Variation drives response to urbanisation: Evolutionary ecology of two introduced birds within anthropogenic environments

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Anthropogenic change causes landscape alteration and fragmentation, which leads to novel challenges for wildlife. Wildlife colonising anthropogenic habitats confront new conditions, such as air and noise pollution, limited space and food resources, higher levels of competition and predator pressures. Such colonists should display a wide spectrum of behavioural, phenotypic, physiological and genetic modifications. Adaptively responding to novel stimuli is a major challenge for urban and rural wildlife and is linked with their fitness. These responses will likely differ between urban and rural habitats as well.

Populations will show behavioural and morphological variation along an urban-rural gradient in response to accompanying environmental changes. Certain behaviours, risk-taking, aggression and exploratory behaviour, will increase opportunities for populations to establish and maintain themselves in novel environments.

I examined behavioural and morphological traits that allow blackbirds (*Turdus merula merula* Linnaeus, 1758) and thrushes (*Turdus philomelos* C. L. Brehm, 1831) to thrive in New Zealand anthropogenic landscapes. Urban blackbirds and thrushes were bolder, more aggressive and more exploratory compared to rural and peri-urban riverside individuals. I assessed the extent to which urban birds showed trends toward using more aggressive behaviour, increased flight duration around a speaker (rather than a signalling response), and decreased duration of singing over the speaker compared to the peri-urban river and rural individuals. The probability of responding with signalling behaviours toward conspecific songs increased in rural and peri-urban river birds. I identified variation in exploratory behaviour and approach response in the presence of a novel object to gather information. Urban birds approached closer to a novel object and had a higher rate of approach at the second attempt. There were inter-specific differences in exploratory behaviour between blackbirds and song thrushes. Blackbirds showed a faster approach response to a novel object compared to song thrushes. However, song thrushes approached closer to the novel object than blackbirds. Morphological traits changed in response to urban-rural landscapes, including increased body mass in rural blackbirds compared to urban individuals. There were morphological variations in response to different regions, including increased tail length for song thrushes and longer bill length for blackbirds in the Canterbury region compared to the Wellington region. Sex-specific traits, such as wing and tail length, varied between male and female blackbirds. There were also differences between the New Zealand populations, isolated for over a century, and their source English populations in tarsus and tail length.

My findings can be used for future investigations into urban wildlife behaviours including risk-taking, aggression and novel avoidance behaviours and morphological variation between individuals. Before conducting conservation and reintroduction programs, we need to understand the behavioural variation between environmental sites and how birds cope with anthropogenic changes and perceive the human presence and potential predators in native and exotic populations. It also shows that morphological and behavioural variation in response to habitat change can occur in spatially adjacent areas, even for highly mobile species.

Keywords: urban ecology, evolutionary ecology, introduced species, *Turdus merula merula*, Western European blackbird, *Turdus philomelos*, Western European song thrush, risk-taking behaviour, anti-predator behaviour, aggression behaviour, exploratory behaviour, flight initiation distance, behavioural syndrome, phenotypic plasticity, morphological variations.

The effect of the Covid-19 pandemic on data collections

After the first lockdown from March to June 2020, data collection activities related to risk-taking and aggressive behaviours and collecting road-killed samples were stopped in the Wellington region. The sample size for this region was reduced and affected the statistical final results compared to data from the Canterbury region. I had part-time employment as an essential worker during the lockdowns and was diagnosed with Rheumatoid Arthritis. After the first New Zealand lockdown in June 2020, I started taking medicines to manage the symptoms but the condition increasingly got out of control. I had to leave Wellington for Christchurch to start data collection although this was delayed by covid travel restrictions. The next lockdown in August 2021 slowed down the morphological measurement of road-killed samples. Due to a compromised immune system and covid-19 delta, I had to remain in my home and postpone the laboratory work until restrictions were lifted. Overall, Covid-19 has impacted my thesis by reducing the amount and timing of data that I would ideally like to have collected.

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Conducting the experimental part of this research was coincide with the Covid-19 pandemic and developing rheumatoid artist in me. Handling active RA, lockdown restrictions and working at the same time created a challenging time. Here, I would like to thank myself for not giving up, always staying positive and helping me to push beyond my limitations for the greater good. For people with RA, ceasing one moment feels like a hand on the hardest day. I shall show my grateful feelings toward Fiona Bellinger for being so kind and supportive.

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Chapter 1 Introduction

Anthropogenic alterations and disturbances in urban environments may impact biotic and abiotic factors in ecosystems (Grimm et al., 2008; McKinney, 2006) which in turn facilitate a wide range of phenotypic plasticity and behavioural changes (Alberti, 2015; Alberti et al., 2017; Alexandrino et al., 2019; Johnson & Munshi-South, 2017). Anthropogenic landscapes create novel challenges for wildlife to which they must respond to survive in these habitats (Thompson et al., 2018). Challenges include anthropogenic noise (Grabarczyk & Gill, 2019; Grunst et al., 2020; Harding et al., 2019), air pollution (Bichet et al., 2013; Eeva et al., 1998), artificial light at night (Arvidsson et al., 2017; Hoffmann et al., 2022; Russ et al., 2017; Touzot et al., 2020; Ulgezen et al., 2019), and animal conflict from predators (Biondi et al., 2020; Gotanda, 2020; Kittendorf & Dantzer, 2021; Timm et al., 2019), other competitors (Dhondt, 2012; Harris & Siefferman, 2014; Maruyama et al., 2010; Pusey & Schroepfer-Walker, 2013) and parasites (Calegaro-Marques & Amato, 2014; Dunn et al., 2011; Giraudeau et al., 2014).

Animals in anthropogenic habitats may need to change behaviourally or phenotypically to benefit from novel resources, such as food and habitats (Lowry et al., 2013; McDonnell & Hahs, 2015; Sol et al., 2013). Many different traits appear to be impacted by urbanisation including clutch size, nestling size, fledging success, growth rate, and nest failure rate (Liu, 2016; Macleod et al., 2005; Magle & Angeloni, 2011; Niemelä et al., 2013; Ophir & Galef Jr, 2003; Perrins, 1965; Sepp et al., 2018; Vaugoyeau et al., 2016), as well as body size, weight and condition (Blackburn et al., 2013; Dulisz et al., 2016; Gillingham et al., 2012; Hutton et al., 2021; Jimenez-Penuela et al., 2019; Liker et al., 2008; Magory Cohen et al., 2021; Meillere et al., 2015; Seltmann et al., 2012).

Animal behaviours that respond to environmental changes may play a functional role in the fast-slow life-history that is explained by the pace-of-life syndrome hypothesis (Réale et al., 2010; Stamps, 2007). This hypothesis suggests that animals with higher aggressiveness, exploration tendencies, and boldness will have higher survival rates and a faster life-history, such as higher growth, increased reproductive efforts and mutation rate (Nakayama et al., 2017; Réale et al., 2010; Wolf et al., 2007). Integrating the pace-of-life syndrome with personality traits has not been addressed in personality-related studies (Bókony et al., 2010; Bokony et al., 2012; Mueller et al., 2013b; Niemelä et al., 2013; Niemelä et al., 2012; Papp et al., 2014; Réale et al., 2010).

Species invasion into urban environments allows a species to colonise and disperse while adapting to this new environment (Winchell et al., 2016). Arrival, dispersal and establishment of invasive species may lead to changes in environmental functioning (Tylianakis et al., 2008) and the structure of animal communities (Kotliar & Wiens, 1990; Levin, 1992; Ricklefs, 1987; Wiens et al., 1993).

Invasive populations size usually become dominant (Melles et al., 2003), such as growing quickly, spreading into many habitats, having a general diet and the ability to adapt to new environments. Selection pressure during the invasion and introduction process (Colautti et al., 2017; Colautti & Lau, 2015) can lead to behavioural and morphological differentiation within native populations (Sakai et al., 2001). Colonisation may take advantage of these differences to allow adaptation to new environments and increase the differentiation from their source populations (Chapple et al., 2012; Le Gros et al., 2016).

The ecological and economic impact of biological invasion encourages scientists to understand those behavioural traits that enable populations and individual to survive in the new environment and promote their invasion success (Chapple et al., 2012; Sih et al., 2012; Wolf & Weissing, 2012). Generally, invasive species show more aggressive, boldness and less neophobic responses compared to non-invasive species (Chapple et al., 2011; Monceau et al., 2015; Short & Petren, 2008; Weis, 2010). The dispersion of established populations may be determined by social interactions and aggression, risk-taking and exploration behaviours (Gruber et al., 2017; Michelangeli et al., 2017; Rehage & Sih, 2004).

There are several behavioural and morphological studies of changes in urban wildlife responses to human presence (Avilla et al., 2021; Berlow et al., 2021; Blackwell et al., 2019; Blumstein et al., 2005; Fernández-Juricic & Schroeder, 2003; Fernández-Juricic & Tellería, 2010; Fernández-Juricic et al., 2004; Fernández, 2005; Heil et al., 2006; Magory Cohen et al., 2021; Mas et al., 2021; Mikula et al., 2018; Rodriguez-Prieto et al., 2009; Zhao et al., 2021). In addition to human presence, response to spatial fragmentation and landscape structure as a result of urbanisation have been studied for several species, such as bobcats (*Lynx rufus*) (Tigas et al., 2002), coyotes (*Canis latrans*) (Atwood & Weeks, 2003), coachwhip snakes (*Masticophis flagellum*) (Mitrovich et al., 2009), bush warblers (*Locustella chengi*) (Nowakowski et al., 2014), and wedge-billed woodcreepers (*Glyphorynchus spirurus*) (Avilla et al., 2021).

Birds are a useful taxon in which to study the effects of urbanisation on species (Sepp et al., 2018). Birds respond to habitat loss and fragmentation with reduced species richness and abundance (Avilla et al., 2021). A fundamental question that remains unresolved in studies of urban colonisation events is the extent to which behavioural adjustments to novel environments are plastic responses.

Population changes in response to urban habitats have been found in many behaviours, such as nest-sites, consuming new food resources (Prasher et al., 2019), avoiding enhanced predator pressure in urban habitats, responses to noise and light pollution (Avilla et al., 2021; Hoffmann et al., 2022; Moiron et al., 2020; Swaddle et al., 2015; Weaver et al., 2019), increased risk-taking (Weaver et al., 2018) and aggression (Moiron et al., 2020; Swaddle et al., 2015; Weaver et al., 2019).

Responses by birds to urbanisation may be measured by comparing urban and rural habitats. It is important to note that rural habitats are also largely anthropogenic landscapes. Most studies have focused on pairs of sites or one location to investigate the differences between populations. Despite considerable work on examining urbanisation effects on population structure and species diversity (Alberti et al., 2017; Marzluff, 2017; Merckx et al., 2018b; Piano et al., 2020), it is still unclear how animals adapt to urban environments (Perrier et al., 2018; Sepp et al., 2018; Short & Petren, 2008).

My study aims to compare behavioural and morphological differences between urban, rural and peri-urban river populations of two species introduced to New Zealand. From European definitions, peri-urban river habitats refer to mixed areas with a rural morphology under influence of urban landscapes (Dekolo et al., 2015; Gonçalves et al., 2017). The reason to select peri-urban river habitats is their global impact role with complex characteristics that act as hybrid transitional zones, creating a new kind of multi-functional landscapes for biodiversity (Banzhaf et al., 2009; Niemelä et al., 2010). Anthropogenic activities cause physical stressors that change the ecosystem related to biological communities (Angela et al., 2015), such as changing water quality and leaking chemical compounds into the aquatic ecosystems (Caroni et al., 2013). The quality of peri-urban river habitats have generally deteriorated over the last two decades.

Urban populations face novel challenges from human disturbances, higher predator pressure and limited spaces that require morphological and behavioural responses. Urban populations may increase their energy investment in behavioural syndromes, such as boldness, exploratory and aggressiveness behaviours, in response to potential predators or intruders, while investing less in responding to stimuli such as human presence (Bentz et al., 2019; Foltz et al., 2015; Hall et al., 2020; Johnson et al., 2020; Łopucki et al., 2020; Møller & Tryjanowski, 2014; Myers, 2013; Samplonius, 2018; Szász et al., 2019; Thibault et al., 2020; Zaman et al., 2019). Body condition related traits, such as weight, and flight-related traits, such as wing and tail length, change in response to food resources and stress as individuals maintain a balance between the risk of starvation and predation (Mitchell & Powell, 2004). As increased disturbance levels lead to shorter foraging bouts in urban birds, they should show bolder behaviour and shorter flight initiation distance in response to a potential predator.

Chapter 2 Literature and background

2.1 Introduction

Urban growth is sprawling across the world and even reaching untouched habitats that may lead to human-wildlife interactions (Soulsbury & White, 2015). Urban dwelling species encounter novel human disturbances and must adapt their pace-of-life traits to these new interactions (Hume et al., 2019). The pace-of-life syndrome explains that variations in behavioural and physiological traits among individuals intervene with their current and future reproduction (Montiglio et al., 2018). The syndrome suggests that closely related species that experience different environmental conditions should be varied in life-history trade-offs (Levin, 1992; Polverino et al., 2018).

Anthropogenic activities can cause habitat loss, isolation and fragmentation over decades due to the construction of structures like buildings and roads (Lindenmayer & Fischer, 2013). Species are forced to deal with spatial and temporal environment changes by adapting (long term) or utilising phenotypic plasticity of traits (short term) (Acasuso-Rivero et al., 2019). Behavioural flexibility or phenotypic plasticity may persist over generations (Martin & Fitzgerald, 2005; Slabbekoorn & Peet, 2003). The main driver behind behavioural responses to urbanisation, whether plasticity or adaptation, is an active question (Lowry et al., 2013). Empirical evidence indicates that there are correlations between different behavioural traits between individuals across ecological conditions (Sih et al., 2004).

The diversity of life-history strategies is at the centre of most evolutionary ecology studies due to its direct link to fitness (Niemelä et al., 2012). Life history theory comprises extrinsic and intrinsic factors: (a) the communication of external factors, such as ecological impacts related to a specific life-history trend, and (b) intrinsic factors, such as interactions among life-history traits and links with a variety of gene expression (Stearns, 2000). These factors include body size at birth/hatching, adult body size, growth rate, clutch size, reproductive success, mortality rate and lifespan (Stearns, 2000).

Birds have been studied to investigate pace-of-life syndromes at the interspecific level (Jimenez et al., 2014; Jones et al., 2008; Pap et al., 2015; Wiersma et al., 2007; Wikelski et al., 2003), and found to vary along different gradients (Jimenez et al., 2014; Londoño et al., 2015). For example, tropical birds have slower metabolic rates and thermogenic metabolic scope compared to species living in temperate habitats (Wiersma et al., 2007). Also, birds have evolved adaptations in their reproductive traits, such as clutch size, nestling success, and incubation period, based on environmental conditions along various latitudinal and altitudinal gradients (Wikelski et al., 2003). Generally, a low fecundity rate is related to slower reproductive potential and increased survival rates at higher elevations and lower latitudes (Hille & Cooper, 2015; Promislow & Harvey, 1990; Ricklefs & Wikelski, 2002).

From a pace-of-life viewpoint, life history has an evolutionary role in avian behavioural and physiological traits (Martin et al., 2007; Niemelä et al., 2013; Réale et al., 2010). For example, 'slow-living' house sparrows (*Passer domesticus*) had strong secondary antibody reactions and immune systems compared to 'fast-living' house sparrows that laid larger clutch sizes over shorter periods (Martin Ii et al., 2006). Also, Mendes et al. (2011) showed a vocal modification along an environmental gradient of urban to rural areas in common blackbirds *(Turdus merula*) probably due to an anthropogenic noise increase from rural to urban environments.

2.2 Urbanisation and biodiversity

2.2.1 The definition of urban area

Urban areas are found all over the world and have brought environmental alternations (Gaston et al., 2015; Marzluff, 2001) and novel conditions (Caizergues et al., 2021). More than half of the world's human population lives in urban areas (Pickett et al., 2001) and this number is projected to reach 66% over the next two decades (Nations, 2018). An urban area is a human settlement with a high human density and built-up environments that comprise cities, towns and suburbs (Blair & Johnson, 2008). In New Zealand, 87.2% of the population live in urban landscapes (Stats, 2020).

2.2.2 Urban landscape changes

A discussion of urbanisation tends to focus on human density in residential and industrial areas and their related impacts (Cringan & Horak, 1989; Evans, 2010; Lowe et al., 2014; Marzluff, 1997; Sol et al., 2017; Sol et al., 2014; Van der Ree & McCarthy, 2005), such as landscape changes associated with a natural habitat reduction and alteration (Adams & Klobodu, 2017; Gil & Brumm, 2014; Marzluff et al., 2001; McKinney, 2002; Xu et al., 2018), highly developed and fragmented habitats and novel stressors (Bauerová et al., 2017; Gaston et al., 2013; Swaddle et al., 2015). Ecosystem patterns and processes are constantly changing due to the fast pace of urbanisation (Grimm et al., 2008; Grimm et al., 2000).

The coexistence of animals with people depends on the extent of vegetation cover (Catterall et al., 1991; Emlen, 1974; Gavareski, 1976; Mills et al., 1989; Morelli et al., 2017; Rosenberg et al., 1987), presence/absence of exotic and novel predators (Brown & Brown, 2013b; Churcher & Lawton, 1987; Ferrari et al., 2015; Paton, 1990), competition interactions among species living with humans over significant periods (Major et al. 1996), the structure of vegetation landscapes (Chace & Walsh, 2006;

Greenberg, 1989; McKinney, 2006; Tweit & Tweit, 1986) and the additional food resources of human origin (Haverland & Veech, 2017; Major et al., 1996; Newsome et al., 2015; Seress & Liker, 2015; Vuorisalo et al., 2003).

Anthropogenic disturbance causes habitat degradation and biodiversity loss in urban areas and affects most species (Seto et al., 2012). Key factors driving the evolution of life histories are pressure of predation and resource availability, and both are theoretically and empirically linked (Gadgil & Bossert, 1970; Reis et al., 2012; Reznick et al., 1990; Stephenson et al., 2015). Despite all being anthropogenic landscapes, depending on the species, urban landscapes can sometimes offer greater resources than other habitats, like rural areas. Urban environments may provide a safe zone for some species from predators compared to rural landscapes (Sepp et al., 2018). Food may be more accessible and in large quantities (Auman et al., 2008; Marzluff & Neatherlin, 2006; Robb et al., 2008; Seress & Liker, 2015) but may be lower in food quality (Murray et al., 2016; Sumasgutner et al., 2014). Predation pressure in urban areas on individuals may be low due to a decreased predator density (Brahmia et al., 2013; Fischer et al., 2012; Newhouse et al., 2008; Stracey, 2011; Valcarcel & Fernández-Juricic, 2009) along with reduced parasite loads (Calegaro-Marques & Amato, 2014).

2.2.3 Urbanisation implications for biodiversity in New Zealand

Despite humans colonising New Zealand only 750 years ago (Wilmshurst et al., 2008), urban areas have become homogenised due to species introduction that started over 150 years ago. Subsequently, many native species have been reduced in numbers and distribution by exotic predators and competitors (Christchurch City Council, 2008). Due to forest clearance and habitat destruction, many native species have been forced to live in urban habitats or isolated in patches with small populations (Amiot et al., 2021; Chakravarthy et al., 2019). Differences between any two landscape structures lead to behavioural and phenotypic variations (Amiot et al., 2021; Biard et al., 2017; Bishop & Byers, 2015; Kozlovsky et al., 2020; Mazza et al., 2019; Moiron et al., 2020; Thompson et al., 2018).

2.2.4 Urbanisation and wildlife behaviours

Urbanisation is a catalyst for significant changes in the environment and living organisms. It can impact local weather conditions (Parlow, 2011). For example, urban areas usually have higher precipitation rates (Pickett et al., 2001) and a heat island effect where there are higher temperatures compared to surrounding rural areas (Borer et al., 2000; Kalnay & Cai, 2003). Urban areas are several degrees warmer after sunset as heat absorbed during daytime is reemitted (Pickett et al., 2001). Animal and plant populations respond to the urban heat island effect with earlier blooming dates and prolonged vegetation growth periods, as well as a reduction in the risk of springtime frosts (Neil & Wu, 2006).

Vegetation phenotypes, such as earlier flowering and fruiting, change insect life cycles and affect food availability for birds. Birds need to quickly adapt to changes in invertebrate prey or risk dissociated interactions between prey and predator (Peñuelas & Filella, 2001; Visser et al., 2004). Warmer climates allow urban birds to enhance their winter survival rate, increasing the breeding population (Chace & Walsh, 2006).

Chemical pollution concentrations in urban habitats are several times higher than the global average (Grimm et al., 2008). The effects of urban pollution move beyond the cities and through the food chain, negatively influencing a wide range of animals and plants, especially birds (Eeva et al., 2003; Eeva et al., 1998). Small insectivorous songbirds are good indicators of pollution levels as they have high metabolic rates and have been well studied for the effects of pollution in cities (Pickett et al., 2001). A number of common urban birds have been analysed for bioaccumulation of heavy metals, including American robins (*Turdus migratorius*) (Hofer et al., 2010), house sparrows (Bichet et al. 2013; Kekkonen et al. 2011; Swaileh and Sansur 2006), and house wrens (*Troglodytes aedon*). Outridge and Scheuhammer (1993) and Eeva and Lehikoinen (1996) measured the synergistic effect of pollutants on bird physiology and concluded that young individuals are generally more vulnerable than older individuals (Scheuhammer, 1987) with higher mortality and lower body mass (Janssens et al., 2003). Eeva et al. (2003) measured the level of lead (Pb) in great tit (*Parus major*) nests and assessed the differences between nestling physiological, plumage and biometrical traits. Nestlings showed a lower rate of survival, smaller body size and fewer health conditions with exposure to lead in areas with higher pollution. Chicks from highly polluted areas had a lower survival rate, decreased health state and smaller body size.

