Preening behaviour, whilst typically not driven by environmental stimuli, has been known to occur in the context of exposure to stressors. A study by Delius (1988) found that birds often exhibited bouts of comfort behaviour following a stressful situation, including brief preening. As such, birds that are not habituated to humans may perform such a bout of comfort behaviour, and thus preening, in response to interactions with people.

With the success of Zealandia's efforts to increase the kākā population of Wellington, direct and indirect interactions between kākā and humans have grown significantly (Cote et al., 2013). While kākā are neophobic (Bond & Diamond, 2004; Wilson et al., 1991), interactions between people and kākā still occur, and at increasing frequency with proximity of the area to Zealandia (Cote et al., 2013). As interactions between kākā and humans occur at an increasing frequency, it is important to understand what impacts this may have on their behaviour, and to understand what behavioural adaptations may already have occurred, as an

indicator of their adaptability to urban environments. By establishing baseline knowledge surrounding the urban and human tolerance levels of kākā, the limitations and boundaries to urban reintroduction efforts may be better informed.

The first aim of this chapter was to explore the influence of human presence and land cover on kākā behaviour. Specifically, I examined how these factors impacted vigilance, foraging, and preening behaviours, and vertical space use (i.e., preferred foraging height) by kākā. To investigate the behaviour and vertical space use of kākā, I conducted focal following samples throughout urban reserves in Wellington, Zealandia, and Kāpiti Island. Focal follow sampling is an established method of behavioural observation that is ideal for focusing on the behaviour of one animal, especially when exhibiting many behaviours rapidly (Lehner, 2002). I predicted that in areas with greater human presence, and in urban reserves as compared to sanctuaries, kākā would spend more time exhibiting vigilant behaviour and less time foraging, as well as spending more time at greater distances from the ground. I also predicted that in areas of urban land cover, individuals would spend less time foraging and be more vigilant. The second aim of this chapter was to determine how human presence and land cover type may affect risk perception in kākā. To estimate risk perception, I performed flight initiation distance (FID) tests. FID is the exact distance at which an animal will begin to flee from a perceived approaching threat (Blumstein, 2003). FID testing is a useful metric for quantifying perception of risk in animals, due to the ease of measurement (Stankowich & Blumstein, 2005), and replicability. FID testing is used in wildlife management to determine set-back zones for wildlife, beyond which wildlife behaviour is not impacted by human disturbance (Fernández-Juricic et al., 2005; Rodgers Jr & Smith, 1995). As highlighted above, FID is typically lower in urban birds as compared to their non-urban counterparts, as such I expected the FIDs of kākā to be greatest at Kāpiti Island, followed by urban reserves, and smallest within Zealandia.

3.2 Methods

3.2.1 Study site and species

The study sites (Otari-Wilton's Bush, Wellington Botanic Garden, Mount Victoria, Waimapihi Polhill Reserve, Kāpiti Island, Zealandia) and study species (kākā) are identical to those described in Chapter 2.

Permissions/Animal Ethics

All permissions and animal ethics approval for fieldwork undertaken in this chapter are identical to those described in Chapter 2.

3.2.2 Procedure

Behavioural Observations

I conducted focal follow observations of kākā at all study sites (Fig. 2) over a 9-month period from March to November of 2021. I opportunistically conducted a focal follow whenever an individual was seen while I was not actively performing the 5-minute bird counts (5MBC) or point-transect distance sampling methods that are described in Chapter 2. Individuals were only recorded if I could assume that I had not performed a focal follow on the individual prior, as determined by bird band combinations for birds with leg bands; birds without leg bands were all treated as unique. Focal follow sampling was undertaken on any kākā seen, excluding kākā seen at known supplementary feeder locations (in Zealandia and Wellington Botanic Garden). The focal follows were conducted by slowly walking along each track between 5MBC count stations, actively scanning surroundings and listening for kākā calls; when a kākā individual was sighted I filmed the bird on a Samsung S8+. While filming, I narrated the behaviours exhibited and the estimated elevation of the bird above the ground to the nearest metre. Behaviours recorded included perching, resting, moving, foraging,
vocalising, preening, courtship/mating, and aggression/fighting. I stayed at least 5 metres away from the individual at all times and only moved when necessary to maintain my line of sight. Each recording lasted up to 5 minutes, or until the bird left the area, whichever occurred first. I also recorded the band combination of each individual where possible to prevent observing the same bird twice.

Focal follow samples were performed on 50 birds across all study sites. All focal follows were conducted during daylight hours, between 9 AM and 6 PM. Focal follows were undertaken on the same days as 5MBCs and point-transect distance sampling, and as such were only done on fine days or days with light precipitation. Data for precipitation, wind speed, cloud cover, canopy height, canopy cover, and human presence for each focal follow was taken from the 5MBC conducted that day at the nearest count station.

Flight Initiation Distance Testing

To measure kākā risk perception, I undertook flight initiation distance testing over a 9-month period from March to November of 2021 at all study sites (Fig. 2). FID testing was conducted on kākā found while walking between 5MBC count stations. These were exclusively undertaken on kākā sitting or standing at a height no greater than 3.5 metres (approximately double researcher height) above the ground, at the beginning of each experiment. This ensured the kākā would perceive me as a potential threat. Kākā at known supplementary feeder sites (Zealandia and Wellington Botanic Garden) were not tested. The test involved approaching the kākā at a steady walking pace until the individual moved away from the position it had been occupying at the start of the test. I stopped moving as soon as the kākā began moving away from me. The distance between myself and the kākā at the time that fleeing was initiated was measured to the nearest metre using a Bushnell rangefinder and recorded as the flight initiation distance. A total of 9 FID tests were conducted across all sites. All FID testing was conducted during daylight hours, between 9 AM and 6 PM. All FID testing was undertaken on the same days as 5MBC and point-transect distance sampling, and as such were only done on fine days or days with light precipitation. Data for precipitation, wind speed, cloud cover, canopy height, canopy cover, and human presence for each FID was taken from the 5MBC conducted that day at the nearest count station.

3.2.3 Statistical Analyses

Behavioural Observations

Analyses of focal follow videos were conducted in BORIS v7.10.3 (Behavioral Observation Research Interactive Software) (Friard & Gamba, 2016). Occurrences of foraging, alert (i.e., scanning), preening, courtship, aggression and moving behaviours, as well as vocalisations and height of each individual above the ground, were extracted from video recordings. The total amount of time each individual spent exhibiting a given behaviour was converted to a proportion of the whole recording duration, as each recording was a different length of time. These proportions were then weighted by the total length of time of the given recording, giving longer recordings more significance in the model than shorter ones.

Data reformatting and analyses were undertaken in RStudio version 1.4.1717 (Integrated Development for R. RStudio, Inc., Boston, MA, http://www.rstudio.com/). Multimodel averaging and inference (using the MuMin package) was used and for all tests the alpha level was 0.05 (i.e., if the 95% confidence interval for a mean effect size estimate did not include zero it was considered a significant association between the predictor and the response). Land cover classes were defined using the method described in Section 2.2.3. Time of day was reformatted to hours after sunrise, rounded to the nearest hour. Due to the very limited number of focal follow observations at Kāpiti Island (n = 2) compared to

Zealandia (n = 35) and Wellington reserves (n = 13), the Kāpiti Island recordings were excluded from analyses, but these data are reported in the results.

For the multi-model averaging separate global models were first created for the average weighted proportion of time spent exhibiting alert, preening, and foraging behaviour, using linear models. Fixed factors included in each global model were land cover type (as numeric with five rank levels in assumed ascending order of preference, based on the existing literature on kākā foraging behaviour and habitat selection (Recio et al., 2016; Vinton, 2008; Wilson et al., 1991); 1=indigenous forest, 2=exotic forest, 3=indigenous scrubland, 4=exotic scrubland, 5=urban), number of people present (as a numeric integer), time of day (numeric as hours after sunrise from 4-9), canopy cover (measured as a percentage, included as a numeric integer), canopy height (as a numeric integer), sanctuary status (categorical with two variables: sanctuary and urban reserve), precipitation (as a numeric integer), cloud cover (measured as a percentage, included as a numeric integer), and wind speed (as a numeric integer). To ensure that canopy height was not correlated with sanctuary status, I also tested for a significant difference in mean canopy heights between sanctuary (mean = 8.00, SE = (0.96) and urban reserve (mean = 9.46, SE = 0.25) environments using a two-tailed T-test for 2 independent means (Social Science Statistics, n.d.b.) and found no significant difference (t = 0.855, p = 0.397). I also tested for a significant difference in human presence between sanctuary (mean = 0.43, SE = 0.25) and urban reserve (mean = 2.94, SE = 0.82) environments using a two-tailed T-test for 2 independent means (T Social Science Statistics, n.d.b) and found significantly greater human presence in urban reserves than sanctuary environments (t = 2.037, p = 0.047).

A global model for time spent at heights above 4 metres was created using a generalised linear model, with a binomial error structure (where 0 was given as the response variable for observations where kākā spent the majority of their time below 4 m and 1 given

to observations where the majority of time was spent above 4 m). This global model included all fixed factors included in global models described above, excluding land cover type and canopy height, as these would inherently influence whether an individual was able to be at heights above 4 metres within a canopy. The preferred height of kākā was determined by continuously recording the estimated height of each kākā from the ground during the focal follow. Estimated heights were recorded in the following bin values: 0-2m, 2-4m, 4-6m, 6m+. Preferred height was then categorised as either above or below 4 metres, approximately twice the head height of the researcher, and higher than the predator-proof fence around Zealandia (and consequently higher than the maximum jumping height of predatory mammals (Zhang et al., 2021)), and thus a height at which the birds are presumably safe from predators based on whether each individual spent more time above or below 4 metres during the focal follow observation.

For each global model, a model set was generated by running all possible combinations of predictors. The five models with the best fits, as well as the intercept only models, are shown in table 3.1, along with their Akaike information criterion corrected for small sample sizes (AICc), the difference in AICc compared to the best-fitting model (Δ AICc), and the Akaike weight (AICw), providing the conditional probability of the model (Burnham & Anderson, 2002). All possible models in the model set were then averaged to provide average model parameter estimates and associate 95% confidence intervals (Burnham & Anderson, 2002). Graphs were then plotted using the ggplot package in R, comparing responses with fixed factors found to have significant explanatory power.

Flight Initiation Distance Testing

Flight initiation distance data was very limited, with only 9 samples recorded, 8 of which were from Zealandia. Due to the limited results, analyses to test differences in FID between sanctuary and urban sites could not be conducted. Consequently, analysis was limited to the measurements recorded from kākā within Zealandia. I ran a spearman's rank correlation test (Social Science Statistics, n.d.a.) to determine the effect of human presence and the distance to the nearest supplementary feeder on the FIDs of kākā that were tested in Zealandia. Human presence data was obtained from the nearest 5MBC conducted on the same day. Estimated distances of each kākā from the nearest supplementary feeder were measured using Google Earth (Google Earth, 2022) by measuring from the nearest 5MBC count site to the nearest supplementary feeder (located at either Tui Terrace or the upper kākā feeders in Zealandia).

3.3 Results

3.3.1 Behavioural Observations

Of the 50 total recordings, there were 35 at Zealandia, nine at Wellington Botanic Garden, two at Waimapihi Polhill Reserve, two at Otari-Wilton's Bush, and two at Kāpiti Island. A total of 48 unique recordings of kākā were analysed, with those from Kāpiti Island excluded, totalling 138 minutes and 1 second. The average recording time was 2 minutes and 45 seconds. On average, kākā spent 17.6% of their time preening (SE=4.68), 28.1% of their time perched (SE= 3.99), and 26.9% of their time foraging (SE=4.65). The remaining time consisted of mating, moving, and aggressive behaviour. Of the 48 recorded kākā, 29 spent the majority of their time while recorded at heights above 4 metres from the ground. For the two recordings of kākā on Kāpiti, birds spent an average of 1.2% of their time preening, 59.3% of their time perched (SE=34.68), and were foraging for 17.9% of their time, and spent most of their time at heights above 4 metres. Standard errors were not calculable for time spent preening or foraging due to only one of the two recordings including these behaviours.