Ecological light pollution is also a problem in urban settlements that affect animal migration, orientation, foraging, communication and reproduction (Dominoni et al., 2018; Hoffmann et al., 2022; Longcore & Rich, 2004; Silva et al., 2020). Such impacts cause novel interactions between competitors (Arvidsson et al., 2017; Petren & Case, 1996), and predator/preys relationships (McMunn et al., 2019; Perry & Fisher, 2006). It occur on a wide range of animals, from flying insects (Eisenbeis et al., 2009) to birds (Gauthreaux Jr et al., 2006), lizards (Thawley & Kolbe, 2020) and toads (Touzot et al., 2020).

Migrating birds often use celestial light sources to navigate and may use urban light instead of natural light on the horizon at night, especially in difficult visibility conditions, such as heavy cloud and fog (Gauthreaux Jr et al., 2006; Møller & Erritzøe, 2014). Migrant species that are disoriented by urban lights may become trapped, have to deal with reduced energy stores or arrive at wintering or breeding destinations late. Urban birds may sing earlier than forest counterparts, which will affect territorial and courtship behaviours (Gauthreaux et al. 2006; Ramos et al. 2016). American robins started singing their dawn song earlier in environments with more artificial light than those living in darker habitats (Miller 2006; Kempenaers et al. 2010). The Eurasian blackbirds exposed to artificial light at night moulted and started their reproductive activities earlier compared to those exposed to dark conditions (Dominoni et al., 2013). Urban blackbirds differed in their chronotype and circadian clocks between forest and urban populations, such that urban blackbirds had longer daily activities and began singing before dawn compared to forest populations (Dominoni et al., 2015b), and those exposed to a higher level of artificial lights at night foraged longer, particularly during spring (Russ et al., 2015).

Anthropogenic noise pollution influences animal communication systems and other behaviours, including acoustic signals involved in territorial defence and courtship displays, alarm calls and other related songs and calls (Hennigar et al., 2019; Warren et al., 2006). European robins (*Erithacus rubecula*) affected by noise level from transportation changed male behaviour in both spatial distribution and singing, avoiding noise sources (McLaughlin & Kunc, 2012). In the case of elevated noise levels, highway noises negatively alter bird behaviour and reproductive success. Great tits (*Parus major*) living near highways with higher noise levels exhibited smaller clutch size and fewer chicks (Halfwerk et al., 2011). Males living in noisy habitats may not be as successful in mating, perhaps because females prefer quieter territories or because anthropogenic sounds cover male singing (Gross et al., 2010; Habib et al., 2007). House sparrows living near highways had their parent-offspring relations negatively affected compared to the control group, as nestling begging calls for food were masked (Schroeder et al., 2012).

Anthropogenic noise may also influence the behaviour of developing organisms (Grunst et al., 2020). For example, urban birds in noisy areas, such as chaffinches (*Fringilla coelebs*), showed more vigilance and less tendency to forage (Quinn et al., 2009). Tree swallows (*Tachycineta bicolor*) were less successful at using parental alarm calls when exposed to increased acoustic noise (McIntyre, 2013). Song thrushes (*Turdus philomelos*) showed significant differences in the minimum and peak frequency of whistle syllables between urban and rural populations (Deoniziak & Osiejuk, 2019). Warren et al. (2006) found that anthropogenic noise is mainly at low frequencies that favour birds singing in high frequencies to avoid being masked by urban noise. Similar responses have been found in a hundred avian taxa (Hu & Cardoso, 2009).

Urban populations may cope with new conditions and noise disturbances by raising frequencies to overcome anthropogenic sounds, such as has been observed in white-crowned sparrows (*Zonotrichia leucophrys*) (Phillips & Derryberry, 2018; Phillips et al., 2020), great tits (Slabbekoorn & den Boer-Visser, 2006; Slabbekoorn & Peet, 2003), common nightingales (*Luscinia megarhynchos*) (Brumm, 2004), song sparrows (*Melospiza melodia*) (Wood & Yezerinac, 2006), and grey-shrike thrushes (*Colluricincla harmonica*) (Parris & Schneider, 2009). In response to daytime anthropogenic noises, diurnal birds can sing at night to avoid masking their songs by acoustic interferences (Fuller et al., 2007). Sound transmission in urban environments was characterised by higher attenuation and reverberation than rural areas and urban individuals preferred to sing short whistles, faster trills, and narrower bandwidth. Faster trills in urban area may result from cultural drift or sexual selection (Phillips et al., 2020).

Roads are prominent features of anthropogenic landscapes and are sources of pollution, alter hydrological systems (Coffin, 2007; Gaston et al., 2013), and increase mortality (Andrews et al., 2008). Animals generally prefer to keep their distance from roads due to traffic noise pollution (Cooke et al., 2019). In a meta-analysis, population densities of birds were found to decrease near roads (Benítez-López et al., 2010). The effects of roads on populations persist kilometres away from the actual site of the road (Benítez-López et al., 2010). Common European species modified their flight initiation distance (FID) to the speed limits of roads, with longer flight initiation distance in high-speed roads (Legagneux & Ducatez, 2013). Some species, including those in Accipitriformes and Falconiformes, benefit from roadkill carcasses as food resources (Novakova et al., 2020).

Buildings are the most obvious sign of urbanisation. Buildings bring people, domestic animals, increased pollution, less vegetation cover, and decreased biodiversity compared to natural habitats, such as forests. A major cause of bird mortality in urban areas is from collisions with buildings and windows, although this varies among seasons and species (Riding et al., 2020).

Species with a tolerance for human presence can benefit from urbanisation (Miller et al., 2001). For instance, buildings can become a winter shelter for arthropods (reviewed by Raupp et al., 2010) and urban individuals may choose to breed and feed in infrastructure such as houses.

The effect of human disturbance on wildlife can be morphological (Evans et al., 2009) or physiological (Partecke et al., 2006), and can lead to behavioural changes. For example, there may be changes in daily activity patterns (McClennen et al., 2001; Riley et al., 2003; Tigas et al., 2002), changes in anti-predator behaviour (Kitchen et al., 2011; McCleery, 2009), enhancement of novel avoidance behaviour (Miller et al. 1998), shifting nest-site locations (Yeh et al. 2007), modification of vocalisations (Brumm, 2004; Foote et al., 2004; Sun & Narins, 2005; Wood & Yezerinac, 2006), changed mate selection by avoiding nesting with males living in noisy habitats (Habib et al., 2007), and changing individual plasticity or micro-evolutionary changes (Miranda et al., 2013).

Habituation allows an individual to gradually decrease their response to repeated stimuli (Blumstein, 2016; Rankin et al., 2009; Rodriguez-Prieto et al., 2009; Vincze et al., 2016). Animal response to human presence occurs through micro-evolutionary changes or habituation (Jiang & Møller, 2017). There is a trade-off between vigilance and foraging behaviours that may shift individuals to spend less time and energy on anti-predator behaviour and more on processing food (Arenz & Leger, 1999; Unck et al., 2009). Grey squirrels (*Sciurus carolinensis*), urban populations do not show any trade-off between foraging and escape behaviour compared to populations at a distance from human settlements (Bowers & Breland, 1996) and this has also been shown in other mammals, birds, and reptiles (Andrzejewski et al., 1978; Blumstein, 2003; Blumstein et al., 2005; Carrasco & Blumstein, 2012; Kerman et al., 2018; Stroud et al., 2019).

Species that are unable to modify their behaviour to urban conditions and that do not respond to novel environments appropriately are likely to go locally extinct (Magle & Angeloni, 2011; McDonald et al., 2008; Van der Ree & McCarthy, 2005). Grey flycatchers (*Empidonax wrightii*) are less able to live in noisy locations due to an inability to shift the frequency of their vocalisations, whereas ash-throated flycatchers (*Myiarchus cinerascens*) occupy both noisy and quiet habitats because they can modify their vocalisation to a higher frequency (Francis et al., 2010).

The consistency of individual differences in behavioural traits and personality have been questioned (Réale et al., 2007) including within populations (Thompson et al., 2018). Individuals living in high anthropogenic areas showed reduced escape behaviour, higher aggressive response and exploratory traits toward the potential predator, intruder and novel object compared to those that live in less intensive anthropogenic landscapes.(Magle & Angeloni, 2011; McDonald et al., 2008; Van der Ree & McCarthy, 2005).

2.2.5 Vigilance and risk-taking behaviour of birds within different habitats

Animals respond to potential predators, including humans, via assessment and scanning a situation, then escape from possible threatening conditions (Bohls & Koehnle, 2017; Engelhardt & Weladji, 2011; Isaksson et al., 2018; Müller et al., 2006). Urban animals must balance between the risk of predation and loss of energy consumption as a result of the escape response, also defined as starvation-predation balance (Dall et al., 2005; Witter & Cuthill, 1993; Ydenberg & Dill, 1986).

Animals should optimise their ability to balance resources and the cost of decreasing predation pressure (Møller et al., 2013). Escaping earlier to avoid potential risk could reduce the time spent foraging, the chance of reproductive activities (Brown & Chivers, 2005; Brown & Kotler, 2004; Cooper Jr & Frederick, 2007; Fernández-Juricic et al., 2003; LaManna & Martin, 2016) and resting (Brubaker &

Coss, 2015; Burger & Gochfeld, 1981; Klein et al., 1995; Manor & Saltz, 2005). It would be wise to escape at the first sight of predator appearance, however, such a decision decreases energy consumption and engagement in social activities (Mbise et al., 2019). In this case, the optimal escape strategy is when the cost of staying will not meet the benefits (Cooper Jr & Frederick, 2007; Ydenberg & Dill, 1986).

Such risk-taking or anti-predator behaviours can be assessed through flight initiation distance (FID), the distance at which individuals take an action by moving in response to an approaching potential predator (Blumstein, 2003; Blumstein, 2006; Blumstein et al., 2005; Burger & Gochfeld, 1981; Heidiger, 1934; Stankowich & Blumstein, 2005). Urbanisation and anthropogenic related factors affect risk-taking and fearfulness behaviour, such as pedestrians, vehicular traffic, bicycles, dog-walking, cats and urban noises (Banks & Bryant, 2007; Bernard et al., 2018; McLeod et al., 2013; Mikula, 2014). FID is correlated with other fear-related factors, such as alert distance (AD), the distance at which the focal bird stops their foraging behaviour in response to an approaching predator, scanning rate, the number of times animals scan a situation while resting or foraging (Blumstein, 2003; Blumstein, 2006; Blumstein, 2010), and potential refuge cover (Eason et al., 2019).

Animals learn over time to stop responding to repeated stimuli, which will reduce the predator pressure and change the risk assessment toward a special predator (Rankin et al., 2009; Shulgina, 2005). This process is referred to as habituation (Blumstein, 2016; Thompson, 2009). Urban animals eventually become inattentive toward human activities (McGowan et al., 2014; Rodriguez-Prieto et al., 2009; Samia et al., 2017; Samuni et al., 2014).

The risk of allocation explains that when animals are exposed to frequently repeated high-risk situations, they will trade-off between anti-predator behaviour and fitness activities and reduced anti-predator responses will lead to more rest and the conserving of energy (Lima & Bednekoff, 1999). FID decreases with the increased density of pedestrians (Stankowich & Blumstein, 2005), which could be the result of habituation and risk allocation (Rodriguez-Prieto et al., 2008).

Intra-specific variation in risk-taking behaviour may be defined by micro-evolutionary changes (Møller, 2008) or phenotypic plasticity (Holtmann et al., 2016; Holtmann et al., 2017) and has been used for programmes regarding conservation decision making (Watson, 2010; Weston et al., 2012). Animals better able to deal with human disturbance will be more successful in colonising human habitats (Scales et al., 2011). Some studies found that wild hunted populations showed larger FIDs than non-hunted individuals, including reindeer and giraffes (Baskin & Hjältén, 2001; Marealle et al., 2010) and changes in human presence may impact FID (Thiel et al., 2007). Birds in urban habitats become bolder and tamer over generations (Møller, 2008c; Weston et al., 2012).

Surviving in urban environments is aided by high levels of boldness, a willingness for individuals to take risks, such as exploring novel conditions and new resources (Wilson et al., 1994). For example, there is a correlation between risk-taking behaviour, exploration of new habitat and heritability of these traits in great tits (Van Oers et al., 2004). Boldness is an individual-specific trait that often varies in a population (Carere & Van Oers, 2004; Reaney & Backwell, 2007; Webster et al., 2009; Wilson & Godin, 2009). If urban environments select for bolder species, then human disturbance will increase the frequency of this trait over time. European birds in urban areas are bolder toward human presence relative to rural populations and this is related to time since urbanisation (Møller, 2008c). Boldness is positively correlated with aggressive behaviour toward conspecifics in a range of taxa, such as sticklebacks (Bell, 2005), great tits (Drent et al., 1996), fiddler crabs (Reaney & Backwell, 2007) and male song sparrows (Evans et al., 2010).

2.2.6 Differences in aggression between urban and rural individuals

Individual habitat selection, along with adjacent human activities and population distribution, may be under the influence of variation in boldness and aggression behaviours (Bejder et al., 2006; Carrete & Tella, 2009; Fernández-Juricic et al., 2002; Meager et al., 2012; Scales et al., 2011). Highly aggressive individuals tend to occupy new habitats but after a few generations, this trait may be eliminated from the population as high aggression is costly for individuals (Duckworth, 2006a; Wingfield et al., 2001). As a result, bolder and more aggressive individuals are usually found in new environments, such as highly human-disturbed areas.

Environmental changes in urban areas may disrupt the equilibrium between signalling and aggressive behaviours (Johnson & Munshi-South, 2017; Searcy et al., 2006; Searcy & Nowicki, 2005). Urban birds show different aggressive behaviours compared to rural individuals of the same species, responding more strongly to intruders during the breeding season (Davies et al., 2018; Evans et al., 2010; Fokidis et al., 2011; Hardman & Dalesman, 2018). When species confront each other with different interests, the signaller may send different intensities of an aggressive message to manipulate the receiver, compromising the trustworthiness of signals (Dawkins & Krebs, 1978).

There may be a significant correlation between other forms of signalling behaviour, such as patrolling territory boundaries and approaching or attacking an opponent (Cain & Langmore, 2016; Cain et al., 2011). The intensity of signalling and aggressive traits may be masked by urbanisation and human activities, such as noise pollution and the receiver individuals who may not be able to understand the messages (Bermúdez-Cuamatzin et al., 2009; Luther & Baptista, 2010; Wood & Yezerinac, 2006).

One useful trait in response to urban noise is singing loudly. Urban animals respond to anthropogenic noise by vocalising at a higher pitch compared to non-urban populations, which is identified as the Lombard effect (Brumm, 2004; Brumm & Todt, 2002; Brumm & Zollinger, 2011; Cynx et al., 1998). Vocalisation variations within different frequency ranges may increase the Lombard effect as well (Brumm & Todt, 2002; Cynx et al., 1998). Another solution for defeating urban noise is singing at a shorter distance to the opponent to ensure the transmission of low amplitude songs in urban environments (Halfwerk et al., 2012; Halfwerk et al., 2011). Approaching the intruder while singing to ensure the receiving of a signal may bring an increased risk of aggressive interactions (Anderson et al., 2012; Templeton et al., 2012).

Urban noise may interrupt effective communication and cause increased aggressive behaviour. The impact of anthropogenic noise on a species social life has been examined (Gil & Brumm, 2014; Shannon et al., 2016). Some studies focused on the singing response to the intruder and whether it was overlapped by urban noise (Helfer & Osiejuk, 2015; Hyman et al., 2004; Naguib et al., 2020; Searcy et al., 2006). When their songs overlapped, birds responded by changing their song rate and duration (Grabarczyk et al., 2020; Hutfluss et al., 2021; Naguib & Mennill, 2010). There was a positive relationship between song overlap and approach distance regarding aggressive behaviours (Brindley, 1991; Hutfluss et al., 2021; van Dongen, 2006; Wilson et al., 2016).

Increased aggression might be costly (Duckworth, 2006a; Wingfield et al., 2001), which could impact habitat selection (Bejder et al., 2006) and species distribution to occupy better territory (Carrete & Tella, 2009; Scales et al., 2011). Highly aggressive behaviour may provide individuals with a higher level of fitness in newly established populations compared to less aggressive conspecific (Duckworth, 2006a; Duckworth, 2006b; Duckworth, 2008). Increased levels of aggressive responses could result from food availability in urban habitats that encourage animals to explore the novel environment and resources and that allow individuals to learn about their spatial surrounding habitats and social interactions (Reader & Laland, 2003; Réale et al., 2007).

2.2.7 Variation of exploratory behaviour and urbanisation

Examining exploratory behaviour in response to novel situations allows understanding of animal personality. The spectrum of responses ranges from ‘bold’ or ‘neophilia’, willing to explore new resources, to ‘shy’ or ‘neophobia’, avoiding new conditions (Dingemanse et al., 2012; Dingemanse & de Goede, 2004; Drent et al., 1996; Sih et al., 2004; Verbeek et al., 1996). Variation in inter-individual personalities may result from differences in ecological contexts (Johnson et al., 2020) that shape the way individuals deal with inter and intra-specific interactions and local environments (Dingemanse et al., 2010; Réale et al., 2010; Sih et al., 2004).

Animal personalities and exploratory behaviour among populations and individuals are linked to differences in habitats and social interactions. For example, shy individuals in grey kangaroos (*Macropus giganteus*) (Best et al., 2015) and zebra finches (*Taeniopygia guttata*) (McCowan & Griffith, 2015) tend to stay with larger groups (Best et al., 2015) and individual free-living house finches (*Haemorhous mexicanus*) showed more exploratory behaviour and a tendency to interact with bold conspecifics rather than shy individuals (Moyers et al., 2018). Social dominance may be promoted by neophobic, boldness and aggressive behaviours (Dingemanse et al., 2004; Dingemanse & de Goede, 2004; Drent et al., 1996; Favati et al., 2014). The extent of habitat exploration results from exploratory behaviours that may impact the type and status of social interactions (van Overveld & Matthysen, 2010).

The correlations between exploratory behaviour with, for example, aggressive behaviour show that animal personalities can impact social interactions (Breck et al., 2019; Moyers et al., 2018; Nacarova et al., 2018). 'Fast' explorers were less neophobic, more aggressive and tend toward exploring novel conditions (Groothuis & Carere, 2005). For example, neophobic three-spined stickleback (*Gasterosteus aculeatu*) (Pike et al., 2008) and great tits tend to stay in small groups or hold a marginal position in their social relationship (Aplin et al., 2013; Stöwe et al., 2010), as a social network lasts longer for shy individuals (Aplin et al., 2013). In a similar study, 'fast' exploring birds with increased risk of predation would visit a winter feeder more frequently than 'slow' explorers (Quinn et al., 2012) and less neophobic pairs showed higher risk-taking behaviour toward predators than more neophobic pairs (Vrublevska et al., 2015).

Urbanisation and anthropogenic alterations create novel environments and objects for animals that modify breeding habitats (Chace & Walsh, 2006; Marzluff et al., 2001). While urban-related stressors could reduce individual fitness (Chamberlain et al., 2009; Halfwerk et al., 2011), many species colonise and thrive within urban habitats due to an ability to adapt to new environments and variable personalities of individuals within a population (Bermúdez-Cuamatzin et al., 2020; Slabbekoorn, 2013; Sol et al., 2011; Sol et al., 2013). Urban animals show 'fast' exploring (Miranda et al., 2013), highly aggressive and bolder behaviours than their rural conspecifics (Thys et al., 2019; van Overveld & Matthysen, 2010; Verbeek et al., 1996). Urban animals also have greater behavioural plasticity that allows urban populations to exploit novel food and space resources (Thys et al., 2019; van Overveld & Matthysen, 2010; Verbeek et al., 1996). The increased degree of exploratory and novelty-seeking for urban populations may make them prone to poisoning (Cowan, 1977; Greggor et al., 2016), novel predators (Brown et al., 2013a; Ferrari et al., 2015) and ecological traps that lead animals to lower quality habitats (Schlaepfer et al., 2010).

Behavioural plasticity and variation in inter and intra-specific responses to environmental changes may impact phenotypic traits of urban wildlife. Some studies found that larger animals may show higher exploratory behaviours toward new situations (Clark, 1994; Meillere et al., 2015), be bolder against potential predators (Møller et al., 2016), and more aggressive toward competitors (McElreath et al., 2007). Variable life histories, behaviours and morphological traits aid animals in colonising and establishing in a new environment (Mowery et al., 2021). The phenotypic difference resulting from selection during the introduction process (Colautti et al., 2017; Colautti & Lau, 2015) may be one of the keys to adaptation and divergence from the source populations (Chapple et al., 2012; Le Gros et al., 2016).

2.2.8 The effect of urbanisation on morphological traits

Intra-specific changes in morphological traits as an adaptive response have been detected in urban wildlife as a mechanism to cope with new conditions (Darimont et al., 2009; Gaynor et al., 2018; Hendry et al., 2008). Studying dispersal and motion-related traits may help us to understand adaptation to new conditions (Cheptou et al., 2017). Body size variations is also an adaptive response to climate changes and habitat fragmentation (Merckx et al., 2018b; Merckx et al., 2018a).