None of the top five models for the time spent alert, foraging, preening, or at heights above 4 metres included the intercept only models (Table 3.1). As such, we can assume that some of the fixed factors tested have some explanatory power for the trends in responses found.

Table 3.1: Supporting data for the top five models for the analyses of various behaviours across all birds (N=48). The intercept only model was not in the top 5 ranked models for any responses but has been included for reference. AICc is the small sample Akaike Information criteria, Δ AICc is the change in AICc relative to the top model, AICw (Akaike weight) is the conditional probability of the model.

Response	Model	AICc	ΔAICc	AICW
	1. canopy height + hour + sanctuary	-0.05	0.00	0.05
	2. hour + sanctuary	0.52	0.57	0.04
time spent alert	3. canopy height + hour	0.72	0.77	0.04
	4. hour	1.11	1.16	0.03
	5. canopy height + cloud cover + land cover + sanctuary	1.64	1.69	0.02
	41. intercept only	4.66	4.71	0.01
	1. cloud cover + hour + precipitation + land cover	42.13	0.00	0.07
	2. hour + land cover	43.26	1.13	0.04
time spent foraging	3. hour + precipitation + land cover	43.36	1.23	0.04
	4. cloud cover + hour + precipitation + land cover + sanctuary	43.45	1.32	0.03
	5. hour + land cover + sanctuary	43.57	1.44	0.03
	138. intercept only	51.44	9.31	0.00
	1. human presence + land cover	48.78	0.00	0.06
	2. canopy cover + human presence + land cover	49.45	0.67	0.04
time spent preening	3. land cover	49.94	1.48	0.03
	4. cloud cover + human presence + land cover	50.27	1.50	0.03
	5. hour + human presence + land cover	50.67	1.79	0.02
	148. intercept only	56.46	7.69	0.00
	1. cloud cover + wind speed	64.14	0.00	0.04
	2. cloud cover	64.56	0.42	0.04
time spent at heights	3. cloud cover + human presence + wind speed	64.82	0.68	0.03
above 4 metres	4. cloud cover + human presence + sanctuary	64.85	0.71	0.03
	5. cloud cover + human presence	65.03	0.89	0.03
	21. intercept only	66.53	2.39	0.01

It was found that one variable, hours after sunrise, had a significant association with the proportion of time individuals spent exhibiting alert behaviour. The relative importance of hours after sunrise as a predictor of time spent alert (RVI=0.89) and foraging (RVI=0.94) was very high (Table 3.2), with hours after sunrise present in all top five models for time spent foraging, and the top four models for time spent alert (Table 3.1), indicating hours after sunrise was a significant explanatory factor for both time spent alert and foraging. The model-averaged effect size estimate predicted that individuals, on average, would spend an additional 5.3% of their time alert with each additional hour after sunrise (mean $\beta \pm s.e. =$ 0.053 ± 0.021 , 95% CI = 0.010 to 0.096) (Table 3.2). From Figure 3.1a we can see that the average proportion of time spent alert by $k\bar{a}k\bar{a}$ was lowest between 5 and 6 hours after sunrise, after which point it steadily increased over the following hours of the day. Hours after sunrise was also found to have a significant association with the time spent foraging. The model-averaged effect size estimate also predicted that individuals, on average, spent 10% less time foraging with each additional hour after sunrise (mean $\beta \pm s.e. = -0.100 \pm$ 0.036, 95% CI = -0.172 to -0.028). Figure 3.1b shows the average proportion of time spent foraging by kākā increases until 6 hours after sunrise, then decreases for the remainder of the day.

Land cover type rank was also a very important predictor for time spent foraging and preening, appearing in 98% of models in the top model set for foraging (RVI=0.98) (Table 3.3), and 94% of models in the top model set for preening (RVI=0.94) (Table 3.4), suggesting land cover type has very strong predictive power for time invested in foraging and preening. Land cover type rank was also found to be a significant predictor of time spent foraging (mean $\beta \pm$ s.e. = 0.141 ± 0.045, 95% CI = 0.050 to 0.131), with the greatest proportion of time invested in foraging in indigenous scrub (rank 3) and exotic scrub (rank 4) environments, though there was only one observation of foraging in an exotic scrub

environment (Figure 3.2a). The proportion of time individuals spent preening was also significantly influenced by land cover type rank (mean $\beta \pm s.e. = -0.129 \pm 0.046$, 95% CI = -0.222 to -0.035), with the greatest relative investment in preening in indigenous forest (rank 1) and exotic forest (rank 2) environments (Figure 3.2b).

Table 3.2: Multi-model averaged parameters for the analyses of the proportion of time spent exhibiting alert behaviour across all birds (*N*=48). For each predictor, the relative variable importance (RVI, calculated as the sum of the AIC weights for all models that contain the predictor), the mean regression coefficient (β), the SE and 95% CI for mean β . Sanctuary status coded as binary (focal follow conducted on an individual either inside or outside a sanctuary environment, inside a sanctuary treated as reference level). Land cover type is ranked from 1-5, with 1 as the most preferred habitat, and 5 the least (1=indigenous forest, 2=exotic forest, 3=indigenous scrub, 4=exotic scrub, 5=urban).

Response	Predictor	RVI	Mean β	SE	95% CI		
	hours after sunrise	0.89	0.053	0.021	0.010	to	0.096
	sanctuary status	0.58	0.146	0.087	-0.028	to	0.320
	canopy height	0.55	-0.008	0.005	-0.018	to	0.002
proportion of	cloud cover	0.28	0.001	0.001	-0.001	to	0.002
time spent	precipitation	0.25	-0.132	0.241	-0.616	to	0.351
alert	land cover type	0.24	-0.012	0.031	-0.073	to	0.050
	canopy cover	0.24	0.000	0.002	-0.003	to	0.004
	human presence	0.22	0.005	0.020	-0.035	to	0.044
	wind speed	0.22	0.000	0.002	-0.005	to	0.005

Table 3.3: Multi-model averaged parameters for the analyses of the proportion of time spent exhibiting foraging behaviour across all birds (*N*=48). For each predictor, the relative variable importance (RVI, calculated as the sum of the AIC weights for all models that contain the predictor), the mean regression coefficient (β), the SE and 95% CI for mean β . Sanctuary status coded as binary (focal follow conducted on an individual either inside or outside a sanctuary environment, inside a sanctuary treated as reference level). Land cover type is ranked from 1-5, with 1 as the most preferred habitat, and 5 the least (1=indigenous forest, 2=exotic forest, 3=indigenous scrub, 4=exotic scrub, 5=urban).

Response	Predictor	RVI	Mean β	SE	95% CI		
	land cover type	0.98	0.141	0.045	0.050	to	0.231
	hours after sunrise	0.94	-0.100	0.036	-0.172	to	-0.028
	precipitation	0.57	0.644	0.400	-0.158	to	1.447
proportion of	cloud cover	0.43	-0.002	0.002	-0.005	to	0.001
time spent	canopy height	0.34	-0.009	0.008	-0.024	to	0.007
foraging	sanctuary status	0.33	-0.148	0.140	-0.429	to	0.133
	canopy cover	0.32	0.002	0.003	-0.003	to	0.008
	wind speed	0.22	-0.001	0.004	-0.009	to	0.007
	human presence	0.21	-0.002	0.030	-0.062	to	0.057

Table 3.4: Multi-model averaged parameters for the analyses of the proportion of time spent exhibiting preening behaviour across all birds (*N*=48). For each predictor, the relative variable importance (RVI, calculated as the sum of the AIC weights for all models that contain the predictor), the mean regression coefficient (β), the SE and 95% CI for mean β . Sanctuary status coded as binary (focal follow conducted on an individual either inside or outside a sanctuary environment, inside a sanctuary treated as reference level). Land cover type is ranked from 1-5, with 1 as the most preferred habitat, and 5 the least (1=indigenous forest, 2=exotic forest, 3=indigenous scrub, 4=exotic scrub, 5=urban).

Response	Predictor	RVI	Mean β	SE	95% CI		
	land cover type	0.94	-0.129	0.046	-0.222	to	-0.035
	human presence	0.67	-0.059	0.031	-0.120	to	0.003
	canopy cover	0.37	-0.003	0.003	-0.009	to	0.003
proportion of	cloud cover	0.35	0.002	0.001	-0.001	to	0.005
time spent	precipitation	0.31	-0.372	0.413	-1.200	to	0.457
preening	sanctuary status	0.27	-0.118	0.169	-0.457	to	0.222
	wind speed	0.26	0.003	0.004	-0.005	to	0.011
	hours after sunrise	0.25	-0.019	0.039	-0.097	to	0.059
	canopy height	0.22	0.002	0.008	-0.015	to	0.019





Figure 3.1: (*a*) The average proportion of time that individuals spent exhibiting alert behaviour at different numbers of hours after sunrise. (*b*) The average proportion of time that individuals spent foraging at different numbers of hours after sunrise. The shaded areas surrounding depict 95% confidence intervals.



Figure 3.2: (*a*) The average proportion of time that individuals spent exhibiting foraging behaviour at different numbers of hours after sunrise. (*b*) The average proportion of time that individuals spent preening at different numbers of hours after sunrise. The whiskers show range, the boxes display interquartile range, and the bold centre line depicts the median value. Land cover type is ranked from 1-5, with 1 as the most preferred habitat, and 5 the least (1=indigenous forest, 2=exotic forest, 3=indigenous scrub, 4=exotic scrub, 5=urban).

None of the fixed factors tested were shown to significantly influence the proportion of time individuals spent at heights about 4 metres (Table 3.5). Effect estimates for all fixed factors tested across height responses had 95% confidence intervals overlapping zero (Table 3.5).

Table 3.5: Multi-model averaged parameters for the analyses of the proportion of time spent at heights above 4 metres from ground level across all birds (*N*=48). For each predictor, the relative variable importance (RVI, calculated as the sum of the AIC weights for all models that contain the predictor), the mean regression coefficient (β), the SE and 95% CI for mean β . Sanctuary status coded as binary (focal follow conducted on an individual either inside or outside a sanctuary environment, inside a sanctuary treated as reference level). Land cover type is ranked from 1-5, with 1 as the most preferred habitat, and 5 the least (1=indigenous forest, 2=exotic forest, 3=indigenous scrub, 4=exotic scrub, 5=urban).

Response	Predictor	RVI	Mean β	SE	95% CI		
	cloud cover	0.73	-0.019	0.009	-0.038	to	0.000
	human presence	0.52	0.272	0.190	-0.111	to	0.655
proportion of	wind speed	0.40	0.033	0.028	-0. 023	to	0. 089
time spent	sanctuary status	0.33	-0.831	0.930	-2.698	to	1.037
above 4m	canopy cover	0.31	0.013	0.018	-0.022	to	0.049
	precipitation	0.27	0.980	2.507	-4.042	to	6.002
	hours after sunrise	0.25	-0.095	0.225	-0.549	to	0.358
	canopy height	0.23	-0.003	0.061	-0.126	to	0.121

3.3.2 Flight Initiation Distance Testing

A total of nine FID tests were conducted from April to November, 2021. Of these tests, eight were conducted within Zealandia, and one within the Wellington Botanic Garden. The average FID for individuals within Zealandia was 4 metres (SE = 0.40), and 7 metres for the individual in the Wellington Botanic Garden. The largest FID of all individuals was the individual tested in the Wellington Botanic Garden (7 m), whereas the greatest FID recorded

within Zealandia was 5 metres. For the tests conducted in Zealandia, no significant correlation was found between FID and the distance to the nearest supplementary feeder (r_s = -0.37, p = 0.37), or human presence (r_s = -0.35, p = 0.39).

3.4 Discussion

Overall, the findings suggest that kākā behaviour is most strongly influenced by the time of day and type of land cover of the area they are in. Land cover type was found to influence the proportion of time individuals invested in foraging and preening. The proportion of time spent foraging and alert was found to be influenced by the number of hours after sunrise. The proportion of time that individuals spent at heights greater than 4 metres was not strongly predicted by any of the fixed factors tested in this study. There was not enough data collected to draw any meaningful conclusions regarding differences in FIDs between sanctuary and non-sanctuary environments.