Food availability and abundance are key factors in forming phenotypic characteristics of animals (Gil & Brumm, 2014; Marzluff et al., 2001; Shochat et al., 2006). Landscape changes, including habitat fragmentation, reduced vegetation cover, and exotic plants, create differences in diet composition between urban and non-urban populations (Avilla et al., 2021). This can cause changes in body mass (Badyaev et al., 2008; Giraudeau et al., 2014). For example, urban house sparrows (*Passer domesticus*), great tits, blue tits (*Cyanistes caeruleus*), and blackbirds (*Turdus merula*) showed shorter tarsus and lower body mass (Bailly et al., 2016; Dulisz et al., 2016; Ibáñez ‐ Álamo & Soler, 2010; Liker et al., 2008; Seress et al., 2011) and differences in bill shape related to novel foods and seed feeders compared to rural conspecifics (Bosse et al., 2017; Giraudeau et al., 2014; Mason & Taylor, 2015). While many morphological traits change throughout life, such as wing and tail length, body mass is often affected by conditions in the early stage of life. For example, Caizergues et al. (2021) found that when there was a decline of insects in urban habitats that insect feeders may be beneficial for adult birds but not for offspring.

Some studies found lower body mass in urban birds compared to rural individuals (Liker et al., 2008; Seress et al., 2011). The differences may be explained with Shochat's credit card assumptions (Shochat, 2004) where it is proposed that urban species tend toward an increased brood size that leads to lower body mass and an increase in survival rate. Overexploitation of food resources by a large number of consumers caused increased intra-and inter-specific food competitions (Anderies et al., 2007). Weaker competitors will reach lower body mass due to feeding on limited high-quality food resources, but the credit card hypothesis assumes that while winner competitors maintain higher body mass, smaller individuals still have high survival rates and include a large part of the population (Anderies et al., 2007).

Besides the abundance of food resources, predator pressure may be another factor determining avian morphology in urban habitats, as increased body mass would increase the rate of survival and reproductive success allowing the storing of more energy (Bednekoff & Houston, 1994; Gosler & Carruthers, 1999; Houston et al., 1993; Owen & Black, 1989; Thomas, 2000). Birds maintain lower body mass in response to predator risk (Cresswell, 1998; Gosler & Carruthers, 1999; Van Balen, 1967; Witter & Cuthill, 1993) to optimise their ability to escape from predators or to increase foraging time to store more energy (Bednekoff, 1996; Brodin, 2000; Brodin, 2001; Krams, 2002; Kullberg et al., 1996; Kullberg et al., 2002; Macleod et al., 2005; Tubaro et al., 2002; Zhao et al., 2021).

Selective forces may reshape the morphology of wildlife introduced beyond their natural geographic boundaries (Blackburn et al., 2013; Cardador et al., 2019). The interactions between abiotic (e.g. temperature) and biotic factors (e.g. increased degree of competition and predation) may allow for the differentiation between introduced and source populations (Blackburn et al., 2009; Davis, 2009). Some studies have found morphological differences between the introduced/invasive and their source populations after colonisation in flight-related traits, such as decreased wing pointedness and length in European starling and blackbirds due to reduced migratory movements (Bitton & Graham, 2015; Djemadi et al., 2019; Mönkkönen, 1995; Saccavino et al., 2018). Phenotypic variations between introduced and source populations may be expected in their motion-related traits and body mass.

2.3 The rationale for this study

2.3.1 Aims

My research aims to better understand the selective forces of evolutionary ecology in anthropogenic habitats, especially urban habitats, for two introduced birds and to provide some urban ecological guidance and options for conservation and reintroduction programs along with urbanisation and anthropogenic-related impacts on wildlife.

2.3.2 Objectives

This research was conducted with fieldwork and data collection on behaviours, carcass sample collections for morphological measurements, and statistical analyses to examine the following objectives.

1. Investigate the risk-taking and anti-predator behaviour of two introduced species, blackbirds and song thrushes, in two regions within urban, rural and peri-urban river habitats. Peri-urban river landscapes are described as a type of land transititioning between urban and rural land (Dekolo et al., 2015; Iaquinta & Drescher, 2000; Ravetz et al., 2013). Questions: Do birds regulate their anti-predator and escape behaviour toward a potential predator according to human density and disturbances? Do sex and dimorphism differences impact anti-predator behaviour? What other factors are associated with risk-taking behaviour? (See **Chapter 3**).
2. Assess the effect of environmental differences and urbanisation on aggression and signalling behaviour of blackbirds and song thrushes in response to conspecific songs and intruders within their territory. Questions: Do urban birds behave more aggressively toward intruders compared to peri-urban river and rural individuals? Do rural and peri-urban river birds warn of intruders more frequently than urban birds? (See **Chapter 4**).
3. Investigate the exploratory behaviour of blackbirds and song thrushes toward a novel object following conspecific songs within their territory. The exploratory responses were examined by the approach distance to the novel object along with the 'bold-shy' range and the frequency of approach response along with the 'fast-slow' spectrum in different habitats. Questions: From how far away do shy and bold individuals respond to a novel object in their territory? Do urban individuals approach more closely at the second attempt to approach the speaker in the presence of the novel object compared to rural and peri-urban river birds? (See **Chapter 5**).
4. Analyse the morphological variation of blackbirds and song thrushes along an urban to rural gradient. Questions: How do flight-related traits and body mass vary between male and female blackbirds? Are there phenotypic variations between the New Zealand and source populations (United Kingdom) since introduction? (See **Chapter 6**).
5. Based on the results above, evaluate the findings and hypotheses of the research and identify the limitations with this research and suggest future studies to further investigate urban and evolutionary ecology of wildlife (See **Chapter 7**).

Chapter 3 Should I stay or should I go? Response of blackbirds and thrushes to approaching potential predators and regulation of risk-taking behaviour.

3.1 Introduction

Over the past century, habitat transformation from natural to anthropogenic landscapes has happened at an unprecedented rate (Klausnitzer, 1989; Marzluff et al., 2001; Shochat et al., 2006). Such transformation changes ecosystem functions and physical structure and composition of the landscape, which, in turn, causes changes in the biotic community (Clergeau et al., 2006; McKinney, 2002; McKinney, 2006). Urbanisation is associated with many human modifications to the landscape and the introduction of many non-native species, forcing native species to cope with new habitats. How species in an urban habitat have adapted and changed their behaviour, physiology, and life history due to this novel environment is the subject of much research (Andrews et al., 2008; Angelier & Chastel, 2009; Baker, 1991; Chace & Walsh, 2006; Chamberlain et al., 2009; Coffin, 2007; Lima & Dill, 1990; Marzluff, 2017; McKinney, 2008; Møller et al., 2016; Sepp et al., 2018; Soulsbury & White, 2015).

Urbanisation provides many challenges (Hall et al., 2020), such as high levels of pollution, competition, and predation by exotic species (Taylor & Hochuli, 2017). These novel conditions favour particular species over others (Shochat et al., 2006), due to novel vacant niches, new food resources, new predator and natural competitor free habitats, and highly heterogeneous landscapes (Callaghan et al., 2019; Møller & Ibáñez-Álamo, 2012; Shochat et al., 2006). For some species, humans are seen as potential predators and they may leave a human area rather than coexist there (Blumstein, 2014). For example, the presence of humans causes problems for bird species with lower tolerance to fear, such collared flycatchers (*Ficedula albicollis*), higher level of corticosterone and longer flight initiation distances (Møller, 2008c).

Anti-predator behaviour consumes time and energy that could be spent on other important behaviours, including foraging and parental care (Lima, 1998). Some species are not threatened by humans and do not perceive humans as a threat (Clucas & Marzluff, 2012), and these gain an advantage in minimising their reactions to humans (Vincze et al., 2016). Some bird and mammal species in urban populations are often less neophobic, show more tendency to explore new resources, display fewer fearful behaviours, and have a shorter fleeing distance in response to humans (Carrete

& Tella, 2011; Cavalli et al., 2016; Clucas & Marzluff, 2012; Engelhardt & Weladji, 2011; Kalb et al., 2019; Metcalf et al., 2000; Møller, 2008b; Rodriguez-Prieto et al., 2009; van Dongen et al., 2015).

Novel stimuli may cause either neophilia and neophobia, or a mix of these two responses (Berlyne, 1950; Montgomery, 1955). Neophilia is the tendency to approach and investigate new conditions, also known as exploratory behaviour (Mettke‐Hofmann et al., 2002). Neophilia allows animals to more quickly and thoroughly map their habitat for food sources, refuges, predators and mates (Renner, 1990) and this affects survival and reproduction success directly or indirectly (Dall et al., 2005; Heinrich et al., 1995; Mettke‐Hofmann et al., 2002). Neophobic animals tend to avoid exposure to risks and new resources and environments (Biondi et al., 2010; Crane et al., 2020; Greenberg, 1989). Neophilia, as exploratory behaviour, is part of an animal's behavioural syndrome (Miranda, 2017) or personality axes (Réale et al., 2007), although, neophilia and neophobia personality traits are not correlated in response to different levels of stimuli (Vonk & Shackelford, 2019) such as novel objects, novel foods and novel environments. Animals may show neophilia responses to novel objects in their natural environments while responding with neophobia toward a familiar object in an unfamiliar environment (Carter et al., 2012).

Habituation, defined as the situation where individuals detect different kinds of stimuli and stop reacting to them over time, may explain some of this behavioural variation in response to anthropogenic changes (Grunst et al., 2019; Metcalf et al., 2000; Rodriguez-Prieto et al., 2009; Uchida et al., 2020; Vallino et al., 2019; Vincze et al., 2016). Habituation to the repeated presence of humans leads to a decreased flight distance by urban wildlife (Blumstein, 2014; Chapman et al., 2012; Metcalf et al., 2000; Rodriguez-Prieto et al., 2009; Whittaker & Knight, 1998). Other hypotheses could explain the reduced fearfulness of urban animals including the local adaptation hypothesis, and the risk allocation hypothesis (Table 3.1).

The local adaptation hypothesis explains that populations are adapted more to their local environment and range rather than other environmental conditions (Quinby et al., 2020), resulting in each population showing the best performance in areas similar to their local environmental conditions (Kawecki & Ebert, 2004). It suggests that natural selection in urban areas favours bold urban phenotypes (Møller, 2008c). Unlike habituation, which includes behavioural plasticity, the local adaptation hypotheses propose that bold and shy responses to human disturbance may vary among individuals due to animal personality (Dingemanse et al., 2010).

The risk allocation hypothesis (Lima & Bednekoff, 1999) proposes that the temporal variation of animal foraging under predator pressure explains the effective allocation of escape behaviour in the face of various kinds of risk. A response of species to predators may be with increasing time of foraging in high-risk environments along with shorter escape distances. When individuals are exposed to dangerous conditions, they will choose to collect more enrgy and spend longer feeding. This has been suggested to drive urban wildlife behavioural changes.

Table 3.1 Risk-taking behaviour hypothesis tested in the current study and outcome variables.

Hypothesis	Description
Habituation	Decreased responses to repeated stimuli.
Local adaptation	Populations are optimised to their local environmental conditions or similar situations.
Risk allocation	Increasing foraging time while decreasing anti-predator responses in high-risk environments.
Flush early and avoid the rush (FEAR)	Animals flush soon after they become aware of an approaching predator to avoid the risks and reduce the cost of possible threats.
Flock size hypothesis	Birds increase their antipredator behaviour by fleeing earlier when they are in a larger group
Conspicuousness-hypothesis	Colourful and more distinctive males escape sooner and show larger DF
Escape strategy	Birds prefer safe regions on the rooftops or in open spaces rather than refuges within bushes with larger FID
Response strategy	Birds choose to show their escape behaviour between two options: walking or flying

A common method of investigating antipredator and risk-taking behaviour in individuals is to record the flight initiation distance (FID), the distance at which a focal individual flees from an approaching observer or predator (Kalb et al., 2019). This risk allocation hypothesis assumes a negative relationship between FID and predator density due to increased predator pressure and decreased tolerance toward predator presence (Rodriguez-Prieto et al., 2009).

FID has been found to be affected by urbanisation, intruder starting distance, habitat type, distance to a refuge, predator behaviour and individual body mass (Allan et al., 2021; Bejder et al., 2009; Blumstein, 2014; Cooper Jr & Frederick, 2007; Stankowich & Blumstein, 2005; Tätte et al., 2018; Ydenberg & Dill, 1986). Human approach often causes responses similar to that of approaching predators (Frid & Dill, 2002). FID to approaching humans is typically less in areas of high human density and activity (Engelhardt & Weladji, 2011; McGiffin et al., 2013). Other influences on FID may be phenotypic plasticity (Blumstein, 2016), personalities (Carrete & Tella, 2013), and selection against fearful individuals (Carrete et al., 2016).

Disturbance tolerance defines individual decision making when facing an approaching predator, fleeing too soon may reduce foraging opportunities while fleeing too late may lead to harm or loss of life (Lima & Bednekoff, 1999). Identifying the optimal distance at which animals ought to escape from a predator as well as the risk of staying, determine the fleeing optimal escape behaviour (Ydenberg & Dill, 1986). FID is affected by alert distance (AD), the distance at which an individual becomes aware of an approaching predator. Due to the difficulties of reliably describing the vigilance behaviour of birds, measuring the alert distance has not been recorded for many studies (Cooper & Blumstein, 2015). In particular, AD explains the ability of individuals to detect the approaching predator and assess the following risks to respond in time. The escape behaviour might be explained by the 'flush early and avoid rush' (FEAR) hypothesis, where individuals decide to escape earlier than is optimal to decrease the cost of constantly monitoring an approaching predator (Blumstein, 2010).

Most variation in FID among different taxa was explained by both body mass and AD (Samia et al., 2013), larger animals showed higher FID and AD in response to approaching predators compared to animals with lower body mass (Mayer et al., 2019; Møller et al., 2016). Both FID and AD approximate the general tolerance of individuals toward a potential predator. However, variation in the relationship between these two factors implies different escape strategies at various levels of predator pressure (Cooper & Blumstein, 2015).

Shorter FID in urban birds may result from a trade-off between the risk of getting caught by predators and gaining longer foraging time that leads eventually to increasing anti-predator behaviours. Smaller buffer distances, i.e., longer FID and shorter AD, indicate faster responses by a bird to an approaching human. A short buffer distance may be related to less tolerance and indicates that birds prefer to increase their monitoring costs (Samia et al., 2017). However, a mathematical artefact could explain the positive relationship between FID and AD rather than a biological factor (Chen et al., 2020). The positive relationship between AD ≥ FID could be due to the randomly selected value of SD (Dumont et al., 2012). In the study, SD was selected based on the protocol suggested by Guay et al. (2013) that a single observer measured SD to have consistency (Guay et al., 2013). It means SD is always larger and/or equal to AD and larger than FID. Such mathematical artefact would need to be distinguished from biological effects (Dumont et al., 2012). The ratio among SD, AD and FID varies among different species of birds and mammals. Different environmental and behavioural factors affect antipredator responses, such as social context, species, inter-individual variation, type of potential approaching predator (Weston et al., 2012).

Another variable suggested by Tätte et al. (2018) is distance fled (DF), the distance from the flushing point (FID) to the next landing spot, also called 'flight distance', 'landing distance', 'distance moved' and ‘flight mode’ (Collop et al., 2016). The relationship between FID and DF is positive for heavier birds, whereas for lighter birds there is not expected to be a relationship between FID and DF, because of the low energetic costs of escaping (Cooper & Blumstein, 2015; Tätte et al., 2018). Distance fled (DF) may match FID patterns influenced by predation pressure, food availability and the importance of parental care (Cooper Jr & Peréz-Mellado, 2004; Samia et al., 2016). For example, griffon vultures (*Gyps fulvus*) displayed ‘costly’ antipredator behaviour while showing shorter FID and bolder responses toward predators during periods of reduced food availability (Zuberogoitia et al., 2010). Incubating Eurasian curlews *(Numenius arquata*) left their nests in response to approaching observers at intermediate FIDs compared to non-incubating individuals with shorter and longer FIDs (de Jong et al., 2013). It is not clear if prey evaluate the risk of predation against the cost of leaving resources while fleeing from a predator (Tätte et al., 2020). I expected that as blackbirds and song thrushes are categorised as light songbirds, there might be a weak relationship between FID and DF.

Studies have been unable to conclude whether spending less time and energy to escape (i.e. shorter FID) is a trait of bolder individuals (Collop et al., 2016). The relationship between FID and DF can be used to indicate different escape strategies among species, for example, some species flush and flee further (Bulova, 1994; Piratelli et al., 2015; Stankowich & Coss, 2007), and in lower food availability and higher competition spent longer time on foraging (Collop et al., 2016).

Species colonising urban landscapes sometimes develop different phenotypic traits compared to rural populations (Møller, 2008c). Differences between urban and rural landscapes provoke stress responses (Wingfield & Ramenofsky, 1999) due to the increased density of potential predators in urban habitats (Fletcher & Boonstra, 2006; Scheuerlein et al., 2001; Ylönen et al., 2006). Measuring DF from a potential predator allows an assessment of perception of risk (Blumstein, 2006), showing the trade-off between the cost of escaping from predators relative to benefits of continuing with other activities (Møller, 2008b). When frequently exposed to a predator, showing anti-predator behaviours will be costly because individuals will take time and energy from other essential behaviours, such as foraging or parental care, to monitor potential predator activities. Living in urban habitats requires an increase in tolerance to human disturbances (Møller, 2008c). I, therefore, hypothesised that urban blackbirds and song thrushes would show shorter FID and higher tolerance to an approaching observer than rural and pre-urban peri-urban river birds. Figure 3.1 illustrates SD, AD and FID from the approaching observer to the focal bird and DF to the refuge.

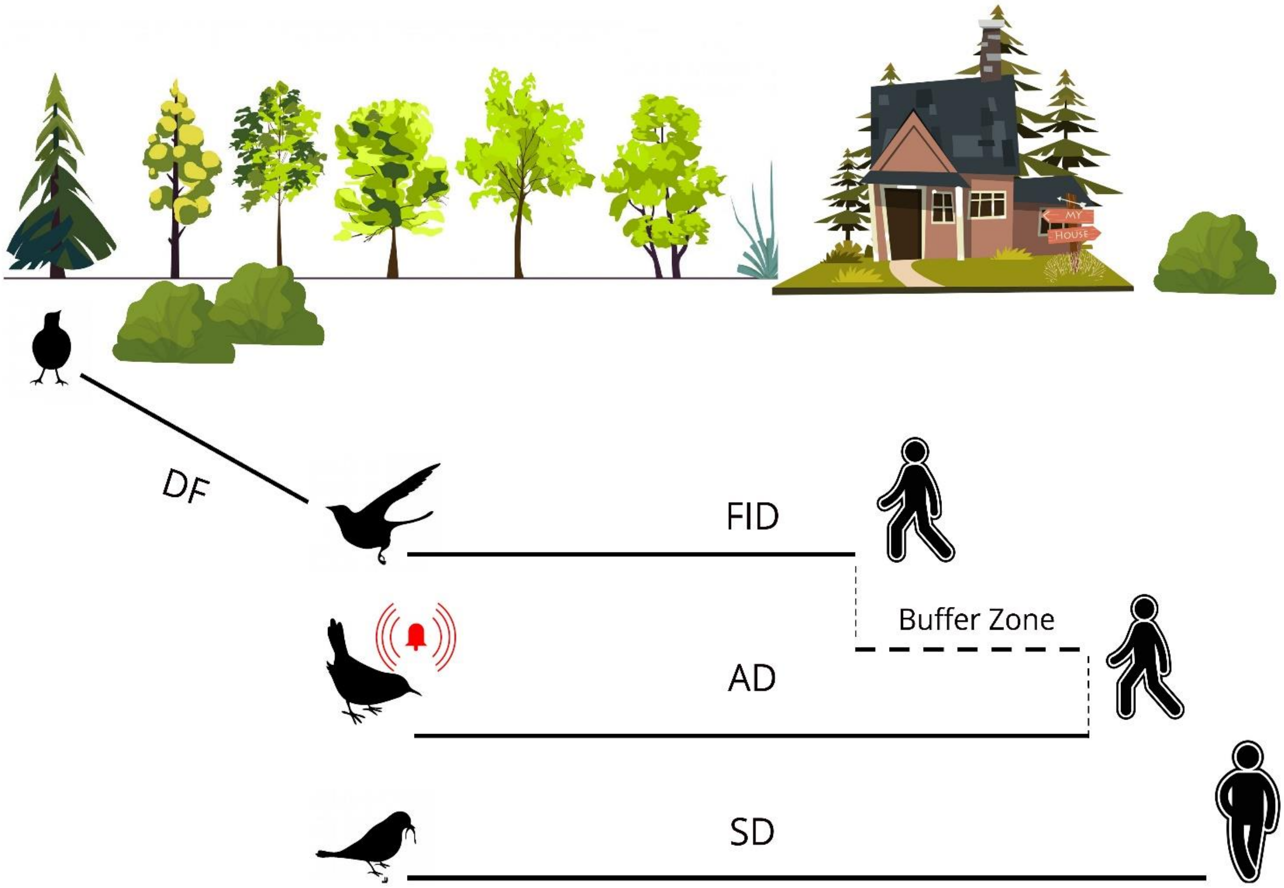

Figure 3.1 Escape response measurements of birds made by an approaching observer. Starting distance (SD), the distance to the focal bird when the approach begins. Alert Distance (AD), the distance at which an individual becomes aware of an approaching predator. Flight initiation distance (FID), the distance at which a focal individual flees from an approaching observer or predator. Buffer zone, the differences between AD and FID. Distance fled (DF), the distance from the flushing point to the next landing spot.