The proportion of time kākā spent alert decreased until between 5 and 6 hours after sunrise, after which point the proportion of time increased over the remainder of the day. Conversely, the proportion of time that individuals invested in foraging increased until between 5 and 6 hours after sunrise, after which it declined over the remaining hours of the day. An early morning peak in foraging behaviour is expected, as energy reserves and fat stores that depleted during a night of fasting need to be (Bonter et al., 2013; Pravosudov & Grubb, 1998). Following this, an extended period of low activity levels is expected, as birds maintain their reserves (Bonter et al., 2013), especially as the ambient temperature increases (Verbeek, 1972). When energy reserves are sufficiently high later in the day, a greater proportion of time can be invested in vigilance behaviour (Pravosudov & Grubb, 1998). As such, vigilance is lowest in the morning, but increases throughout the day as foraging

behaviours decrease with reduced demand for energy gain. This is consistent with the findings of Ward & Low (1997), who suggested that time spent foraging increased as time spent alert, or vigilant, decreased. As birds are unable to simultaneously scan their surrounding environments for predators and feed, these behaviours are mutually exclusive, and thus it follows that as the proportion of time invested in one behaviour increases, the other decreases. The vigilance behaviours of kākā may also be reflective of the behaviours of predatory species with which kākā coevolved, such as the kārearea /New Zealand falcon, which are known to hunt fledgling kākā (Powlesland et al., 2009). Kārearea hunt most intensely during the morning and evening; the increased vigilance behaviour later in the day in kākā may reflect the increased hunting activity of karearea (Fox, 1977), while the lower vigilance in the morning may be a trade-off in order to ensure sufficient energetic replenishment.

Kākā investment in foraging in areas of indigenous scrub environments may be reflective of the distribution of land cover types across the study sites. Indigenous scrub was strongly represented by observations in Zealandia, with 18 of 19 focal follows in indigenous scrub environments occurring in Zealandia. As such, the greater investment in foraging in indigenous scrub environments may more strongly reflect differences in foraging behaviour between Zealandia and the urban reserves of Wellington. As kākā living in the predator-free Zealandia sanctuary may have reduced perception of predation risk, they may feel more comfortable investing time in foraging, due to both a lower risk of being preyed upon while foraging, as well as a lessened risk of predation from increased levels of feeding (Bonter et al., 2013). Typically, birds can be expected to invest highly in foraging in the morning to replenish energy reserves that were depleted during the night (Bednekoff & Houston, 1994; McNamara et al., 1994). A period of reduced foraging occurs between morning and evening, as the increased weight of birds resulting from feeding causes increased vulnerability to predation, due to a reduced capacity to quickly escape from an approaching predator (Bonter et al., 2013; Macleod et al., 2005). Given the reduced risk perception that resident kākā of Zealandia may have, they may feel comfortable investing heavily in the morning due to the generally low predation risk. Additionally, foraging investment is likely greater in areas of indigenous scrub due to the dietary preferences of kākā, who feed on species such as five-finger (*Pseudopanax arboreus*), mahoe (*Melicytus ramiflorus*), kohekohe (*Dysoxylum spectabile*), and rewarewa (*Knightia excelsa*) (Miskelly 2018; Watts et al., 2014), all of which are present in Zealandia's regenerating native scrub.

These species are well represented amongst the indigenous scrub of Zealandia. Furthermore, the absence of competing mammalian species such as possums in Zealandia suggests the food resources available in Zealandia are less likely to be over-browsed by species such as possums, and thus food availability would be higher (Moorhouse et al., 2003; Wilson et al., 1998).

The proportion of time spent preening was greatest in areas of indigenous and exotic forest. This may be reflective of the higher perch heights available in forested areas. At greater perch heights, birds tend to exhibit decreased risk perception (Nyatanga et al., 2021). As such, k $\bar{a}k\bar{a}$ may feel safer to preen when in such environments as forests. While preening is an important behaviour for maintenance of body condition, the timing of it is not critically dependent on environmental stimuli, rather, it is considered somewhat of a spare-time activity, conducted when there is no more important activity to do (Delius, 1988). It is possible that individuals are not inherently more likely to invest in preening when in forested areas had greater canopy heights (mean=9.50, *SE*=1.312), and thus likely provided higher available perches than areas of scrub (mean=6.70, *SE*=0.97), possibly creating an environment of lower perceived risk.

Flight initiation distance was found to be lower, on average, in Zealandia than the botanic garden, though there was not enough data to make any meaningful comparison. There was no correlation between FID and the distance to the nearest supplementary feeder for individuals tested within Zealandia. This may be a reflection of the strong flying abilities of kākā, as individuals tested near the feeders are not necessarily different from those tested further from the feeders. As kākā are a highly mobile species (Moorhouse, 1997; Moorhouse et al., 2003), individuals that frequent the feeders are also likely to be found in other areas of Zealandia, as well as nearby urban reserves. The difference in FID between the individuals in Zealandia and the kākā tested in the Wellington Botanic Garden may be reflective of habituation to approaching mammalian species amongst the kākā of Zealandia. Individuals within Zealandia would likely have experienced many non-harmful interactions with humans and have lower levels of exposure to predatory mammals such as cats, rats, and stoats as compared to individuals nesting in the urban reserves of Wellington. Individuals residing in the Wellington Botanic Garden, however, would be more likely to have had potentially harmful exposure to mammalian predators, and thus may be more wary, or have become sensitised (Blumstein, 2014).

The finding that human presence and sanctuary status were not explanatory factors for any of the behaviours explored here may reflect habituation of the kākā population of Wellington to humans and the urban environment. This may be a result of high levels of exposure of kākā to humans across Wellington City, both within Zealandia and across the urban reserves, especially as a neophobic species (Wilson et al., 1991). Given the relatively recent history in New Zealand of human-wildlife interaction, and of predatory mammalian introductions (Maloney & McLean, 1995, Worthy & Holdaway, 2002), the threshold for habituation to humans in kākā may be relatively low, allowing the levels of exposure experienced by individuals in both sanctuary and urban environments to result in habituation.

Alternatively, as proposed by the differential colonisation hypothesis, the kākā individuals that chose to settle outside of the sanctuary environment and in more urbanised areas may have bolder personality types and be more tolerant of the environmental stressors of an urban landscape (Carrete & Tella, 2010). As such, these individuals may show no significant difference in behaviours such as vigilance compared to kākā living in Zealandia, despite the expectation for greater investment in vigilance to overcome the sensory stress of the loud and more densely populated urban environment (Merrall & Evans, 2020). Human presence has also been found not to influence foraging rates in birds, but rather the use of green spaces for leisure by humans can reduce available foraging areas (Prestes et al., 2018). As such, it follows that foraging rates were comparatively low in urban areas, wherein human leisure activity is more common, as opposed to the indigenous scrub of Zealandia, where leisure activity is restricted to established tracks.

Overall, the findings suggest that kākā behaviour and risk perception was not directly influenced by human presence in Wellington. However, the city environment did indirectly influence behaviour in the sense that urban areas are associated with changing land cover use and land cover type rank was associated with foraging and preening behavioural changes in kākā. Time of day was the only other factor found to predict any of the behaviours measured, though cloud cover was very close to significant in predicting time above 4 metres. Unfortunately, due to limited data, meaningful analysis of FIDs as a measure of fearfulness was not possible. In future, an alternative method of measuring risk perception would likely be more effective, such as a study design exploring vigilance behaviour specifically, rather than a broader behavioural study such as this one, as a very low number of individuals were found at low enough heights from the ground to conduct an FID test.

3.5 Conclusion

This study has provided some of the first analyses of how the behaviour of urban-dwelling kākā is influenced by human presence and habitat types. Human presence and sanctuary status was not found to influence kākā behaviour, though this may reflect some shortcomings in sample sizes. Vegetation land cover was, however, found to influence foraging and preening behaviours. This study supports the need for a broader understanding of how species behaviour is influenced by increasing urbanisation and human disturbance, in order to better manage and increase vulnerable species populations. I encourage future researchers to further investigate how risk perception in kākā is affected by human presence and the urban environment, to better understand how tolerant kākā are of urban spaces and manage conservation efforts accordingly.

Chapter Four: General Discussion

4.1 Research Summary

The overall aim of this study was to determine how kākā behaviour and distributions are influenced by interactions with the urban landscape and humans, and thus gain a better understanding of their capacity to adapt to cities. The main objectives were: 1) to examine how habitat availability and human presence influence the relative abundance of kākā across the Greater Wellington and Kāpiti Coast Regions; 2) to provide some of the first density estimates for kākā in the Wellington region; 3) to explore the influence of human presence and land cover on behavioural flexibility and risk-taking behaviours in kākā; and 4) to determine how human presence and land cover type may affect risk perception in kākā.

Observations of the relative abundance and density (Chapter 2) of kākā across Wellington showed the distribution of kākā across the landscape of Wellington city was not uniform, with far greater relative abundance of kākā in Zealandia than the urban reserves throughout the city. This is consistent with the findings of other studies, wherein kākā distributions were found to align most strongly with resource distribution across the city, especially supplementary food sources, which are provided supplementarily in Zealandia (Recio et al., 2016). Additionally, this study successfully provided a density estimate of Wellington's kākā, and found that densities of kākā were greater within Zealandia than in the urban reserves of Wellington. The number of distance sampling observations, however, was quite low despite efforts, and furthermore, kākā violate the assumption that detection probability is based on proximity to the observer, as they are highly conspicuous birds with loud vocalisations. As such, alternative frameworks such as mark-recapture (Lettink & Armstrong, 2003) may be able to more accurately quantify kākā density in future projects. The extent of human presence at each site was not, however, shown to be influential in determining the spatial distribution of kākā. This may be indicative of a degree of habituation resulting from continued exposure (St Clair et al., 2010), allowing kākā to better tolerate human presence in order to utilise the resources present in otherwise inaccessible areas (Cavalli et al., 2018; Frid & Dill, 2002). Furthermore, areas with greater human presence in Wellington are associated with lower mammalian predator presence due to intensive management (Balls, 2019; Greater Wellington Regional Council, 2007). The level of predator management intensity at each site was not, however, able to be accounted for in the bird counts, due to convergence errors when attempting to run the model for analysis. This could be overcome in future in a study looking more specifically at the impact of varying predator control intensities on the relative abundance of kākā, rather than accounting for a wide breadth of variables as this study has done. While the type of land cover broadly influenced distributions of kākā, no specific land cover type was found to be preferred over any other, suggesting their space use within the landscape is more strongly driven by other factors, such as the supplementary food resources available within Zealandia (Gouws, 2020; Karori Sanctuary Trust, 2013). The greatest difference in land cover preference found was between indigenous and exotic scrub, which was likely driven by the high representation of indigenous scrub cover in Zealandia and Waimapihi Polhill Reserve, a halo reserve of Zealandia. Rather, the relative detectability of kākā was found to be most strongly linked to the time of day, with greater numbers detected in the morning and evening, likely driven by higher ambient temperatures at midday reducing kākā activity as individuals conserve their energy (Blake, 1992; Lynch, 1995).

The second study (Chapter 3) indicated that kākā behaviour is most strongly influenced by land cover and time of day. Variation in investment in foraging and vigilance behaviours over the course of the day is expected, as individuals must recoup their energy in the morning following a period of overnight fasting (Bonter et al., 2013), driving higher

foraging levels during the early hours of the day. Vigilance investment reflects foraging investment, as they are mutually exclusive behaviours (Ward & Low, 1997), as such, individuals are less vigilant when spending more time foraging, and vice versa, explaining lower levels of vigilance in the morning, increasing over the day. Foraging behaviour was greatest in areas of indigenous scrub, a vegetation cover that was strongly represented within Zealandia. The investment into foraging, vigilance, and preening behaviours was not significantly lower in areas of urban land cover compared to other land cover types, nor was investment in these behaviours found to be predicted by whether an individual was outside of the sanctuary environment as compared to within it. Furthermore, none of the behaviours were significantly influenced by differing levels of human presence. Considering all of these factors together, these results suggest kākā have habituated and adapted to the urban environment to some degree, as we would expect notable differences in behaviours if they had not (Partecke et al., 2006; Sih et al., 2011; Tuomainen & Candolin, 2011). We are not able to definitively conclude, however, that the city environment did not indirectly influence kākā behaviour, as land cover type as a whole was associated with changes in preening and foraging behaviours. The behavioural observations were potentially impacted by the baseline human presence for all observations being one person, due to the observer's presence. As such, none of the observations were able to quantify kākā behaviour without some degree of human presence. This could potentially be overcome through the use of motion detected cameras recording behaviour without the need for a person to be present, though this method could also have issues with consistent data collection and would require many hours of labour to review the footage. Further studies are needed to confirm whether risk perception of humans varies in kākā with differing levels of exposure to people and the urban environment, which is critical to more deeply understanding the degree of habituation kākā have undergone. Due to the limited number of FIDs conducted, analysis of risk perception