The 'flock size' hypothesis suggests that foraging behaviour in a large flock size of conspecific or heterospecific individuals may affect FID and AD. Birds responded to approaching predators earlier in large flock size compared to their conspecifics in smaller group sizes (Deboelpaep et al., 2018; Morelli et al., 2019). Measuring foraging behaviour allows us to test risk-taking behaviour in similar threat situations (Tätte et al. 2018). It is worth noting that birds moving from one branch to another may not be related to escape behaviour, exploration, or foraging behaviour (Tätte et al., 2018).

There are two contradictory hypotheses associated with sexual dimorphism or plumage dichromatism regarding flight behaviour and conspicuousness (conspicuousness-hypothesis) (Møller et al., 2016). The first hypothesis suggests highly conspicuous individuals within a species are vulnerable to predators due to being more detectable (Slagsvold et al., 1995). A second hypothesis proposes that conspicuous prey are aposematic and are disturbed less (Götmark, 1992). In support of the first hypothesis, cryptic frog individuals (*Craugastor bransfordii*) individuals showed shorter FID than aposematic frogs (Blanchette et al., 2017; Ozel & Stynoski, 2011). A sexually dichromatic species, the common flat lizard (*Platysaurus intermedius wilhelmi*) had more conspicuous males taking fewer risks and escaping at larger FID than females (Lailvaux, 2020; Lailvaux et al., 2003). Hensley et al. (2015) claimed that bird plumage vividness did not indicate at what distance birds would flee from predators, however, they did not consider sex differences. Despite sexual dimorphisms in blackbirds, both blackbird males and females are dark in colour. I expect to see no differences in escape behaviour between male and female blackbird populations.

Species show different escape responses, such as fleeing into the cover or open space. Cover may be considered as a dangerous or safe place to hide from predators (Engelhardt & Weladji, 2011; Lazarus & Symonds, 1992). For example, black redstarts perceived cover as risky and prefered to flee to open spaces (Kalb et al., 2019). Animals tend to escape to cover when FID decreases and but escape to open spaces as FID increases (Engelhardt & Weladji, 2011; Martín & López, 2000; Møller, 2012). Most ground-foraging birds show their anti-predator responses either by walking or flying from the approaching predator (Rodriguez-Prieto et al., 2008). Birds reduce potential risks by flying away and increasing the vertical and/or horizontal distances from predators, but the consequence is spending more energy on flying (Butler, 1991; Nudds & Bryant, 2000) and less time on foraging activities (Cooper Jr & Peréz-Mellado, 2004; Engelhardt & Weladji, 2011). However, when escaping by walking, prey is still in a dangerous situation when the escaping response is too slow and the predator can approach the remaining distance faster (Nuevo, 2004), but the energetic cost is lower than flying and individuals have a longer foraging time and do not leave a profitable foraging spot (Butler, 1991). Walking away from potential risks allows birds to gather more information about the threatening situation and avoid unnecessary reactions (Rodriguez-Prieto et al., 2008).

In this chapter wild animal variation in response to urban habitat was examined by measuring the frequency distributions of antipredator behaviour. The risk-taking behaviour was tested toward human activities and the extent to which habituation plays a role to respond to the human disturbance for a gradient population from urban to rural areas for blackbirds (*Turdus merula merula*) and song thrushes (*Turdus philomerus*) in the Wellington and Canterbury regions of New Zealand. There were three main habitats in this study: urban, peri-urban rivers, and rural landscapes. In relation to the risk-taking behaviour, I hypothesis three assumptions (a) birds in larger flock size may escape earlier than birds in smaller flock size, (b) there would not be significant sex-related antipredator between female and male blackbirds due to dark-colour plumage for predators and (c) the probability of escape to cover would increase when birds choose to fly away from the approaching observer rather than walk to the open spaces.

Urban populations generally showed shorter FID than rural individuals (Samia et al., 2017; Samia et al., 2015). Samia et al. (2017) defined three variables as important for explaining variation in anti-predatory behaviour as measured by FID, starting distance (SD - the distance to the focal bird when an observer's approach begins), alert distance (AD), prey buffer distance (AD minus FID - the distance at which an alerted bird continues to stay in its position (Cooper & Blumstein, 2015). In the present research, the values of SD, AD and FID for blackbirds and song thrushes were measured from urban, river-edge and rural habitats according to human presence from two different New Zealand regions: Wellington, (North Island), and Canterbury (South Island).

3.2 Methods

3.2.1 Study sites

Data were collected from three sites in the Wellington and Canterbury regions of New Zealand. Urban sites were characterised by a minimum of 50% of lands occupied by multi-story buildings and houses, > 10 buildings/ha with parks and streets and the residential population is at least 10 people/ha. Rural sites are described as low to medium density development where 5-20% of the land is covered by human settlements, with a population of 1 to 10 people/hectare, with less than 2.5 buildings per hectare (Clergeau et al. 2006; Loss et al. 2001; Møller et al. 2015; Møller and Garamszegi 2012; Morelli et al. 2016; Samia et al. 2017). Pre-urban river habitats are found in the interaction of urban and rural landscapes (Griffiths et al., 2010). In a European definition, peri-urban landscapes surround urban sprawl and contain woodlands, agricultural, rivers and large open areas (Zasada et al., 2011).

Wellington City, including the Hutt Valley (https://forecast.idnz.co.nz/wellington/home), is the second-largest city in New Zealand with a population of 417,790 people (June 2021) (https://www.health.govt.nz/new-zealand-health-system/my-dhb/hutt-valley-dhb/population-hutt-valley-dhb) (Figure 3-2). The distance between urban sample points was between 1 and 30 km. The Hutt River flows through the southern North Island, from the southern Tararua Range, for 56 kilometres, forming fertile floodplains (Figure 3-4, top). Rural habitats in the Wellington region are located mostly in the Hutt Valley, with farmlands containing vegetables, wheat, domestic farm animals (including cows, sheep, lama, horses) grasslands, orchards, open green spaces, and scattered houses (Figure 3-3).

Christchurch City, the largest city in the South Island, is populated with 394,700 people in 2021 (https://populationstat.com/new-zealand/christchurch). Rural areas were located at the periphery of the city, where open green spaces are used for farming with fences and narrow roads. In the present research, these landscapes included two locations: (a) the Selwyn River/ Waikirikiri flows from the Southern Alps to the east, for 80 km, to reach Lake Ellesmere/Te Waihora south of Banks Peninsula (https://gazetteer.linz.govt.nz/place/7435). (b) within Christchurch, there is the Avon River/Ōtakaro that flows through the red zone of Burwood, a northeastern suburb of Christchurch. The total area of the red zone is 602 hectares including in the Port Hills, Waimakariri, Southshore, South New Brighton, Brookland. This zone that contained several thousand homes was severely damaged by the 2010 and 2011 earthquakes and has been cleared of housing due to soil liquefaction (Figure 3-4, lower figure). The land is currently an area of publicly accessible open, mowed grassland with scattered trees left from the original gardens. Rural areas were located at the periphery of the city, predominantly pastoral farming of sheep and dairy cows, interspersed with fences, narrow roads and woody shelter (for map site see Figure 4-1).

3.2.2 Observations

Data collection in Wellington was in the non-breeding season (mid-June to early August 2019) and breeding season (September to November 2019), while data collection in Canterbury was in the breeding season (September to December 2020). Sampling took place from 8:00 until 17:00, but mostly from 8:00 to 12:00. Every location was visited only once to avoid pseudo-replication.

One observer was used throughout the data collection. The observer consistently wore dull coloured clothes to decrease the possible impact of variable visibility on bird behaviours. A standard protocol (Blumstein, 2006) was used where only adults contributed to data collection. Where possible, the sex of the birds was recorded, but this was only possible for blackbirds: males are black and females are dark brown (Kalb et al., 2019). This kind of classification only applied to blackbirds due to obvious sexual dimorphisms.

Binoculars were used to locate birds that were foraging on the ground (Samia et al., 2017) to decrease the effect of the approaching observer on escape behaviour (Fernández-Juricic et al., 2002). In previous studies, the altered behaviour of blackbirds was determined by observers from 35 ± 1.6 m, almost twice the largest AD recorded (Fernández-Juricic et al., 2001; Fernández-Juricic et al., 2001). I identify AD as when a focal bird stopped foraging and raised its head to scan the area. Therefore, the observer approached from a maximum SD recorded for rural and peri-urban-river habitats starting at a shorter SD than for urban areas. The closest suitable focal bird at a site was at least 20 to 25 m from the observer in urban habitats and between 40 to 45 m in rural sites. The distances to initiate approaching toward birds were chosen according to a bird's behaviour, at which they stopped foraging and scanning. The observer started walking before observing alert behaviours, such as head-up, looking around. Those birds who were aware and stopped feeding on the ground were not approached. Birds living in rural and river-edge sites walked or flew away at distances less than 40 m. The observer did not get any responses from rural and river-edge birds at distances of more than 45 m. After conducting a few pilot experiments in each habitat, the starting distances for urban, rural and river-edge birds were selected for all individuals.

The studied sites were selected according to weather and commuter vehicles. All experiments were conducted on working days, sunny, partially cloudy, without rain and less than 19 km/h wind. Those highly vigilant or aware individuals, such as singing birds, interacting with other individuals, especially those near nests or sitting on eggs were not approached. The observer walked calmly at a steady speed (~ 0.5 m/s) toward each focal bird in a direct line (Blumstein et al., 2015; Díaz et al., 2013).

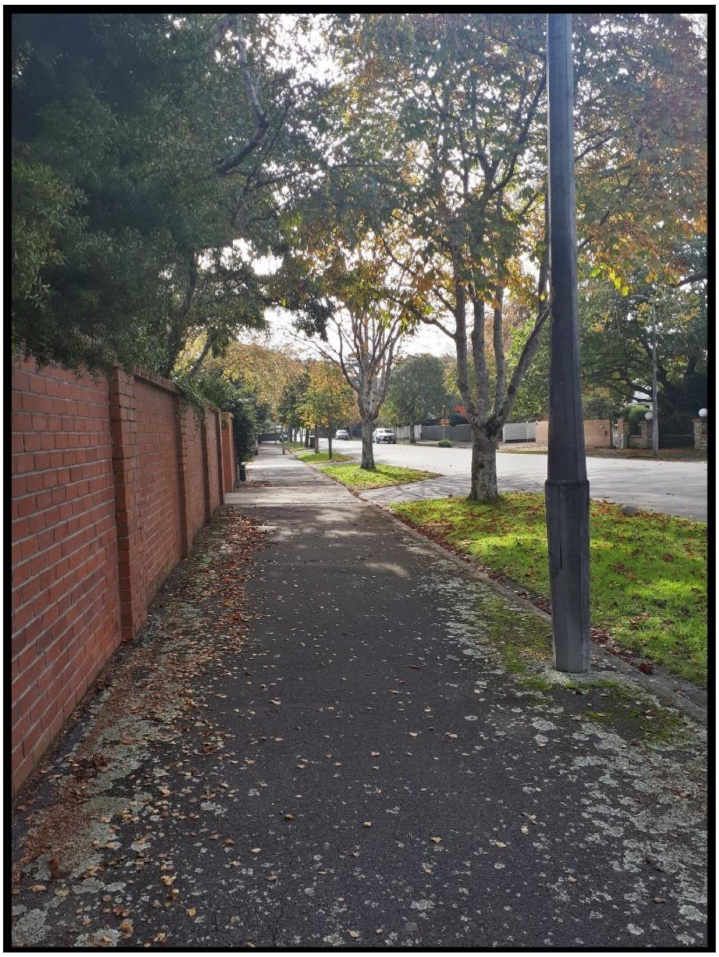

Figure 3.2 The urban landscape within the Wellington and Canterbury region included urban green spaces and streets.

Figure 3.3 Rural landscapes included private farmlands, roads, scattered houses and green spaces.

Figure 3.4 Peri-urban River landscapes (Hutt River; top, and Avon River; down) within the Wellington and Canterbury regions.

The measured values were starting distance (SD), alert distance (AD), flight initiation distance (FID), and distance fled (DF) (Battle et al., 2016). When the observer started walking toward the focal bird, they stopped foraging or raised their head to scan around, an object was dropped to mark the stop and the distance to the focal bird was measured with a laser rangefinder (AEG LMG50). Birds responded by either flying or walking to open or covered spaces and was recorded. The observer approached linearly without obscuring vegetation or object obstacles to be potentially visible to the focal bird. The number of birds initially located in a 15 m radius around a focal bird (the closest to the observer) was recorded as the 'flock size' but was only recorded in Wellington in the non-breeding season (Møller et al., 2016; Morelli et al., 2019; Samia et al., 2017; Tätte et al., 2020; Tätte et al., 2018). During the breeding season in the Wellington region, birds tended to be more territorial and spend time within their territorial boundaries. Therefore, no data were collected for the flock size for this season. However, during the non-breeding season, territory boundaries were dissolved and birds spent more time foraging together.

3.2.3 Statistical analysis

In total, in the Wellington region, for the non-breeding season, 182 adult blackbirds (115 males, 67 females), and 54 song thrushes were observed. During the breeding season, 162 adult blackbirds (100 males, 62 females), and 68 song thrushes were observed. In the Canterbury region, 119 adult blackbirds (70 males, and 49 females), and 66 song thrushes were recorded during the breeding season. All data for blackbirds and song thrushes were combined into two species.

The Shapiro–Wilk test was used to check the normality of the data and the data were not normal. Transforming the normal distribution using log-10 did not make it normal. As the data were not normally distributed, Spearman Rank Order correlation was used to test for significant relationships between the following variables both within and between the Canterbury and Wellington regions for each species: FID, SD, AD, and DF, and flock size only for the non-breeding season in the Wellington region. Due to SD variation across different habitats, the Spearman rank correlation was tested within each habitat. The correlation between AD and flock size was tested by using Spearman Rank Order.

A Linear Mixed Effects Regression (LMER) Using 'lme4' and 'lmerTest' packages (Bates et al., 2014) was run to examine the effect of the regions (Wellington and Canterbury), season (breeding and non-breeding), habitat types (urban, peri-urban river and rural) and sex (only for blackbirds), and SD (random effect) on FID.

A generalized linear model (GLM) with Quasi-Poisson distribution, package lme4 and lmerTest (Bates et al., 2014; Kuznetsova et al., 2017), was used to test how FID (fixed factor), independent factors including escape strategy (cover and open space), different habitat types (classified as urban, peri-urban river and rural), DF and AD (explanatory factor) would affect the response strategy (walking and flying). Each model was run individually for each species. To examine the effect of flock size for birds in the non-breeding season (fixed factor), habitat types (independent factor) and SD (random effect) on FID, an LMER model was run.

A Chi-square test in ANOVA for each model was run to identify whether there is a significant association between the categories of the two variables. A post-hoc test with "Tukey" and "holm" adjustment, using the glht function from the 'multcomp' package, was used to compare which habitat showed differently antipredator behaviour from one to another (Bretz et al., 2016; Hothorn et al., 2008; Hsu, 1996; Searle & Gruber, 2016). All statistical tests were conducted with R 4.0.3 software (R Development Core Team 2013).

3.2.4 Results

FID was positively correlated with SD and AD in all samples except for DF and flock size for song thrushes. There was a weak and negative relationship between FID and flock size for blackbirds. There was also a positive correlation between SD and AD in all samples (Table 3.2). The Spearman Rank test showed a weak and negative correlation between FID and flock size for blackbirds in the non-breeding season but there was no significant linear regression between them. There was no significant relationship between sex and FID (Table 3.3, 3.4).

There were no significant correlations between FID and regions and seasons for birds. The antipredator behaviour in blackbirds was significantly related to habitat types (Table 3.3, 3.4). FID was significantly varied among habitats but the comparison between urban and rural blackbirds was significantly different from one to another (Table 3.5, Figure 3.5).

FID for song thrushes was significantly affected by habitat type (Table 3.6). There was no correlation between regions and seasons with FID (Table 3.7). The difference among different habitats related to FID showed that the most distinctive difference was between FID of urban and peri-urban river individuals in response to the approaching observer. The differences between FID of urban and rural song thrushes were significant. Rural and peri-urban river song thrushes showed similar antipredator behaviour toward the approaching observer (Table 3.8, Figure 3.5).

Table 3.2 Correlation between FID and other approach variables tested using Spearman's rank correlation. 'Flock size' was the number of birds initially located in a 15 m radius around a focal bird (the closest to the observer).

Species	Fixed factor	Variable	Rho	*p*-value
Blackbird	FID	SD	0.78	< 0.00001***
		AD	0.86	< 0.00001***
		DF	0.14	0.002**
		Flock size	-0.14	0.06
	AD	SD	0.82	< 0.00001***
Song thrush	FID	SD	0.81	< 0.00001***
		AD	0.81	< 0.00001***
		DF	0.03	0.66
		Flock size	-0.13	0.41
	AD	SD	0.67	< 0.00001***

Significant independent variables are depicted with: <0.00001 '***', <0.001 '**'.

Table 3.3 Effect of the regions (Wellington and Canterbury), habitat types (urban, peri-urban river and rural), sex (male and female), flock size (only for the non-breeding season) on FID in blackbirds using LMER with SD as the explanatory effect.

Variables	Estimate	Std. Error	*p*- value
Intercept	17.47	3.23	5.4
Region: Wellington	1.01	1.009	1.007
Season: non-breeding	0.83	0.83	0.99
Habitat: Peri-urban river	4.77	1.92	2.47
Habitat: Rural	6.7	1.95	3.42
Sex: male	-0.47	0.6	-0.8
Flock size	-0.08	0.13	-0.6

Table 3.4 Effect of independent variables on FID in blackbirds using ANOVA (Chi-square) for LMER.

	Chisq	Df	Pr (> Chisq)
Region	1.01	1	0.31
Season	0.98	1	0.32
Habitat	14.38	2	0.0007***
Sex	0.63	1	0.42
Flock size	0.40	1	0.52

Significant independent variables are depicted with<0.00001 '***'.

Table 3.5 The comparisons among habitat types with FID for blackbirds in using post-hoc test (Tukey).

Linear Hypotheses	Estimate	Std. Error	z value	Pr (>|z|)
Peri-urban river – Urban = 0	4.77	1.92	2.48	0.02*
Rural – Urban = 0	6.7	1.95	3.42	0.001**
Rural – Peri-urban river = 0	1.91	0.79	2.41	0.02*

Significant independent variables are depicted with<0.001 '**' <0.01, '*'.

Table 3.6 Effect of the regions (Wellington and Canterbury), habitat types (urban, peri-urban river and rural), flock size (only for the non-breeding season) on FID in song thrushes using LMER with SD as the explanatory effect.

Variables	Estimate	Std. Error	*p* value
Intercept	17.96	2.10	8.52
Region: Wellington	0.31	1.17	0.26
Season: non-breeding	1.48	1.94	0.76
Habitat: Peri-urban river	4.04	1.25	3.2
Habitat: Rural	3.61	1.44	2.5
Flock size	-0.09	0.33	-0.27

Table 3.7 Effect of independent variables on FID in song thrushes using ANOVA (Chi-square) for LMER.

	Chisq	*Df*	Pr (> Chisq)
Region	0.07	1	0.78
Season	0.58	1	0.44
Habitat	10.32	2	0.005 **
Flock size	0.07	1	0.78

Significant independent variables are depicted with<0.001 '**'.

Table 3.8 The comparisons among habitat types with FID for song thrushes in using a post-hoc test (Tukey).

Linear Hypotheses	Estimate	Std. Error	z value	Pr (>|z|)
Peri-urban river – Urban = 0	4.04	1.26	3.19	0.004**
Rural – Urban = 0	3.61	1.44	2.5	0.024*
Rural – Peri-urban river = 0	-0.43	1.03	-0.42	0.67

Significant independent variables are depicted with: <0.001 '**' <0.01, '*'.

3.2.5 Escape and response strategy

Blackbirds and song thrushes fled to a safe place to keep their distance in response to the approaching observer. The response strategy was significantly correlated with escape strategy, habitats and DF for blackbirds and song thrushes (Table 3.9, 3.12). The probability of walking to open spaces at a short distance to the next point (DF) will increase for urban birds as they showed larger FID (Table 3.10, 3.13). There was a trend toward the higher probability of flying to cover as FID and AD increased, but it was insignificant (Table 3.10). There were no significant differences between rural and peri-urban river habitats on escape strategy in blackbirds, however, urban landscapes showed significantly different and opposite effects on escape strategy compared to rural and peri-urban river areas (Table 3.11).

There was a weak probability of flying to cover for peri-urban river song thrushes and flying to open space within rural landscapes, but the response strategy was not associated with habitats (Table 3.12, 3.13). Therefore, a post-hoc test was not applied for examining the differences among habitats for song thrushes.

Table 3.9 Effect of FID, escape strategy (cover and open space), habitat types (urban, peri-urban river and rural), DF and AD (explanatory factor) on response strategy (walking and flying) in blackbirds using GLM.

Variables	Estimate	Std. Error	t value	Pr(>|z|)
Intercept	0.54	0.54	0.99	0.31
FID	0.03	0.02	1.44	0.14
Escape: open space	4.00	0.5	8.03	< 0.00001***
Habitat: Peri-urban river	-1.17	0.50	-3.43	0.0006***
Habitat: Rural	-1.60	0.51	-3.12	0.001**
DF	-0.06	0.01	-4.90	<0.00001**
AD	-0.01	0.03	-0.55	0.58

Significant independent variables are depicted with: <0.00001 ‘***’, <0.001 ‘**’.

Table 3.10 Effect of independent variables on FID in blackbirds using ANOVA (Chi-square) for GLM.