regarding humans in kākā was not possible. An alternative study design may be necessary in future assessments of human tolerance, owing to the preference of kākā to spend time in the mid to upper canopy (Cote et al., 2013), making FID testing difficult. A study design looking explicitly at vigilance behaviour could better determine habituation and risk perception in kākā. It would also be very impactful for a future study to look into behavioural flexibility and innovation in kākā in urban areas as compared to non-urban or rural spaces, as a measure of adaptation to the urban environment (Lefebvre et al., 1997; Evans et al., 2011).

Overall, the observations made in this study indicate that while kākā abundance is greatest in Zealandia relative to the urban reserves of Wellington, their behaviour and spatial distributions do not appear to be strongly influenced by human presence or the urban environment, but rather resource availability and time of day. As such, these findings suggest kākā have been able to adapt to the urban environment to an extent, especially considering the number of kākā in Wellington continues to increase as the population increasingly proliferates into the residential areas and suburbs of the city (Gouws, 2020; Recio et al., 2016).

4.2 Management Implications

With the ongoing pest management being undertaken (Vinton, 2008), the continued supplementary feeding by Zealandia and Wellington residents (Galbraith et al., 2014), and ongoing forest regeneration providing increased natural food and habitat resources (O'Donnell & Dilks, 1994), it is likely that the kākā population of Wellington will continue to increase. The success of Zealandia has already seen greater numbers of kākā in Wellington, and a greater presence in the city beyond the sanctuary fence, leading to more frequent human-kākā interactions (Linklater et al., 2018). This, especially, has been noted in the

neighbourhoods bordering Zealandia, where many residents have enjoyed their increased presence, and thus been more likely to interact with the birds (Chug, 2010). These increasingly frequent interactions between people and kākā, wherein it is not uncommon for residents to provide food for the birds (Cote et al., 2013), have likely assisted in the birds becoming less neophobic and more habituated to human presence.

As interaction between people and wildlife within cities continues to increase in frequency around the world, the potential for conflict must be managed, as it poses a threat of hindering progress and support for conservation (Charles, 2013; Madden, 2004). Increasing densities of people in urban spaces drives not only greater disturbance, but also increased potential for community-led predator management, which has proven to be effective in Wellington (McArthur et al., 2017). Furthermore, the increased presence of an endangered endemic species such as kākā within a city is likely to convey benefits to the human community, through increased opportunity for people to connect with nature, potentially leading to more positive attitudes towards urban conservation and conservation as a whole (Galbraith, 2016). Within New Zealand, the public aspect of conservation support is especially critical, owing to the considerable contributions to biodiversity conservation made by community groups and volunteers (Charles, 2012). As the number of people dwelling in cities grows, conservation action is becoming increasingly dependent upon the experiences people have with wildlife (Snep et al., 2016); consequently, it has been argued that wildlife interactions are equally important as conservation action itself (Fernández-Juricic & Jokimäki, 2001; Savard et al., 2000). In suburban areas of cities, biodiversity is commonly driven by human values and preferences, wherein socioeconomic status, culture, ethnicity, and social norms commonly drive national and local regulations and legislation (Kinzig et al., 2005). As such, in order to ensure the success of future reintroduction efforts, conservation

managers must take a socio-ecological approach, both providing adequate habitat conditions for the target species, and maintaining positive human-wildlife interactions.

Reintroductions of extirpated species into modified anthropogenic landscapes is always complex, and requires consideration of many novel challenges, such as the highly modified landscape of private gardens, parks, and reserves (van Heezik & Seddon, 2018). While urban environments often do present degraded and modified habitats for species, they still host significant promise in enhancing animal species populations within cities (van Heezik & Seddon, 2018). Successful reintroduction of a species such as kākā into an urban landscape requires they develop a degree of tolerance to human presence and habituate to the urban environment in order to successfully utilise the foraging, nesting, and breeding grounds available, without incurring excessive energetic cost from overestimating risk posed by humans. The results indicating the development of tolerance and habituation in kākā suggest they are adaptable and thus could be introduced to other urban spaces within the country.

The success of Wellington's kākā population has been largely driven by Zealandia, through the provision of supplementary food, and the anti-predator fence (Gouws, 2020). It may be possible, however, for a reintroduction of kākā into another urban landscape that does not feature a predator-free refuge, but rather maintains suppressed numbers of mammalian predators and competitors, and reliable sources of food (Gouws, 2020). As pest mammal species, namely cats, rats, and dogs, have been identified as the predominant limiting factor for urban reintroductions of kākā (van Heezik & Seddon, 2018), intensive pest management could still allow a population to thrive in lieu of a predator-free sanctuary. Such pest management would likely require the involvement of the local council, alongside residents, volunteers, and community-led groups, further highlighting the importance of a socioecological approach to conservation action (Baker et al., 2005; van Heezik et al., 2010). If

managed and implemented effectively, future reintroductions of kākā into urban spaces could be incredibly beneficial through increasing the population of a threatened endemic species and providing urban residents with greater opportunity for wildlife interaction, thus enhancing their engagement and appreciation of nature and conservation (Gouws, 2020).

Based on the IUCN 2013 guidelines for reintroductions, there are five key aspects concerning the selection and management of release sites (IUCN/SSC, 2013). The site should be within the species' indigenous range; the habitat and landscape requirements of the species must be sufficient and likely to be maintained at the site; the site should have adequate carrying capacity to account for continued growth of the population; there must be identification and eradication of previous sources of population decline; and finally in areas wherein the release site has suffered significant degradation, habitat restoration should be initiated (IUCN/SSC, 2013). These guidelines do not specify, however, that the release site ought to be unmodified. In New Zealand, most urban restoration projects have focused on improving habitat quality, through projects involving riparian planting, forest remnants, stream rehabilitation, and plant and pest control (Clarkson & Kirby, 2016). These projects operate on the assumption that improving the natural conditions of an environment will increase the capacity to support native species abundance and diversity (van Heezik & Seddon, 2018).

Reintroduction is an increasingly successful means of population restoration (van Heezik & Seddon, 2018), and the number of reintroduction projects occurring worldwide is increasing (Seddon, 2011). Globally, urban reintroduction projects have been undertaken with great success, such as the reintroduction of peregrine falcons (*Falco peregrinus*) into cities after being placed in the U.S. Endangered Species list (Heinrich, 2005; Seddon, 2011). Within the cities into which the peregrines were released, the tall buildings effectively

mimicked the cliff-nesting habitats of the birds, and the falcons successfully increased their population sizes within the cities with no specific post-released habitat management (Seddon, 2001). The reintroduction was so successful that New York City now hosts one of the world's highest concentrations of peregrine falcons (Luniak, 2004). In Japan, reintroductions of both Oriental white stork (*Ciconia boyciana*) and Japanese Crested Ibis (*Nipponia nippon*) into urban contexts were undertaken at a time when both species were extinct in the wild due to agricultural pesticide use and management of the rice paddy field systems that the species used for foraging (Naito & Ikeda, 2007; Sado City Government, 2010; Seddon, 2011). Both species were successfully reintroduced, with the implementation of traditional paddy field agriculture, the reduction of pesticide use, and the restoration of the paddy field conditions playing critical roles in their population growth (Seddon, 2011). Strikingly, in both the case of the peregrine falcon, and the Oriental white stork and Japanese crested ibis, the success of the species within the landscape involved dependence on the highly modified landscape (Seddon, 2011).

This suggests that urban landscapes are not inherently detrimental to wildlife, especially endangered species, but rather that through management of the landscape it is possible to have habitat modifications that serve to assist population growth, through increased availability of food resources, foraging grounds, and nesting sites. Furthermore, these urban populations may be able to act as sources for areas outside of the city landscape, allowing recolonisation of more natural habitats. It also does seem likely that some native species are more adaptable to urban landscapes than previously presumed (Seddon, 2011). The issues driving the population declines that such species experienced may be addressed without needing to restore a habitat to pristine condition (Seddon, 2011). Additionally, it is possible that ongoing management of species will not always be necessary, as seen in the peregrine falcon reintroduction to cities (Seddon, 2011), and from the evidence suggesting that some kākā within Wellington have become independent of Zealandia (Gouws, 2020).

While ongoing management is not always necessary, it certainly can provide great benefit to not only the target species, but to ecosystems as a whole. In order to provide the best conditions within a city for the survival of birds, it is recommended that habitats be sufficiently well-connected in order for populations to be established (Seddon, 2011). Furthermore, the structure and composition of the vegetation present must be appropriate for the birds; native vegetation has the capacity to support significantly greater bird diversity, abundance, biomass, and breeding pairs as opposed to urban patches with non-native vegetation (Burghardt et al., 2009). Additionally, predation and disturbance by pets and introduced predators must be managed, especially within New Zealand, where this is a prevalent driver of species decline (Lowe et al., 2011; Møller, 2008; Møller & Ibáñez-Álamo, 2012; Moorhouse, 1997; Towns et al., 2011). Human presence is a complex issue, as many urban birds have developed a tolerance to human presence, yet humans still cause disturbance for birds when foraging, nesting, or at rest (Fernández-Juricic & Tellería, 2000).

The evidence presented in this study, wherein it is suggested that a threatened, deeply endemic, neophobic, forest-dwelling bird has been able to not only adapt and habituate to an urban environment, but to thrive and experience continued population growth, is very promising for urban reintroductions as a means of both bolstering populations of endangered species and bringing more wildlife into the city. As such, the results of this study in the context of existing literature support the movement for increased urban reintroduction programmes, and the inclusion of native and endangered species given the predominant factors driving past declines have been remedied.

4.3 Future Directions

Research regarding how kākā perceive and are affected by risk posed by humans remains highly limited yet could be of great ecological significance and provide significant conservation value. Through a greater understanding of how risk perception varies in kākā in relation to human presence and the urban environment, conservation management could more effectively minimise sources of disturbance and stress, thereby increasing fitness and reproductive outcomes in kākā (Crino & Breuner, 2015; Gill, 2007; Kleist et al., 2018). As such, a long-term research project could also assess the influence of human activity and intensity of urbanisation across the landscape on reproductive success and survival rates in kākā as a measure of how the urban environment affects kākā fitness (Both et al., 2005).

Beyond the scope of kākā in Wellington, it would be worthwhile to investigate the possibility for the reintroduction of kākā into other urban environments around New Zealand, given the success of the Wellington population. Another urban kākā population does exist in New Zealand with a stable population of about 50 individuals in Dunedin, where the Orokonui Sanctuary plays a similar role to that of Zealandia in Wellington (Forrest, 2021). Orokonui Sanctuary, however, is within a less intensely urban landscape than Zealandia, being located 15 km north of Dunedin city (Schadewinkel, 2013). It would be especially interesting to investigate the differences between the cities of Dunedin and Wellington, and the populations of kākā within each city, to determine why the Wellington population has experienced continued population growth (Linklater et al., 2018), whereas the Dunedin population is much more stable in size (Forrest, 2021). Such studies could provide substantial knowledge regarding the factors limiting the success of reintroductions of not only kākā, but avifauna generally, and could aid research and management of other species around the globe.

4.4 Concluding Remarks

This thesis explored the influence of the urban environment and human presence on the behaviour and spatial distributions of kākā. It focused on investigating which factors drove differences in the behaviour, relative abundance, and density of kākā. The findings are promising in indicating that kākā are able to adapt and tolerate urban environments. This research has laid the foundation for follow-up research that specifically addresses the influence of the urban environment on risk perception in kākā, and to explore the variations in behavioural flexibility and innovation between urban and non-urban kākā populations. It is hoped that the findings of this thesis can assist and inform future urban wildlife research projects, the ongoing conservation management of kākā populations nationwide, and future urban reintroductions of endangered native species.

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