Variables	Chisq	Df	Pr (> Chisq)
FID	2.18	1	0.13
Escape	144.71	1	< 0.00001***
Habitat	13.03	2	< 0.00001***
DF	29.46	1	< 0.00001***
AD	0.30	1	0.58

Significant independent variables are depicted with: <0.00001 ‘***.

Table 3.11 The comparisons among habitats types with escape strategy for blackbirds in using post-hoc test (Tukey).

Linear Hypotheses	Estimate	Std. Error	z value	Pr (>|z|)
Peri-urban river – Urban = 0	-1.72	0.50	-3.43	0.001**
Rural – Urban = 0	-1.60	0.51	-3.12	0.003**
Rural – Peri-urban river = 0	0.11	0.35	0.33	0.73

Significant independent variables are depicted with: <0.001 ‘**’.

Table 3.12 Effect of FID, escape strategy (cover and open space), habitat types (urban, peri-urban river and rural), DF and AD (explanatory factor) on response strategy (walking and flying) in song thrushes using GLM.

Variables	Estimate	Std. Error	t value	Pr(>|z|)
Intercept	1.64	0.96	1.71	0.08
FID	-0.02	0.03	-0.50	0.61
Escape: open space	4.02	0.88	4.56	< 0.00001***
Peri-urban river habitat	-1.12	0.84	-1.33	0.18
Rural habitat	0.27	0.87	0.30	0.75
DF	-0.11	0.03	-3.44	0.0006***
AD	0.27	0.87	0.30	0.75

Significant independent variables are depicted with: <0.00001 ‘***’.

Table 3.13 Effect of independent variables on FID in song thrushes using ANOVA (Chi-square) for GLM.

Variables	Chisq	Df	Pr (> Chisq)
FID	0.25	1	0.61
Escape	36.2	1	< 0.00001***
Habitat	5.6	2	0.06 ·
DF	22.04	1	< 0.00001***
AD	0.3	1	0.6

Significant independent variables are depicted with: <0.00001 ‘***’’.

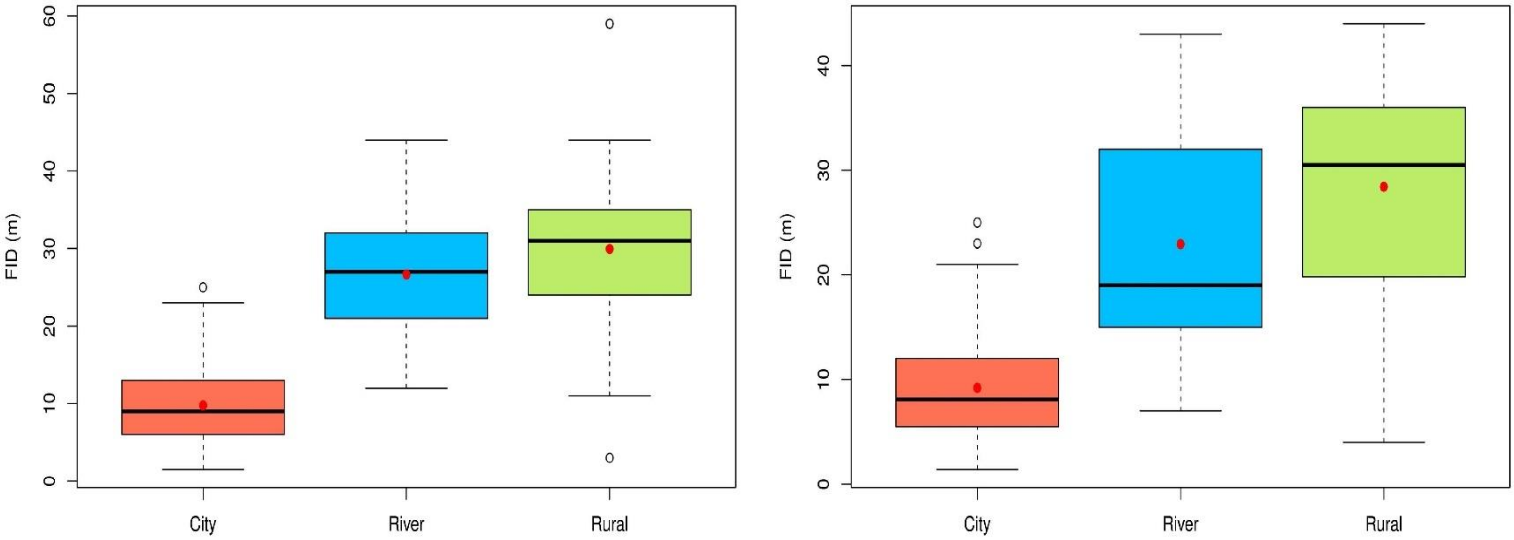

Figure 3.5 FID variations among different habitat types for blackbirds (right) and song thrushes (left). The y-axis represents the value of FID (in meters). Box plots show, mean (red circle), upper and lower quartiles, maximum and minimum values (vertical lines), and outliers (white dots).

3.3Discussion

Blackbirds and song thrushes allow the observer to approach closer in urban environments and respond and flush earlier in peri-urban river-edge and rural areas. Flight initiation distance differed significantly among individuals living in urban, rural, and peri-urban river areas. Birds inhabiting rural, and peri-urban river habitats flushed consistently from longer distances than birds occupying urban habitats. Moreover, risk-taking behaviours were associated with environmental characteristics, such as vegetation cover, human density and activities, urban noise pollution, and pedestrians disturbance. Birds modified their antipredator strategy in places with higher pedestrian traffic by reducing FID (Mikula, 2014). The distribution and connectivity of green spaces within urban habitats provide shelter and food resources for urban wildlife (Tryjanowski et al., 2017). Open spaces in urban areas were important predictors of differences in boldness-shyness and anti-predator behaviour of birds occupying different habitat types.

The correlation between SD and FID was positively significant, as is proposed by many studies (Blumstein 2003; Kalb et al. 2019a; Stankowich and Blumstein 2005) but habitat types were the only independent factor that affects escape behaviour (FID). The significant differences between urban landscapes with rural and peri-urban river areas where birds allowed the observer to approach closer. The variation of SD was dependent on the environmental site, which means SD effects on FID were completely confounded with habitat effects. The results indicated a positive correlation between SD and AD, but it did not find a significant correlation and their effect on FID.

Individuals often modify their behaviours, including risk-taking and antipredator behaviours, according to the intensity of novel situations, and urban individuals in urban landscapes experience many novel situations (Ditchkoff et al. 2006; Møller and Ibáñez-Álamo 2012). Previous studies have proposed that escape behaviour changes along urban-rural gradients, with shorter FID in urban individuals (Biondi et al. 2020; Morelli et al. 2018; Salido and Vicente 2019; Samia et al. 2017). The peri-urban habitats were perceived to be the same as rural habitats by blackbirds and song thrushes.

Anthropogenic noise, such as road noise, is more common in urban areas than in rural and peri-urban river habitats. It may lead to reduced fearful behaviour unless the road noise is associated with negative results (Van Donselaar et al. 2018). Many urban living songbirds showed adaptation behaviour to a noisy environment (Gravolin et al. 2014; Proppe et al. 2013) instead of showing avoidance behaviour. For example, noisy miners (*Manorina melanocephala*) living in rural habitats had a more aggressive response to the high level of noise compared to urban birds (Lowry et al. 2011). I speculate that urban birds regulate their fearfull responses according to level of threat and danger and consider them as a need to respond immediately or save more energy on foraging with higher fear tolerance and reduced escape behaviour.

The positive relationship between response strategy and DF may be related to the 'Flee Early and Avoid the Rush', or FEAR rule (Blumstein, 2010) where rural and peri-urban river blackbirds and song thrushes flushed at a longer distance (DF) than urban individuals to reduce the risk of a potential predator. Furthermore, it is difficult to accurately measure AD when birds are highly alarmed and vigilant. Blackbirds and thrushes are continuous visual foragers and use hearing while hunting prey (invertebrates). The interaction between AD and FID depends on habitat types, the speed of the observer, and different taxa (Cooper et al. 2009; Tätte et al. 2018). This might happen due to the persistence of the approacher rather than keeping a safe distance from the approaching observer (Blumstein 2003; Cooper et al. 2009; Glover et al. 2011; Harbour et al. 2019; Weston et al. 2012). Birds should create their safe buffer zone (the distance between SD and AD) to have more time for foraging and storing more energy. Similarly, Samia et al. (2017) indicated that urban individuals had larger differences between SD and AD. One suggestion is that food availability and abundance in urban habitats cause individuals to sacrifice their vigilance to obtain more time to forage and reduce their escape behaviour (Bonnot et al., 2017; Chace & Walsh, 2006). Animals showed behavioural plasticity against environmental challenges (Piersma and Drent 2003; Thomson et al. 2012).

Flock size was not correlated with the FID of blackbirds and song thrushes. Also, there was no relationship between DF and flock size. However, the weak and negative correlations between AD and flock size may indicate the role of group size on buffer zone and scanning time in blackbirds. They showed a shorter AD when in larger groups. Nevertheless, my results contrast in part with those reported by García-Arroyo and MacGregor-Fors (2020), where found positive relationships between flock size and AD and FID in house sparrows. However, they did not find a significant association with flock size in orange-breasted bunting (*Passerina leclancherii*) similar to our study where there were no AD and FID differences in song thrushes regarding flock size. The differences in antipredator responses between blackbirds and song thrushes may occur as social behaviour varies across taxonomic families (Winkler et al., 2020). Birds in larger flock sizes may benefit from the early warning communication to adjust their AD with risk (Barnard, 1980; Hingee & Magrath, 2009; Stankowich & Blumstein, 2005). The present results showed that group foraging does not act as a refuge or allow the birds to feel safer, which is, in contrast, to Kalb et al. (2019).

The test of the conspicuousness hypothesis showed that FID was not correlated with sex differences in blackbirds. It is speculated that due to the dark colour of blackbirds, they are not distinctive as a potential predator. It is suggested that the dark colour of blackbirds did not make them more conspicuous and FID is related to other factors. My results are in line with a similar study by García-Arroyo and MacGregor-Fors (2020), where they did not find significant differences in the AD and FID of male and female orange-breasted bunting in the flushing behaviour.

The findings showed that DF in blackbirds is not associated with FID, AD and SD but, rather, with habitat types, escape and response strategies, which was in line with those reported by Cooper and Blumstein (2015); Rodriguez-Prieto et al. (2008); Samia et al. (2016), where birds did not display a significant association between their antipredator behaviour and DF. My results were not in line with Tätte et al. (2018) where a positive relationship between FID and DF in black redstarts was found. They showed that birds fled at a shorter distance to the safe spot in decreased FID. Urban blackbirds decreased their buffer zone (AD) and allowed closer observer approaches, shorter FID, before escaping at shorter DF.

Larger FID in rural habitats would reduce the risk of predators for a bird that moved a greater distance to an adjacent landing spot and reduced its buffer zone (AD) and tolerance of potential predators. It determines that birds may bear a minimum approach distance before they are disturbed. The benefits of delaying the flush (shorter FID), and shorter DF, would allow urban birds to have another opportunity to resume foraging at the same spot shortly after the risk is eliminated. Here, blackbird and song thrush decisions about how far to escape depends on the type of response to flush and escape to cover or open spaces and environmental sites.

At larger FID, the optimal response for birds is walking to open spaces, such as open grass, fences rather than to cover in vegetation. Walking a short distance to open spaces at larger FID may reduce the risk of capture while flying long distances to cover when the predator is closer would decrease the higher risk of capture. Blackbirds and song thrushes spent more energy on a costly flying response at a longer distance to cover, which there is a risk of ambush predators, such as cats. My results are in line with findings by Kalb et al. (2019); Kalb and Randler (2017), where black redstarts frequently flee to open structures because they perceived cover as dangerous due to the possible presence of predators.

My findings support the response and escape strategies examined by Rodriguez-Prieto et al. (2008) where blackbirds made their escape (FID) decision shape of '*when'* to flush, which then directed them in '*how'* to respond (i.e. escape strategy), which determined '*how far'* to flee (DF). It would be interesting to investigate whether blackbirds and song thrushes perform different escape strategies depending on different kinds of predators, including aerial and terrestrial predators.

3.4 Conclusion

This chapter has confirmed that standard FID protocols are practical tools to examine risk-taking behaviour in birds in response to approaching humans across habitats and times. The differences among landscape structures shaped by anthropogenic activities shaped the bird's response and escape strategies and FID. Other species may respond differently to FID due to different social networking and foraging behaviours. Flock size is sometimes affected when individuals decided to escape and avoid risks. FID methods are a simple but understandable way to perform comparative analyses to interpret the variation of behavioural traits in the presence and absence of perceived threats such as predators.

My results indicated that escape strategy and FID are strongly related to habitat types and that these effects are consistent across two related species and two different regions from the North and South Island. The role of habitat types on response strategy, escape strategy and DF was substantial. The type of landscape determined *how far* and *which way* would be optimal to respond to risky situations. Birds regulated their risk-taking behaviours according to habitat structure and it may show that results from one region with different habitats are extrapolate to other parts of New Zealand.

The present research investigated the risk-taking behaviours of birds in response to human presence. I studied two introduced bird species in New Zealand and their responses to approaching humans within different habitats. Native New Zealand birds have been through anthropogenic changes and habitat loss for several centuries. Changing their natural habitats into urbanised landscapes and introducing exotic mammals, such as dogs, cats and possums create novel challenging environments.

My findings suggest examining the risk-taking behaviour of native birds and identifying to which extent they may recognise predators and risks in new habitats, the effect of body mass and conditions, food availability and environmental pollutions on escape strategy. My understanding of relationships between life and natural history with risk-taking and escape behaviour will develop insight into how species thrive anthropogenic changes and respond to environmental variations.

Chapter 4 Where do angry birds live? Analysing aggressive behaviour in response to an intruder

4.1Introduction

Urban animal populations often display different behaviours compared to rural counterparts, such as the tendency to be more sedentary (Partecke & Gwinner, 2007), increased habituation to human presence (Atwell et al., 2012; Breck et al., 2019; Kalb et al., 2019; Moller, 2010; Pearish et al., 2019; Scales et al., 2011; Tätte et al., 2020), higher song frequencies (Hennigar et al., 2019; Luther & Baptista, 2010; Luther & Derryberry, 2012; Ma et al., 2010; Nemeth & Brumm, 2009; Slabbekoorn & Peet, 2003; Wood & Yezerinac, 2006), and species-specific differences in aggression (Hasegawa et al., 2014; Newman et al., 2006; Scales et al., 2011; Szász et al., 2019). These differences may be related to light and noise pollution (Dominoni et al., 2015a; Grunst et al., 2019; Hu & Cardoso, 2009; Longcore & Rich, 2004; McIntyre, 2013; McMunn et al., 2019; Phillips et al., 2020; Slabbekoorn & Ripmeester, 2008; Thawley & Kolbe, 2020), different predator pressure (DeCandido & Allen, 2006; Eötvös et al., 2018; Rodriguez-Prieto et al., 2009), anthropogenic structures (Benítez-López et al., 2010; Li et al., 2010; Nichols et al., 2018; Peralta et al., 2011), changes in green spaces (Carbó-Ramírez & Zuria, 2011; González-oreja et al., 2012), and differences in availability of food resources (Fedriani et al., 2001; Heiss et al., 2009; Marzluff & Neatherlin, 2006).

Differences in behavioural traits along a gradient of urban to rural habitats are often driven by plasticity and environmental effects (Bermúdez-Cuamatzin et al., 2009; Estevez et al., 2002; Rodriguez-Prieto et al., 2009; Stevenson & Rillich, 2013). Intraspecific variations in behavioural traits result from a trade-off between potential risks and optimal decisions, which depends on intrinsic factors, such as physiological state (body condition and hormonal changes) (Moiron et al., 2019; Moschilla et al., 2018), and external factors, such as predator pressure, spatial and food resources (Heithaus & Dill, 2002; Verdolin, 2006). Anthropogenic disturbance is one of the external factors that may alter animal behaviours (Ditchkoff et al., 2006).

Urban habitats, one form of anthropogenic disturbance, may favour more aggressive individuals that can outcompete less aggressive conspecifics to access more resources (Duckworth, 2008), at least in the short-term, even though there ultimately may be an increased cost of aggressiveness (Duckworth, 2006). There may be a significant role of genes and environmental characteristics on aggressive responses (Coss et al., 2002; Eccard & Rödel, 2011; Edwards et al., 2015; Felden et al., 2018; Grunst et al., 2019; Kukekova et al., 2011; Marks et al., 2005; McGhee & Travis, 2013; Mueller et al., 2014; Rollins et al., 2015). The “set point” of aggressive behaviour is related to the cost and benefit of expression in a habitat (Estevez et al., 2002; Stevenson & Rillich, 2013) and differs among urban and rural populations with various habitat conditions (Foltz et al. 2015). Another factor associated with territorial aggression behaviour is habitat quality (Fox, Rose, and Myers 1981; Santangelo et al. 2002; Scales et al. 2013), which has been studied in blackbirds (Miranda et al. 2013; Riyahi et al. 2015, 2017).

Birds use territorial behaviour to partition space and defend resources from inter-and intra-specific individuals (Depino & Areta, 2019). They defend their territories through direct approach or long-distance signals (Grether et al., 2009; Orians & Willson, 1964). Birds generally use long-distance vocalisations during a territorial announcement and mostly do not respond to other species vocalisations (Emlen, 1972). Most birds perceive intra-specific individuals as intruders, but some will defend their territories against inter-specific individuals as well (Catchpole, 1978; Depino & Areta, 2017; Freeman, 2016; Martin et al., 1996; Prescott, 1987; Robinson & Terborgh, 1995). For example, I have observed blackbirds and song thrushes chase larger New Zealand tui (*Prosthemadera novaeseelandiae*).

Aggressive signals may be categorised based on the cost of signal creation (Akçay et al., 2020). There is an evolutionary optimality between signalling, such as call and display, and non-signalling responses, including attacking without prior signalling (Searcy & Nowicki, 2005). Urban species have significantly stronger responses to simulated territorial intrusions than rural conspecifics in birds (Akçay et al., 2020; Ali & Anderson, 2018; Moseley et al., 2019; Phillips et al., 2020), mammals (Chapman et al., 2012; Luniak, 2004; Uchida et al., 2020), and reptiles (Baxter-Gilbert et al., 2019; Moore et al., 2020; Storks & Leal, 2020; Stroud et al., 2019). Signalling and aggressive behaviours work separately as behavioural characters (Akçay et al., 2014). Ecological conditions in urban areas, such as high noise levels, may impact signal transmission and detection, and signalling responses are likely to be affected more than aggressive behaviours and be performed with reduced effectiveness and reliability (Brumm & Slabbekoorn, 2005; Phillips & Derryberry, 2018; Slabbekoorn & Smith, 2002).

A common response to higher urban noise levels is vocalising at higher amplitudes, known as the Lombard effect (Brumm, 2004; Brumm & Todt, 2002; Brumm & Zollinger, 2011). Urban birds often sing at a higher intensity to display their dominance instead of using soft, low pitch songs (Akçay et al., 2020). The Lombard effect predicts that there will be an increase in the frequency of use of loud songs by urban individuals in response to intruder calls compared to rural habitats. Two distinct predictions have been considered for this hypothesis: (a) soft song frequency will decrease in urban habitats compared to rural areas while loud songs will increase, and (b) urban birds will be more likely to ultimately attack intruders and will signal their intention with loud songs (Akçay et al., 2020).

The level of resource defence is correlated with the availability of the resource. Limited or spatially clustered resources should lead to more frequent defensive behaviour (Brown, 1964; Davies et al., 2018; Grant, 1993; Stamps, 1994). Urbanisation may play an important role in modifying the defence of resources (Davies et al., 2018; Sprau & Dingemanse, 2017) as well as imposing novel experiences on wildlife (Sih et al., 2011). Loss of natural resources, such as food, space and increased human disturbances, including sound and air pollution, present wildlife with altered kinds of risks and rewards (Senar et al., 2017). Defensive and aggressive behaviours of territorial songbirds have been studied using a stuffed decoy bird placed in the centre of the territory to simulate territorial intrusions. Urban birds use more intense aggression in territorial defence compared with rural counterparts (Abolins-Abols et al., 2016; Evans et al., 2010; Fokidis et al., 2011; Foltz et al., 2015; Garamszegi & Herczeg, 2012; Scales et al., 2011), although some species show the opposite trend (Atwell et al., 2012).

There is a significant relationship between phenotypic and environmental variation (Gienapp et al., 2017; Sih et al., 2015; Stearns, 1989; Wong & Candolin, 2015), which includes behavioural plasticity in response to urbanised areas (Brown et al., 2013; Damas-Moreira et al., 2019; Fisher et al., 2020; Levey et al., 2009; Reaney & Backwell, 2007; Sih et al., 2004; Sol et al., 2013). For example, songbirds, such as nightingales (*Luscinia megarhynchos*), great tits and blackbirds (Ripmeester et al., 2010) adjust their song amplitude (Brumm, 2004) and frequency (Slabbekoorn & den Boer-Visser, 2006) in response to urban noise. With increasing predator pressure, boldness and risk-taking traits are positively correlated with aggression against conspecifics, such as within populations of stickleback (Bell, 2005), great tits (Drent et al., 1996; Gienapp et al., 2017), fiddler crabs (Reaney & Backwell, 2007), and song sparrows (Evans et al., 2010). While increased aggression might be costly (Duckworth, 2006b; Wingfield et al., 2001), individuals can benefit from higher initial fitness in comparison to less aggressive counterparts in some situations (Abolins-Abols et al., 2016; Ali & Anderson, 2018; Fisher et al., 2020; Hasegawa et al., 2014). More aggressive individuals declined gradually and after a few generations, they are removed from the population (Akçay et al., 2020; Hardman & Dalesman, 2018).

Differences in boldness and aggression among individuals impact habitat selection (Bejder et al., 2006; Carrete & Tella, 2011), species distribution (Scales et al., 2011) and occupancy of high-quality nesting and territory sites (Forsman et al., 2007; Jaakkonen et al., 2015; Samplonius & Both, 2017). The local adaptation hypothesis suggests that populations increase their performance as a response to local environments or similar conditions (Colautti & Lau, 2015).

Social and physical impacts and their overlap and interaction are affected by aggressive behaviour. Generally, aggressive behaviour shows a significant negative relationship with the availability of resources, including food, vegetation cover and space (Camfield, 2006; Ewald & Carpenter, 1978; Fox et al., 1981; Lore et al., 1986; Maruyama et al., 2010; Paola et al., 2012; Snekser et al., 2009; Toobaie & Grant, 2013), and with inter-and intra-specific competition over resources (Lacava et al., 2011; Paola et al., 2012; Perrin et al., 2001; Pusey & Schroepfer-Walker, 2013; Yoon et al., 2012). Higher population density also increases the level of aggressive interactions (Bohlin et al., 2002; Yoon et al., 2012).

Territorial aggression occurs when an individual defends space and resources from conspecifics (Szász et al., 2019), which plays a major role in sexual selection, with a direct or indirect impact on the survival and reproductive success of individuals (Davies et al., 2018; Szász et al., 2019; Szász et al., 2019). Aggressive individuals typically occupy higher quality territories at the beginning of the breeding season (Duckworth, 2006; Robinson & Terborgh, 1995; Rosvall, 2008; Scales et al., 2013), and will defend the territory efficiently (Yasukawa, 1979; Yasukawa & Searcy, 1982). The timing of breeding and quality of a nest site is significantly related to reproductive success (Bensch & Hasselquist, 1991; Ens et al., 1992; Verhulst et al., 1995). Females choose suitable males and either avoid or select more aggressive males (Kontiainen et al., 2009; Kunc et al., 2006; Ophir & Galef Jr, 2003; Ophir et al., 2005; Otter et al., 1999; Sandell & Smith, 1997; Szász et al., 2019). Females can benefit from this interaction to identify higher-quality territories (Berglund et al., 1996) or individuals suitable for parental care (Candolin, 2000). Male songbirds use their territory to attract females by singing and displaying (Garamszegi et al., 2009).

Aggression behaviour plays a significant role in ejaculate quality, and therefore, paternity (Mora et al., 2017), extra-pair paternity (Spoon et al., 2007; Van Oers et al., 2008) and copulation frequency (Ophir et al., 2005). Hatching and fledging success are influenced by aggression through nest-site quality, different maternal provisioning (Grenna et al., 2014; Szász et al., 2014) or parental care activity, which have a negative relationship with aggression (Mutzel et al., 2013).

Aggression carries positive and negative consequences in reproductive success. Males should balance their territory defence time and energy investment between male-male competition and female mate selection. Regulating trade-offs relationship between aggression and reproductive success, strategies that emphasise more or less aggressive behaviours may lead to the same overall results (Davies et al., 2018; Szász et al., 2019). For example, in parental care activities, aggression may have a positive impact on nest defence and a negative consequence on incubation and provisioning (Mutzel et al., 2013).

Aggression may change throughout the season, driven by changes in food availability during winter in urban habitats (Chamberlain et al., 2009; Gaston et al., 2005; Schoech et al., 2007), predation risk (Ibanez-Alamo et al., 2018; Ibáñez-Álamo & Soler, 2010; Ibáñez ‐ Álamo & Soler, 2010; Leighton et al., 2010; Lindsay et al., 2008), and the value of present and future reproduction (Szász et al., 2019; Szász et al., 2019; Williams, 1966). Age is one of the factors that cause individuals to behave differently (Van Noordwijk & de Jong, 1986). Experiencing the intensity of risks and threats throughout life should enable birds to optimise their decision. Aggression has been linked with the exploration of new areas (Drent et al., 1996; Garamszegi & Herczeg, 2012; Hardman & Dalesman, 2018), but may increase parasite load (Dunn et al., 2011). Risk-taking and anti-predator behaviour can associate with aggression to form a behavioural syndrome (Garamszegi et al., 2015).

I hypothesised that urban blackbirds and song thrushes show more aggressive behaviour toward an intruder within their territory boundaries during the breeding season compared to rural and peri-urban river individuals. I examined (a) the level of aggressive and signalling responses toward a speaker that broadcast conspecific songs within the three different habitats, (b) compared patterns of variation in aggressive and signalling behaviours of birds in the Wellington and Canterbury regions of New Zealand to test local adaptation of traits, and (c) identified the intra- and inter-specific differences in response to interactive playback within focal birds territories.

4.2Methods

4.2.1 Study Area

The study was conducted at three habitats including urban, rural, peri-urban river habitats in the Wellington and Canterbury regions, New Zealand (Figure 4.1).

4.2.2 Experimental Procedures

I conducted experiments between September to December 2019 in the Wellington region and from September to December 2020 in the Canterbury region during blackbird and song thrush breeding seasons. All observations were made between 8:00 and 14:00 hours. Distances between sites were > 50 m, to decrease the probability of duplicate sampling of territorial birds.

4.2.3 Aggression test

Song thrushes and blackbirds are obvious in their behaviour as they protect their territories and nests during the breeding season. Territory boundaries were determined by locating singing focal males. Before the experiment trials, the songs of territorial males from each habitat were recorded using a digital voice recorder (recording bit rate: 1536 Kbps) from the neibourhood with at least 500 metres distance from broadcasting spot. These songs were imported into Raven Lite 2.0.1 to remove background sounds and low-frequency noises. I played the song to target territorial males from the same habitat type through a bird caller speaker (model 48W E388A, specs sensitivity of

53Bbv/108MHz) The speaker was camouflaged and covered with leaves and branches of the same tree.

I used protocols from similar studies to compare the responses of individuals to the conspecific's song being broadcast in their territory (Evans et al., 2010; Hyman & Hughes, 2006; Hyman et al., 2004; Nowicki et al., 2002; Scales et al., 2011). During the trial, the following responses were recorded: (1) flight duration around the territory (s), (2) the proportion of time within five metres of the speaker, (3) the closest distance that the bird approached the speaker (cm), (4) duration of singing in response to the speaker (s), (5) the number of times the target bird flew over the speaker (Akçay et al., 2015; Akçay et al., 2020). The distances were measured by a laser rangefinder (AEG LMG50).

Before setting up the experiment, the focal bird was located using song or visual presence. I only proceeded when there was no external distraction, such as passing pedestrians. I waited for at least five minutes to confirm that the bird was in its territory and that it kept singing, then mounted the speaker to hedgerows or tree branches, 1.5 m in height from the ground. The focal bird could then approach the speaker without getting too close to the ground. I stood approximately 20 to 25 m from the playback speaker, with the remote control. When playback began and broadcast two or three different songs of blackbird and song thrush in the subject's territory, I recorded the responses of the focal bird for 5 minutes. I combined each from the Wellington and Canterbury regions into a single analysis (see Table 4.1 for the number of tested individuals). Following testing aggression behaviour, I mounted a novel object next to the speaker to examine novelty avoidance-seeking behaviour (see Chapter 5). All experimental trials were conducted on a sunny or cloudy day, without rain and less than 19 km/h wind.

Table 4.1 The number of song thrushes and male blackbirds in each habitat that had song playback trials.

	Blackbird		Song thrush	
Region\Habitat	Wellington	Canterbury	Wellington	Canterbury
Urban	26	26	11	13
Peri-urban river	34	24	18	10
Rural	24	24	15	18
Total	84	74	44	41

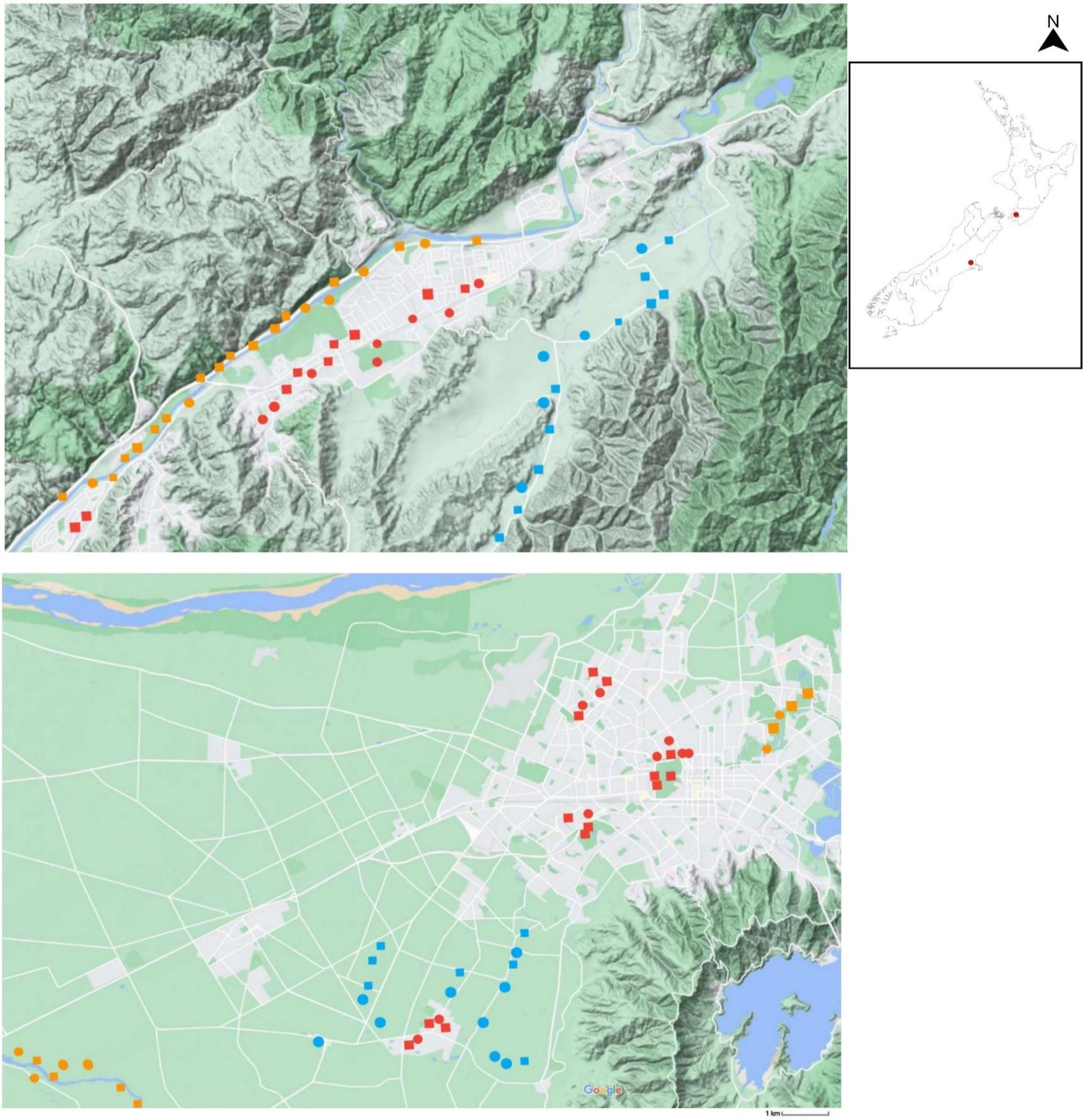

Figure 4.1 Location of data collection for both blackbirds (square) and song thrushes (circles) in the Wellington (upper, left) and Christchurch regions (lower, left) within urban (red), rural (blue) and peri-urban river (orange) habitats.

4.2.4 Statistical Analysis

To determine the strength and direction of the relationship of the recorded responses, correlation coefficients were calculated using the Spearman test.

A Generalised Linear Model (GLMs, R package lme4) with a Quasi-Poisson error distribution due to significant overdispersion (Zeileis et al., 2008) was used to test the effect of habitat types on each response, including the closest distance to the speaker, the number of flights over the speaker, duration of singing in response to the playback song and the time spent near the speaker in a five-meter radius as the fixed factors, and the region as an explanatory factor. An ANOVA F test was run to assess relationships for each GLM model between these five responses and habitat types.

To create one aggression score for analysis, a principal components analysis (PCA) was run to summarise the five aggression measures using the "prcomp" function in R (Jolliffe, 2002). Two PCA scores were used in a GLM (Gaussian error distribution) to examine the effect of habitat types on PCAs as a fixed factor in two separate models. I mapped the PCAs variables using ggplot2 package in R.

A post-hoc test with "Tukey" and "holm" adjustment, using the glht function from the 'multcomp' package, was run to examine the comparisons among all habitats (Bretz et al., 2016; Hothorn et al., 2008; Hsu, 1996; Searle & Gruber, 2016).

All statistical tests were conducted with R 4.0.3 software (Team, 2013). (R Development Core Team 2013).

4.3Results

4.3.1 Relationships between aggression and signalling responses

After testing the possible correlations between behavioural traits in blackbirds and song thrushes, the results showed differences in the behavioural variables collected from two species from different types of habitats in response to human disturbances. Based on the Spearman rank test, there were no significant correlations between the duration of singing as a signalling behaviour to other behavioural traits in blackbirds or song thrushes (Table 4.2).

Table 4.2 Aggression responses interactions for blackbirds and song thrushes in the Wellington and Canterbury regions using Spearman's rank correlation.

Interactions	Blackbird		Song thrush	
	Rho	*p*- Value	*Rho*	*p*- Value
Flight duration with the number of flights	0.63	< 0.00001***	0.72	< 0.00001***
Flight duration with the closest distance	-0.48	< 0.00001***	-0.18	< 0.00001***
Flight duration with time spent within 5 m	0.41	< 0.00001***	0.70	< 0.00001***
Closest distance with time spent within 5 m	-0.35	< 0.00001***	-0.25	0.02*
Closest distance with the number of flights	-0.50,	< 0.00001***	-0.37	0.0004**
The number of flights with time spent within 5 m	0.34	< 0.00001***	0.62,	< 0.00001***
Closest distance with the duration of singing	0.07	0.4	-0.08,	0.43
Duration of singing with the number of flights	0.06	0.44	-0.07,	0.48
Duration of singing with flight duration	-0.08	0.34	-0.01,	0.9
Duration of singing with time spent within 5m	0.07	0.40	0.3,	0.76
Flight duration with the duration of singing	-0.83	0.34	-0.1,	0.89

Significant independent variables are depicted with: <0.00001 '***', ≤ 0.001 '**' ≤0.01, '*' .

4.3.2 Effect of habitats and regions on aggression and signalling responses

The aggression and signalling behaviours of blackbirds and song thrushes were significantly affected by habitat types and regions. However, the results had no significant correlations between the number of flights over the speaker and the flight duration with regions in blackbirds (Table 4.3). The behavioural responses showed negative correlations with peri-urban river and rural habitat except for the closest approach distance to the speaker (Table 4.4). There was a weak correlation between time spent within 5 m of the speaker and habitats.

Fight duration, time spent within 5 m and the number of passes over the speaker were affected by habitat types in song thrushes, and the correlations were significantly negative in peri-urban and rural areas. The correlation between the closest distance approach speaker was significantly negative with regions (Table 4.5). There was a non-significant trend towards a shorter duration of singing over the speaker in peri-urban river song thrushes (Table 4.6).

Table 4.3 Effect of habitat types on each behavioural response to the speaker for blackbirds using GLM and region as an explanatory factor.

Fixed factor	Behavioural responses	Estimate	Std. Error	t value	P value
Intercept	Closest distance	5.129	0.10	51.73	< 0.00001***
	Flight duration	4.9	0.07	63.4	< 0.00001***
	Time spent within 5 m	5.13	0.09	60.40	< 0.00001***
	Number of flights	1.77	0.11	16.13	< 0.00001***
	Duration of singing	4.50	0.12	35.95	< 0.00001***
Peri-urban river	Closest distance	0.66	0.12	5.5	< 0.00001***
	Flight duration	-0.77	0.14	-5.37	< 0.00001***
	Time spent within 5 m	-0.34	0.13	-2.53	0.01*
	Number of flights	-0.75	0.15	-4.9	< 0.00001***
	Duration of singing	-0.86	0.23	-3.66	0.0003***
Rural	Closest distance	0.65	0.12	5.43	< 0.00001***
	Flight duration	-1.10	0.16	-6.77	< 0.00001***
	Time spent within 5 m	-0.11	0.12	-0.88	0.37
	Number of flights	-1.006	0.17	-5.9	< 0.00001***
	Duration of singing	-0.35	0.20	-1.72	0.07
Region Wellington	Closest distance	-0.29	0.09	-3.3	0.001**
	Flight duration	0.19	0.11	1.63	0.10
	Time spent within 5 m	0.27	0.10	2.56	0.01*
	Number of flights	0.22	0.12	1.76	0.08
	Duration of singing	-0.98	0.19	-4.98	< 0.00001***

Significant independent variables are depicted with: <0.00001 '***', ≤0.001 '**'≤ 0.01, '*' .

Table 4.4 Effect of habitat types and regions on behavioural responses in blackbirds using ANOVA (Chi-square) for GLM.

Behavioural responses	Independent variables	Chisq	df	Pr(>Chisq)
Closest distance	Habitat	41.65	2	< 0.00001***
	Region	10.9	1	0.0009***
Flight duration	Habitat	65.93	2	< 0.00001***
	Region	2.7	1	0.1
Time spent within 5m	Habitat	6.95	2	0.03*
	Region	6.64	1	0.009**
Number of flights	Habitat	48.42	2	< 0.00001***
	Region	3.13	1	0.08
Duration of singing	Habitat	15.13	2	0.0005***
	Region	28.03	1	< 0.00001***

Significant independent variables are depicted with: <0.00001 '***', ≤ 0.001 '**' ≤0.01, '*'.

Table 4.5 Effect of habitat types on each behavioural response to the speaker for song thrushes using GLM and region as an explanatory factor.

Fixed factor	Behavioural responses	Estimate	Std. Error	t value	P value
Intercept	Closest distance	5.20	0.11	44.17	< 0.00001***
	Flight duration	5.1	0.13	38.08	< 0.00001***
	Time spent within 5 m	5.27	0.11	46.87	< 0.00001***
	Number of flights	1.82	0.13	14.37	< 0.00001***
	Duration of singing	5.05	0.13	37.36	< 0.00001***
Peri-urban river	Closest distance	0.19	0.17	1.12	0.26
	Flight duration	-0.4	0.17	-2.27	0.02*
	Time spent within 5 m	-0.10	0.14	-0.74	0.45
	Number of flights	-0.54	0.17	-3.21	0.002**
	Duration of singing	-0.20	0.17	-1.21	0.22
Rural	Closest distance	0.32	0.14	2.23	0.02*
	Flight duration	-1.13	0.21	-5.43	< 0.00001***
	Time spent within 5 m	-0.48	0.15	-3.3	0.001**
	Number of flights	-1.45	0.22	-6.63	< 0.00001***
	Duration of singing	0.18	0.13	1.45	0.15
Region Wellington	Closest distance	-4.45	0.55	-8.16	< 0.00001***
	Flight duration	-0.05	0.15	-0.32	0.74
	Time spent within 5 m	-0.02	0.11	-0.22	0.84
	Number of flights	-0.07	0.15	-0.45	0.65
	Duration of singing	0.18	0.13	1.45	0.15

Significant independent variables are depicted with: <0.00001 ‘***’, ≤0.001 ‘**’ ≤ 0.01, ‘*’.

Table 4.6 Effect of habitat types and regions on behavioural responses in song thrushes using ANOVA (Chi-square) for GLM.

Behavioural responses	Independent variables	Chisq	df	Pr(>Chisq)
Closest distance	Habitat	5.15	2	0.07
	Region	356.22	1	< 0.00001***
Flight duration	Habitat	33.17	2	< 0.00001***
	Region	0.10	1	0.74
Time spent within 5m	Habitat	12.16	2	0.002**
	Region	0.04	1	0.82
Number of flights	Habitat	5.43	2	< 0.00001***
	Region	0.20	1	0.65
Duration of singing	Habitat	5.25	2	0.07
	Region	2.11	1	0.14

Significant independent variables are depicted with: <0.00001 ‘***’, ≤0.001 ‘**’ .

4.3.3 PCA variables of aggressive and signalling behaviour within habitats and regions

For blackbird individuals, the first principal component (PC1) was positively correlated with flight duration toward the speaker. The high score of this PC showed more active responses to the speaker with a longer latency to fly (Table 4.7). The second principal component (PC2) was negatively related to the duration of singing over the speaker and explained 46.01% and 19.95% (in total 65.63%) of the variations in these five responses. I used PC1 and PC2 in all statistical analyses as the aggression score for blackbirds (Table 4.8, Figure 4.2, A). Also, for song thrush individuals, the first principal component (PC1) of this PCA explained 57.22% of the variance and was characterised by loadings of flight duration toward the speaker. A high negative score on this PC indicates a shorter latency to fly close to the speaker for the first time. The second principal component (PC2) explained 20.70% of the variance and was related to a negative loading of the duration of singing (in total 77.92%) (Table 4.9, 4.10, Figure 4.2 B).

The variability of the first and second PCA was significantly affected by habitat types and regions for blackbirds (Table 4.11, Figure 4.3 and 4.4 A). The correlation with habitat types had a higher score on PC1, related to flight duration around the speaker (Table 4.12). The correlation was negative with peri-urban and rural habitats, which means that blackbirds displayed increased flight duration in urban areas compared to the peri-urban river and rural habitats while there were no differences between the peri-urban river and rural individuals for flight duration (Table 4.13). The variability of the negative PC2, correlated with the duration of singing over the playback speaker, showed a weak and positive correlation with habitat, but a strong and positive correlation with regions (Table 4.12). Peri-urban river blackbirds showed a slightly decreased duration of singing compared to urban individuals and there were no significant differences between rural individuals with urban and peri-urban blackbirds. The strong correlation between PC1 and PC2 with regions showed that individuals from the Canterbury region displayed shortened duration of flying and duration of singing compared to individuals in the Wellington region (Figure 4.3, Table 4.11).

The first PCAs of song thrushes were affected by habitat types but not with regions. The second PCAs were related to duration of song and showed a weak relationship with habitat (Table 4.14, Figure 4.4, B). There was a trend towards a higher probability of increased duration of singing in the rural and peri-urban river habitats compared to urban individuals (Table 4.15). Habitats had higher scores on the PC1 axes, respectfully, which means that they displayed increased flight duration in urban habitats compared to peri-urban and rural areas, decreased duration of singing in rural song thrushes compared to urban individuals (Table 4.15). There was also a weak effect of habitat types on PC2 (Table 4.15, *p* = 0.09), in the Tukey corrections of significance level, I was able to detect a weak and negetive significant differences in duration of singing between rural and peri-urban river individuals, which means that peri-urban river song thrushes showed increased duration of singing over the playback song compared to rural individuals (Table 4.16).

Table 4.7 Primary PCA results among the five responses to aggression behaviour in blackbirds.

	PC1	PC2	PC3	PC4	PC5
Standard deviation	1.51	0.99	0.89	0.78	0.53
Proportion of variance	0.4601	0.1995	0.1618	0.122	0.056
Cumulative proportion	0.46	0.65	0.82	0.94	1.00

Table 4.8 Final PCA results among the five responses to score as aggression behaviour in blackbirds.

Responses	PC1	PC2	PC3	PC4	PC5
Closest distance	-0.46	-0.21	0.10	-0.84	0.03
Flight duration	0.56	-0.04	0.28	-0.29	-0.71
Time spent in 5 m	0.38	0.14	-0.83	-0.35	0.09
Number of flights	0.55	-0.03	0.41	-0.21	0.69
Song duration	0.11	-0.96	-0.18	0.15	0.009

Table 4.9 Primary PCA results among the five responses to aggression behaviour in song thrushes.

	PC1	PC2	PC3	PC4	PC5
Standard deviation	1.69	1.01	0.73	0.64	0.39
Proportion of variance	0.57	0.20	0.10	0.084	0.03
Cumulative proportion	0.57	0.77	0.88	0.97	1.00

Table 4.10 Final PCA results among the five responses to score as aggression behaviour in song thrushes.

Responses	PC1	PC2	PC3	PC4	PC5
Closest distance	-0.44	-0.22	0.84	0.03	0.20
Flight duration	0.53	-0.05	0.43	-0.1	-0.71
Time spent in 5 m	0.49	-0.11	0.11	0.78	0.34
Number of flights	0.52	0.02	0.16	-0.61	0.57
Song duration	0.02	-0.96	-0.23	-0.10	-0.033

Table 4.11 The effect of habitat types on PCA variables in blackbirds using GLM, region as an explanatory factor.

Fixed factors	PCA variables	Estimate	Std. Error	t value	P-value
Intercept	Flight duration PC1	0.92	0.19	4.75	< 0.00001***
	Duration of singingPC2	-0.67	0.14	-4.8	< 0.00001***
Peri-urban river	Flight duration PC1	-1.82	0.24	-7.53	< 0.00001***
	Duration of singingPC2	0.22	0.17	2.73	0.006**
Rural	Flight duration PC1	-1.9	0.24	-7.8	< 0.00001***
	Duration of singingPC2	0.22	0.17	1.24	0.21
Region Wellington	Flight duration PC1	0.55	0.2	2.77	0.52
	Duration of singingPC2	0.90	0.14	6.27	< 0.00001***

Significant independent variables are depicted with: <0.00001 ‘***’, ≤ 0.001 ‘**’ ≤0.01, ‘*’ .

Table 4.12 Effect of habitat types on PCA variables in blackbirds using ANOVA for GLM.

	Independent variables	Chisq	df	Pr(>Chisq)
Flight duration PC1	Habitat	79.05	2	< 0.00001***
	Region	7.67	1	0.005**
Duration of singingPC2	Habitat	7.5	2	0.02*
	Region	39.36	1	< 0.00001***

Significant independent variables are depicted with: <0.00001 '***', ≤0.001 '**' ≤0.01, '*'.

Table 4.13 Differences in aggressive and signalling behaviours of blackbirds among habitats types using a post-hoc test (Tukey).

Fixed factors	PCA variables	Estimate	Std. Error	t value	P-value
Peri-urban river – Urban = 0	Flight duration PC1	-1.82	0.24	-7.53	< 0.00001***
	Duration of singingPC2	0.5	0.17	2.73	0.01*
Rural – Urban = 0	Flight duration PC1	-1.89	0.24	-7.8	< 0.00001***
	Duration of singingPC2	0.22	0.17	1.24	0.3
Peri-urban river – Rural = 0	Flight duration PC1	-0.07	0.24	-0.3	0.766
	Duration of singingPC2	-0.26	0.18	-1.45	0.3

Significant independent variables are depicted with: <0.00001 '***', ≤0.001 '**' ≤ 0.01, '*' .

Table 4.14 The effect of habitat types on PCA variables in song thrushes using GLM, region as an explanatory factor.

Fixed factors	PCA variables	Estimate	Std. Error	t value	P-value
Intercept	Flight duration PC1	-0.93	0.30	-3.05	0.003**
	Duration of singing PC2	0.32	0.27	1.15	0.4
Peri-urban river	Flight duration PC1	0.98	0.38	2.62	0.01*
	Duration of singing PC2	0.32	0.27	1.15	0.25
Rural	Flight duration PC1	2.05	0.36	5.7	< 0.00001***
	Duration of singing PC2	-0.30	0.26	-1.13	0.25
Region Wellington	Flight duration PC1	-0.31	0.3	-1.06	0.3
	Duration of singing PC2	-0.35	0.21	-1.61	0.11

Significant independent variables are depicted with: <0.00001 '***', ≤0.001 '**' ≤ 0.01, '*'.

Table 4.15 Effect of habitat types on PCA variables in song thrushes using ANOVA for GLM.

	Independent variables	F	df	*p*-Value
Flight duration PC1	Habitat	18.25	2	< 0.00001***
	Region	0.41	1	0.52
Duration of singing PC2	Habitat	2.41	2	0.09
	Region	2.61	1	0.10

Significant independent variables are depicted with: <0.00001 ‘***’.

Table 4.16 Differences in aggressive and signalling behaviours of song thrushes among habitats types using a post-hoc test (Tukey).

Fixed factors		Estimate	Std. Error	t value	P value
Peri-urban river – Urban = 0	Flight duration PC1	-0.98	0.40	-2.45	0.01*
	Duration of singing PC2	0.32	0.27	1.11	0.49
Rural – Urban = 0	Flight duration PC1	-2.28	0.38	-5.97	< 0.00001***
	Duration of singing PC2	-0.30	0.26	-1.13	0.49
Peri-urban river – Rural = 0	Flight duration PC1	-1.30	0.37	-3.50	0.0009***
	Duration of singing PC2	-0.62	0.25	-2.42	0.04*

Significant independent variables are depicted with: <0.00001 ‘***’, ≤0.001 ‘**’ ≤0.01, ‘*’.

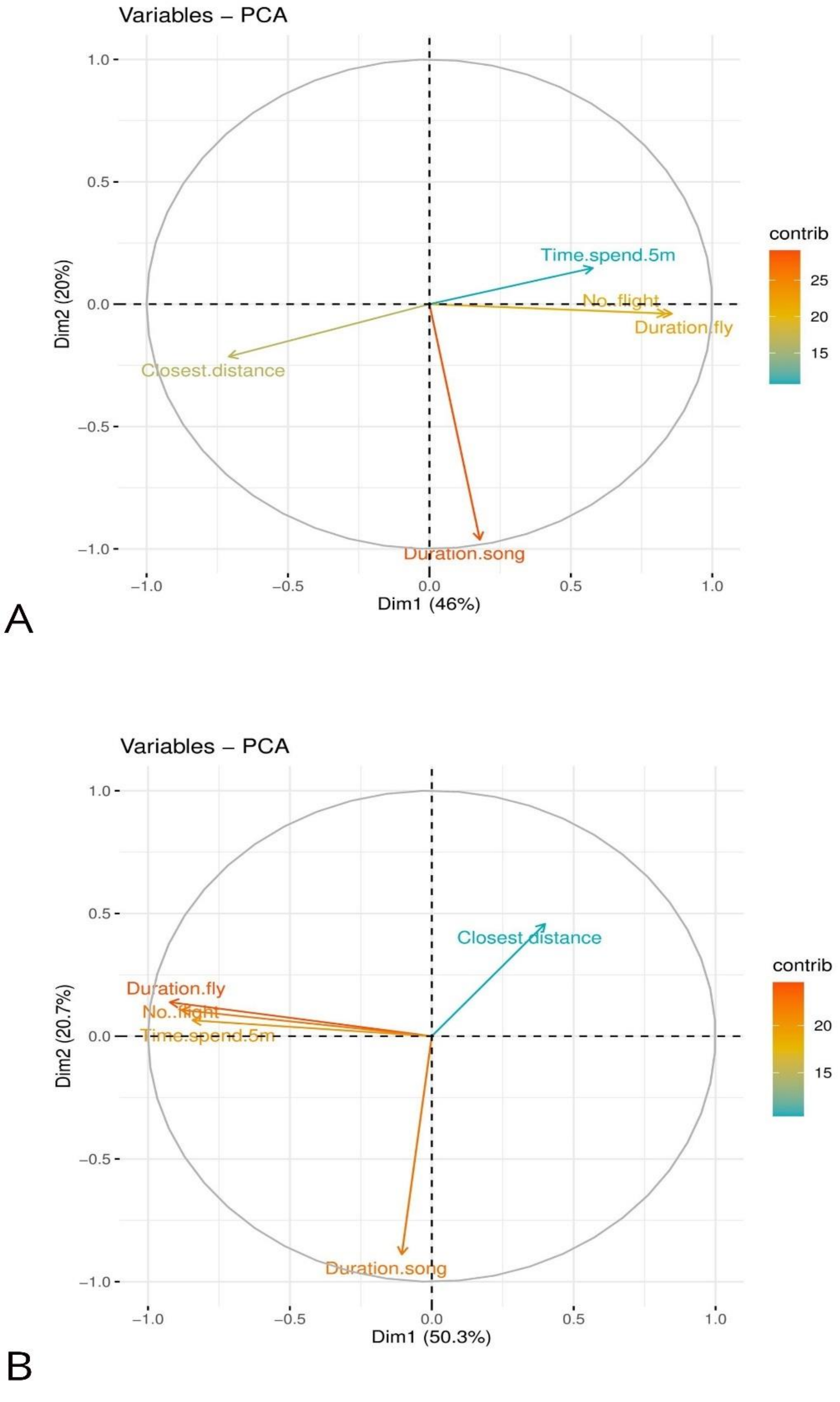

Figure 4.2 Aggression and signalling responses of blackbirds (A) and song thrushes (B) using PCA. The axes show the PC loads for each response on the first two PC axes, which combined explained 65.63% and 70.93% of the variations for blackbirds and song thrushes, respectively.

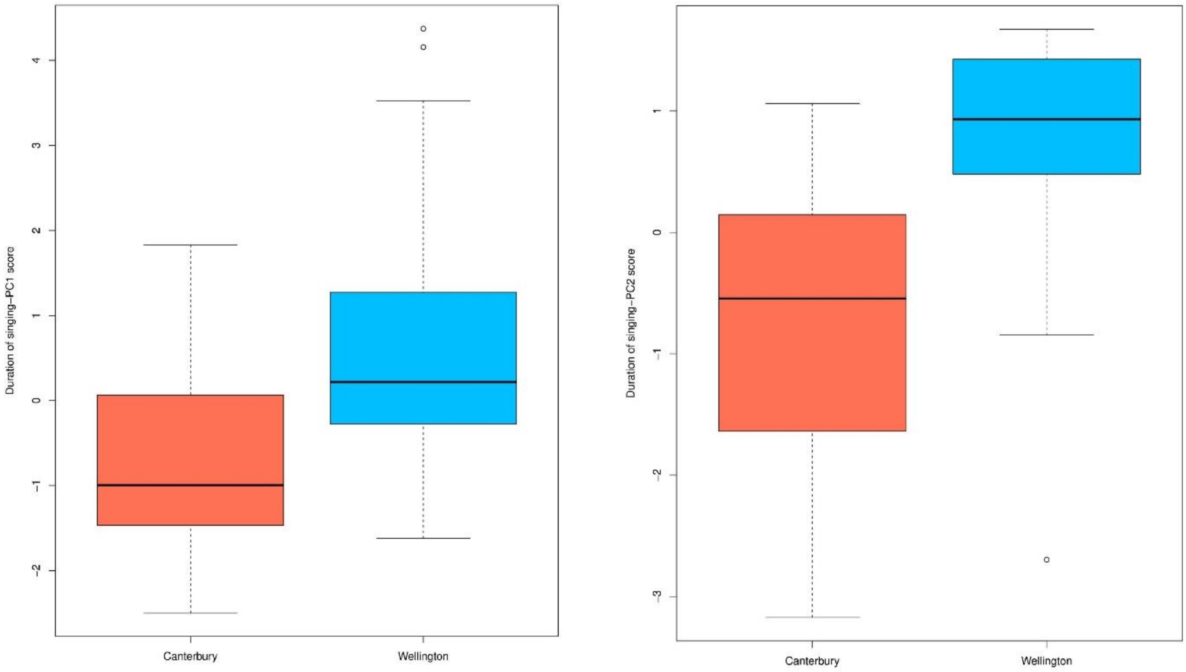

Figure 4.3 Scores of aggressive (PC1) and signalling behaviour (PC2) of blackbirds within different regions.

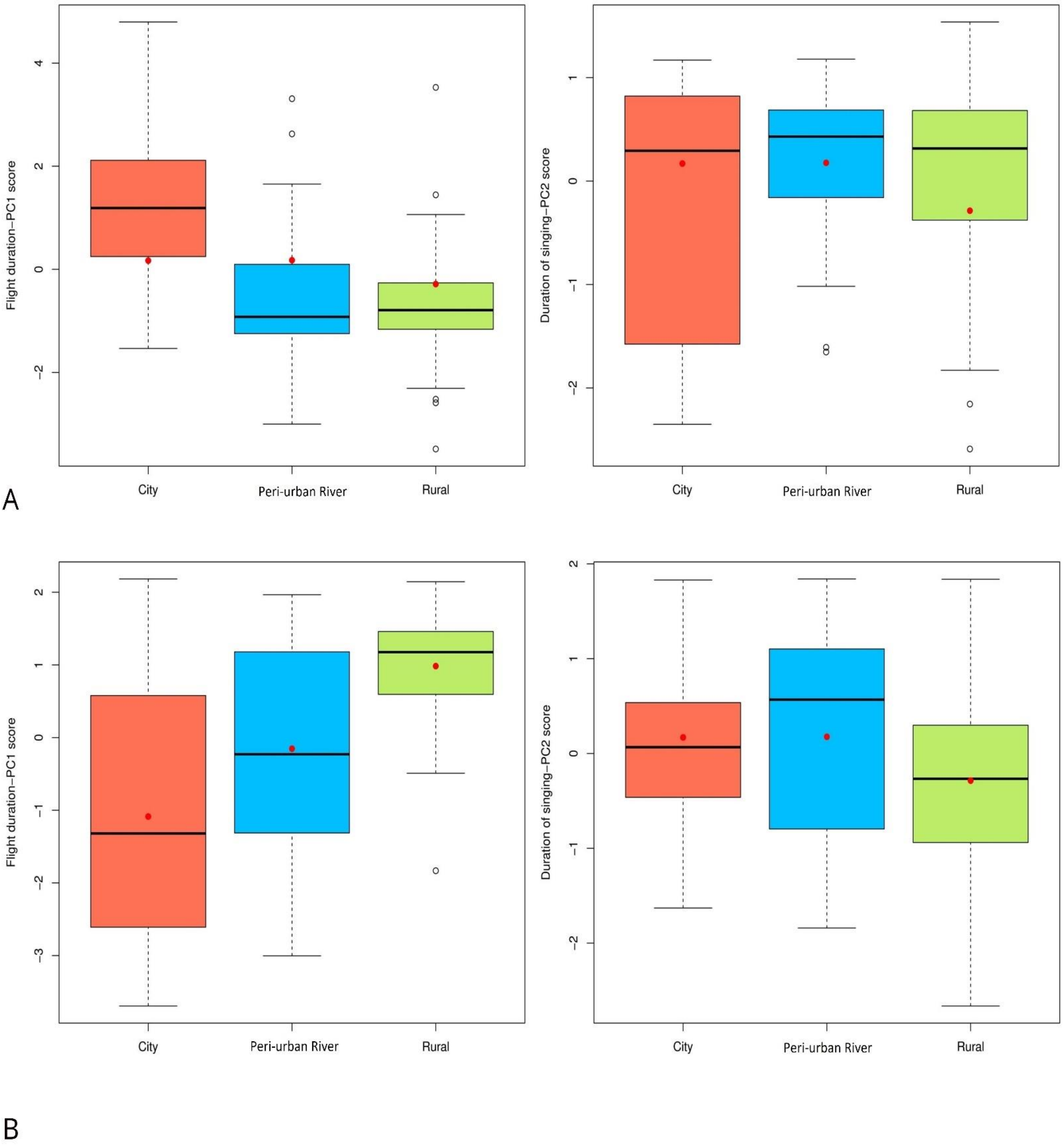

Figure 4.4 Scores of aggressive (PC1) and signalling behaviour (PC2) of blackbirds (A) and song thrushes (B) within different habitats.

4.4Discussion

The first goal of this study was to test the hypothesis that urban birds would be more aggressive compared to peri-urban and rural birds. Urban birds responded to conspecific songs with aggressive behaviours, while rural birds responded with signalling behaviours. I also measured the effect of habitat types and regions on flight duration, song duration, and time spent within 5 m of the speaker and how they were correlated with aggressive and signalling behaviours. The results showed that urban birds were more likely to respond with aggressive behaviours, including increased flight duration around the playback speaker, while the peri-urban river and rural birds respond with signalling behaviours, including increased duration of singing over the playback songs. The probability of increased duration of singing was higher in rural song thrushes compared to peri-urban river individuals. While, the results did not find a significant relationship between signalling behaviours with aggressive behaviours, the effect of habitat types on aggressive and signalling behaviours were negatively correlated with peri-urban river and rural habitats. It means that the probability of showing more aggressive behaviour was higher in urban birds than in peri-urban river and rural birds. This is consistent with other studies that have found song rates to be negatively correlated with aggressive behaviours (e.g. Akçay et al., 2020; Araya-Ajoy & Dingemanse, 2017).

Aggressive and signalling behaviours were affected by different regions. Blackbirds in the Wellington region showed trends toward the higher probability of increased approach distance, increased flight duration, increased time spent within 5 metres around the playback speaker, higher number of passes over the speaker and decreased duration of singing compared to the individuals in the Canterbury region, but it was non-significant with flight duration and the number of passes. Song thrushes and blackbirds showed similar behavioural responses, and show that behavioural traits conform within taxonomic families (Winkler et al., 2020). This may support the local adaptation hypothesis that suggests that populations are adapted to their local environment and range rather than other environmental conditions (Quinby et al., 2020), resulting in each population showing the best performance in areas similar to their local environmental conditions (Kawecki & Ebert, 2004). The aggressive and signalling behaviours of song thrushes were not affected by regions except for the closest approach distance to the speaker which showed that the was a higher probability of increased approach distance in individuals from Wellington than song thrushes from Canterbury regions.

Among aggressive and signalling behaviours, two behavioural responses explained the variability of the data. The measured level of flight duration around the playback speaker (PC1) and the duration of singing (PC2) was affected by habitat types and regions, although not regions for song thrushes. The findings indicated that urban birds were more likely to increase flight duration, as an aggressive response, and shorten the duration of singing over the speaker, as a signalling response, compared to peri-urban river and rural birds where there were no significant differences between them.

The first PCA axis positively associated with the flight duration had negative correlations with peri-urban river and rural habitat types which means that birds from these habitats are more likely to reduce flight duration around the playback speaker. The negative correlations of rural and peri-urban habitats on PC2, which is negatively related to the duration of singing, showed that song thrushes from these habitats trend toward an increased duration of singing in response to the speaker compared to urban birds that were likely to increase their decreased of singing as flight duration increased. The effect of regions in blackbirds indicated that individuals in the Canterbury region correlated with PC1 and PC2 which means they tend toward decreased flight duration and the duration of singing compared to individuals in the Wellington region.

The Lombard effect would predict that birds would sing loudly to overcome the conspecific song in urban habitats. The noisy conditions of urban habitats may explain why urban birds are more likely to show more aggressive responses, including increased flight duration rather than singing over the speaker as a signalling behaviour. My results support the idea that urban birds used the strategy of approaching closer to ensure the receiving of their intention in noisy habitats (Brumm & Slater, 2006). Urban birds are more likely to use aggressive responses, including flying around the speaker, to gain more information about the intruder and engage in actions. Rural birds tended to increase their duration of singing compared to urban individuals. In areas with loud and constant anthropogenic noise, birds often shift from signalling to visual aggressive behaviours (Grafe et al., 2012; Partan, 2017; Patricelli & Blickley, 2006; Ríos-Chelén et al., 2015). This would fit with my study where urban blackbirds and song thrushes switched to using more visual aggressive behaviours, including increased flight duration rather than singing or flying over the speaker. Due to having behavioural changes between two regions, I assumed that the Lombard effect may explain the variation as well. Differences in background noises and the effect of wind speed in noise distortion may affect duration of a song in Wellington individuals.

The most predictable signal of aggressive behaviour was the duration of flying around the playback speaker and was similar to previous studies (Akçay et al., 2020; Moseley et al., 2019; Phillips et al., 2020; Wood & Yezerinac, 2006) where they found that more aggressive birds are less likely to use song overlapping as a signal of aggressive intent. The closest approach distance had a negative correlation with flight duration in birds. I assumed that approaching the speaker may increase the chance of engaging an intruder and of getting hurt. Urban birds preferred flying around the territory to show dominance and to warn intruders. When the territory owner got close enough to the speaker to gain information on the level of threat, they did not waste more energy and time flying around the territory. A potential explanation for these different responses within the same habitat could be the low level of resource availability in some rural areas as well as urban habitats (Enquist and Leimar 1987; Grafen 1987; Lindström and Pampoulie 2005). Depending on how limited resources are in a territory, the costs of not engaging in defending may be higher than the costs of fighting and protecting against more aggressive and higher-quality individuals or provoking a fight (Smith and Parker 1976). There were urban birds that sat on the speaker, or next to it (I used a camouflaged speaker), for around 30 to 60 seconds and stopped singing to the playback.

4.5 Conclusion

I found correlative and comparative evidence that territorial defence aggression of male blackbirds and song thrushes during the breeding season vary in response to habitat. The territorial aggression responses toward conspecific songs were related to different habitats and regions that may be explained by the local adaptation hypothesis. The behavioural variations toward the conspecific songs appear to be dependent on the intensity of anthropogenic landscape changes. Urban habitats with relatively high rates of disturbance favour more aggressive males. Rural and peri-urban river areas with less level of anthropogenic stressors, such as buildings, noise and air pollution, provide individuals with broader spaces and signalling behaviour that may function better to avoid aggressive contact intruders. The next works may be investigate the variations in background noise and the effect of wind speed in singing amputer and pitche in response to intruder. Territorial defence aggression would increase the chance of territorial males holding their space and reproductive success in the long term. Future work could examine and identify the aggression responses toward a stuffed decoy bird in the centre of the territory and compare the behavioural responses towards playbacks songs and the combination of conspecific playback songs and a motionless decoy.

Most aggression-related studies have focused on inter-specific interactions, thus more future studies should add intra-specific interactions with species with over-lapped territorial boundaries (Akçay et al., 2019; Anderson et al., 2012; Hyman & Hughes, 2006; Ophir et al., 2005; Pradhan et al., 2010; Szász et al., 2019; Szymkowiak & Kuczyński, 2017). Territorial defence aggression is not exclusively a seasonal behaviour. Some species hold their territory boundaries during winter, as a territory to cache and store food for the next season. I suggest evaluating and comparing the aggressive behaviour of food caching species during winter and comparing sex differences. The next step may be identifying and investigating to what extent the intensity of connectivity, structure and composition of anthropogenic landscapes impact behavioural differences. I examined aggression behavioural variations within two established introduced passerines to New Zealand. Evaluating the behavioural changes in native species in response to anthropogenic alterations would help us to understand and plan conservation programs. Behavioural variations can potentially change population fitness. Human interventions, such as captive-breeding and hand-feeding may modify animal behaviours, including foraging, anti-predator and aggressive behaviours where it can alter the effectiveness of conservation and reintroduction strategies. My findings highlighted the importance of considering intra-specific and individual-specific behaviour in studying anthropogenic effects on behavioural traits.

Chapter 5 Hide or seek? How birds deal with novel objects.

5.1 Introduction

Urbanisation and anthropogenic changes create novel environments for wildlife. Such conditions may make colonising and dispersing within urban habitats difficult given anthropogenic stressors, such as urban noise, artificial light, introduced predators, and exposure to new parasites and competitors (Thompson et al., 2018). How animals respond to novel stimuli and resources will largely depend on their fear of novelty (neophobia) (Lowry et al., 2013; McDonnell & Hahs, 2015; Mettke-Hofmann, 2017; Sol et al., 2013; Thompson et al., 2018). Novelty avoidance behaviour may reduce an animal's risk from fitness reducing situations, such as poisoning and predators, but novelty-seeking behaviours may allow animals to examine and explore potential new resources (Greenberg, 2003).

Animal personalities and tendencies may adapt to living in urban environments over generations (Réale et al., 2010; Réale et al., 2007). Urban wildlife typically shows greater boldness, aggression and neophilia behaviours toward predators, competitors and novel challenges than those in less anthropogenic landscapes (Miranda, 2017; Miranda et al., 2013). Urban habitats confront species with new challenges and threats that can alter their abundance and diversity, or provide an opportunity to compete with other species and expand their distribution (Case, 1996; Sol et al., 2014). Succeeding in urban habitats requires behavioural, morphological and physiological traits that enhance species ability to disperse and reproduce in novel habitats (Evans et al., 2009; Partecke et al., 2006; Winchell et al., 2016).

The survival rate in anthropogenic areas is influenced by an individual's response to novel stimuli (Crane et al., 2020; Robertson et al., 2013). Response to novelty may have a positive or negative impact on their success, based on the costs and benefits resulting from the novelty (Greggor et al., 2016b). Impacts may affect spatial distribution, intra- and interspecific interactions, and critical decisions (Crane et al., 2020). While increased object neophobia can help individuals avoid risks, such as predators or toxins, decreased object neophobia can prevent animals from exploring and approaching advantageous new resources (Greenberg & Mettke‐Hofmann, 2008).

5.1.1 Neophobia at the individual level

The combination of neophobia and neophilia, at the species level, can be predicted by a two-factor model containing the motivation to (a) *explore* and (b) *avoid* novel situations and habitat characteristics, such as habitat complexity, predators and competition pressure or foraging patterns, including the degree of generalism or specialism, and social interactions (Greenberg & Mettke‐Hofmann, 2008; Mettke‐Hofmann et al., 2002).

Different types of neophobia may be categorised based on different ecological contexts. The main contexts are gustatory, social, predator, object, and spatial (briefly described in Table 5.1). Different kinds of environments can influence phenotypic variations among individuals, resulting in a large range of neophobic responses (Mettke-Hofmann, 2017). Variation in the level of neophobia among individuals suggests that it should be considered as a personality trait (Stieb et al., 2005). Some studies have found positive relationships between neophobic responses among individuals across contexts, such as house sparrow food neophobia (Bókony et al., 2010), Corvidae object neophobia (Greggor et al., 2016b), and spatial neophobia in female mice (Walker & Mason, 2011). Others have not found a consistent correlation between food (Bókony et al., 2010; Walker & Mason, 2011), spatial and object neophobia in starlings (Boogert et al., 2006). For example, there was no correlation between boldness in a novel object and novel odour in wild-caught guppies (*Poecilia reticulata*) (Brown et al., 2018). Captive-reared individuals showed consistent and significant relationships between exploratory behaviour and novel food among individuals based on their evolutionary history (Fountain et al., 2013; Greggor et al., 2016; Mason et al., 2013). There is phenotypically plastic neophobia in which animals respond according to ontogenetic experience (Zhao et al., 2021), which can lead to variable neophobic responses (Brown et al., 2013a).

The 'dangerous niche hypothesis' provides a rationale for how individuals can benefit from neophobia (Greenberg, 2003). The level of neophobic responses is determined by the intensity of danger, leading to increased neophobia (Brown et al., 2014; Brown et al., 2015). Moreover, environmental factors, such as climatic variables, poor food resources, scarce mates and refugia, and the presence of predators and competitors, may impact their intensity of response toward risk across spatial and temporal scales (Lima & Bednekoff, 1999). Individuals may also deal with risks that are unfamiliar because of stochastic ontogenetic and environmental variation, or lack of experience (Crane et al., 2020). Animals face uncertainty as a result of environmental unknowns and unpredictability, which arises from incomplete information (Dall, 2010). The level of danger and spatio-temporal patterns of threats may be variable and unpredictable making assessment even more difficult (Ferrari et al., 2018; Ferrari et al., 2016; Feyten et al., 2019).

Long-term anthropogenic and environmental changes can act as a selective pressure that is driven by the balance between the cost and benefit of a neophobic phenotype (Crane et al., 2020). For example, birds with a generalist diet show a decreased level of food neophobia compared with specialists (Greenberg, 1989). Migratory animals have decreased levels of spatial neophobia than sedentary species (Mettke-Hofmann et al. 2009). Differences in food and spatial neophobia can lead to speciation, either through habitat selection or habitat changes (Crane et al. 2020). For example, urban chimango caracaras (*Milvago chimango*) (Biondi et al., 2020), black-capped chickadees (*Poecile atricapillus*) (Jarjour, 2019), and oriental reed warblers (*Acrocephalus orientalis*) (Shen et al., 2020) showed fewer neophobic responses than rural individuals. In the rural house sparrow, there was a negative correlation between object and food neophobia that was not found in urban populations, implying that differences in population-level habitats can change the relationships among species traits (Bókony et al., 2010; Bokony et al., 2012). Invasive populations of cane toads (*Rhinella marina*) (Candler & Bernal, 2015) and house sparrows (Martin & Fitzgerald, 2005) also show a lower level of neophobia than non-invasive conspecifics. Successful population spread may require a low level of neophobia (Crane et al., 2020).

There is no agreement about the optimal level of object neophobia for urban individuals (Greggor et al., 2015; Greggor et al., 2016b; Greggor et al., 2016). Living in urban areas with human food waste favours decreased neophobia that allows individuals to explore and innovate with novel foods or objects in novel environments (Greenberg, 2003; Martin & Fitzgerald, 2005). For example, common mynas (*Acridotheres tristis*) living in highly urbanised environments show a lower level of neophobia than conspecifics in low urbanisation areas (Sol et al., 2011) and house sparrows from urban habitats were faster and bolder at solving problems compared with rural populations (Liker & Bókony, 2009). Such object neophobia and fear-related traits regarding novel stimuli in urban and anthropogenic environments have been measured by flight-initiation distance (FID), discussed in the third chapter (Biondi et al., 2020; Clucas & Marzluff, 2012; McCleery, 2009; Møller & Liang, 2013; Morelli et al., 2019) and physiological responses, such as corticosterone levels (Abolins-Abols et al., 2016; Angelier et al., 2018; Atwell et al., 2012; Bonier, 2012; Grunst et al., 2014).

A low level of object neophobia may expose animals to increasingly dangerous situations, such as generalist predators or toxic contaminants (Brown et al., 2013; Greenberg, 2003) that are often common in urbanised habitats (Evans et al., 2009; Sims et al., 2008; Sorace, 2002; Sorace & Gustin, 2009). Fish in a manipulated predator pressure environment respond plastically to the risk of predators in the environment (Brown et al., 2013). In cases of colonising high-risk environments, the ability to adapt to predator pressure may affect survival success (Ferrari et al., 2015). Moreover, over time, less neophobic individuals are likely to be selected for living in urban habitats (Greggor et al., 2016).

Anthropogenic environments offer new sources of food, habitat types and dangers compared to more natural areas (Crane & Ferrari, 2017; Greggor et al., 2014; Lehmkuhl Noer et al., 2016). The richness of wild species is typically lower in urbanised habitats than in nearby natural areas (Chace & Walsh, 2006; Loss et al., 2009; McKinney, 2008; Pal et al., 2019) due to habitat destruction and converting natural landscapes into anthropogenic landscapes (Murphy, 1988). However, some bird species survive and settle in urban areas successfully (Croci et al., 2008; Kark et al., 2007; Møller & Erritzøe, 2014; Shochat et al., 2006).

Successful settling in urban environments may be related to an individual's ability to adjust to new conditions by modifying foraging and breeding behaviour (Betini & Norris, 2012; Ducatez et al., 2020; Kark et al., 2007; Shochat et al., 2006; Sol et al., 2002). Behavioural flexibility allows individuals to reduce their costly and unessential fearfulness behaviours or increase risk-taking attitudes toward novel objects (Davidson et al., 2015; Lee et al., 2011; Levey et al., 2009).

Sometimes individuals may identify novel stimuli because they have had an experience with similar novel objects, which is known as stimulus generalisation (Griffin et al., 2001). Animals reduce their novelty-avoidance responses toward novel conditions after experiencing them repeatedly (Mitchell et al., 2013), which requires an individual assessment and categorisation (Crane et al., 2020). Individuals separate the recognition of stimuli into two categorisations: (a) a response according to evolutionary experience, and (b) a response that is learned, based on individual experience (Brown & Chivers, 2005).

Generally, birds perceive information about threats in two ways: (1) directly from an individual known to be an intruder or predator, or (2) indirectly from social information acquired from other individuals perceiving dangers (Dall et al., 2005). Birds use alarm calls to attract both conspecific and interspecific neighbours; the 'calling for help' hypothesis (Hurd, 1996; Rohwer et al., 1976). Alarm calls bring benefits for neighbours, alerting them to the presence of dangers or predators (Grimm et al., 2008), and signallers, driving out invaders or reducing the risk of being hurt (Goodale & Ruxton, 2019). Individuals use social and heterospecific signals to provide optimal information for habitat selection (Seppänen et al., 2007) or predator risk-avoiding behaviour information, (Fuong et al., 2014; Goodale & Ruxton, 2019; Shen et al., 2020). In some cases, birds recognise and respond to a conspecific's alarm calls (Francis et al., 1989; Magrath et al., 2007; Marler, 1957; Seyfarth & Cheney, 1990; Vitousek et al., 2007; Walton & Kershenbaum, 2019). Most studies have focused on alarm calls in response to predators per se; moreover, most use playback sounds close to nests to investigate the behaviours of conspecific individuals toward alarm calls (Walton & Kershenbaum, 2019; Yu et al., 2019; Yu et al., 2016; Yu et al., 2017).

Blackbirds and song thrushes share many resources in the same environment, from trees and bushes for building nests to food sources, like worms and insects. They also have common predators, such as domestic cats, and parasites. Studying the Turdidae family allows us to identify whether exploratory behaviour toward a novel object within a bird's territory, while conspecific songs were playing, would vary with different habitat types based on anthropogenic development and environmental features.

I tested and compared responses of wild individuals toward novelty and exploratory behaviour in blackbirds and song thrushes in different habitat types based on human presence and urban, rural and peri-urban river habitat. Based on similar studies (Evans et al., 2010; Riyahi et al., 2017; Scales et al., 2011; Smit & van Oers, 2019), I predict that individuals living in urban territories will be both more aggressive and more exploratory to novel objects than their rural dweller counterparts. I wanted to understand how birds evaluate different threats using vocal and visual information.

Table 5.1 Brief descriptions of the different kinds of neophobia. Depending on whether an individual perceives the novel situation as a predator, food or habitat structure, there may be overlap among different kinds of neophobia (Crane et al., 2020; Crane & Ferrari, 2017).

Type	**Description**
Gustatory	Fear of tasting and eating novel food resources even when palatable (reviewed by Dovey et al., 2008; Greenberg & Mettke-Hofmann, 2001). This behaviour may prevent individuals from developing food poisoning but may also decrease the chance of identifying new food resources and incorporating them into their diet (Greenberg, 2003). A limited diet may result from long-lasting food neophobia, known as “dietary conservation” (Marples et al., 2007).
Social	Fear of novel social networks and the tendency of animals to participate in group activities (Crane et al., 2020). Examined by novel sexual interactions in animals. This kind of fear occurs in aggressive or competitive contexts, leading to decreased probability of intra-specific aggression (Crane et al., 2020) but may reduce with mate copying. Well studied in birds (Dardenne et al., 2013), and mammals (Laviola et al., 2004; Prather et al., 2001; Vitale & Udell, 2019).
Predator	Fear of stimuli is perceived as an increased predation risk (Crane & Ferrari, 2017). Usually investigated by exposing novel objects or odours to an individual (Crane et al., 2020; Crane & Ferrari, 2017). Responses toward potential predation threats include freezing, fleeing, vigilance, and social grouping. While, this kind of response increases the survival rate against the novel predator, misplaced fear of non-predatory situations could cause individuals to miss opportunities (Brown et al., 2013a).
Object	Fear of novel objects (Concepción et al., 2016; Elvidge et al., 2016; Greenberg, 1990; Mettke‐Hofmann et al., 2009; Moretti et al., 2014). Often measured by placing novel objects near a territory, nest or food resources. A conflict between avoiding and approaching could happen (Crane et al., 2020).
Spatial	Fear of novel environments (Brown et al., 2013; Cohen et al., 2015; Elvidge et al., 2016; Greenberg & Mettke‐Hofmann, 2008). Often associated with population dispersal and migration and usually is measured through the level of reluctance or willingness of an individual to respond to a novel environment (Greenberg & Mettke‐Hofmann, 2008; Mettke‐Hofmann et al., 2009). It might provide animals with the opportunity of home range expansion.

5.2Methods

5.2.1 Study Area

The study was conducted in three habitats (urban, rural, and peri-urban river) in the Wellington and Christchurch regions of New Zealand (Table 5.2). The urban habitats had buildings, private gardens and urban parks. Rural individuals lived in habitats with open fields, lawns, and woods. Individuals classified as occupying peri-urban river habitats were within 100 to 250 metres of the Hutt River and other parts of the Hutt Valley in the Wellington region. The peri-urban river habitats in the Canterbury region were Selwyn/ Waikirikiri River in the Selwyn district and Avon River in the Christchurch Red Zone (see Figure 4-1).

5.2.2 Experimental Procedures

The methology followed the previous aggression behaviour testing (refer to chapter 4, section 4.2.3). Daytime songs of blackbirds and song thrushes were recorded at all sites to minimise the impact of an unfamiliar song and dialect on a bird's behaviour. Songs were playbacked that were recorded from neighbouring conpecific individuals from at least 500 metres distance. I recorded at least 10 songs for each habitat. Song thrushes are monomorphic and the sex of the singing bird was usually unclear. Blackbirds are sexually dimorphic and male blackbirds were used in my tests. Alarm calls were not included in the daytime songs. Songs were recorded using a digital voice recorder (recording bit rate: 1536 Kbps).

A speaker was placed in an area near a focal bird about 1.5 metres above the gound. The observer waited 20 to 25 metres aways for three minutes. And then, a remote was used to activate the speaker and one or two conspecific songs were broadcast for intrested individual for five minutes and the closest approach distance to the speaker was recorded. The observer stopped the playback song, waited until the focal bird shows non-vigilance behaviour, such as returning to the first spot, resuming feeding the nests, stopping singing or flying around the territory. Then, a novel object (a woollen red hat) was placed next to the speaker, 1.5 m above the gound, where it was visible for the experimental bird. Placing the novel object was done carefully to ensure it was not noticed by the focal bird. The observer waited for three minutes to monitor whether the focal bird approached the novel object without playback song. The song was played by the speaker. The behaviour of the observed individual was recorded for the next three minutes to measure the closest approach distance to the novel object (Evans et al., 2010; Hyman et al., 2004; Nowicki et al., 2002; Scales et al., 2011). I examined whether the focal bird approached the speaker in the presence of the novel object for each territorial male and measured as the approach response to the novel object (for more details see Chapter 4, Figure 4.1).

The experiments were conducted from September 2019 to February 2020 in the Wellington region and from September to December 2020 in the Christchurch region, during the breeding season (Figure 5.1). I assumed that because blackbirds and song thrushes are territorial during the breeding season, they most likely stay and sing within their territorial boundaries. The observer checked whether their nest was built on the considered tree. All data were recorded between 8:00 and 14:00 hours. Distances between sites were > 50 m, to decrease the probability of duplicated sampling of territorial birds. It was assumed that a closer approach to the speaker indicated greater aggression (Scales et al., 2011; Searcy et al., 2006) and/or novelty-seeking and is repeatable within seasons (Hyman et al., 2004; Nowicki et al., 2002) and across years (Hyman & Hughes, 2006).

Table 5.2 The number of individuals observed in each habitat for each species in each region.

Habitat	Blackbird		Song thrush	
	Wellington	Canterbury	Wellington	Canterbury
Urban	26	26	11	13
Peri-urban river	34	24	18	10
Rural	24	24	15	18
Total	84	74	44	41

5.2.3 Statistical Analysis

A Generalised Linear Model with a binomial error distribution was used to examine the effects of different habitats (fixed factor) and the region as explanatory factors on the probability that birds approached the novel object during the trial. An LMER (multivariate linear mixed-effects model, package lme4) was used to test the effect of habitat type (fixed factor), regions and the closest distance to the speaker (random factor, see chapter 4) on the approach distance to the novel object (Zeileis et al., 2008). The significant correlations were checked using ANOVA (package car) for each model (Fox et al., 2012).

Birds that did not approach the novel object at all were excluded from the LMER of approach distance. Scatter plots and box plots were used to visualise the relationship between distance to the novel object and distance to the speaker without the novel object according to habitat effect by running ‘ggplot2’ package (Wickham et al., 2016).

A post-hoc test with “Tukey” and “holm” adjustment, using the glht function from the ‘multcomp’ package, was used was run to examine the comparisons among all habitats (Bretz et al., 2016; Hothorn et al., 2008; Hsu, 1996; Searle & Gruber, 2016).

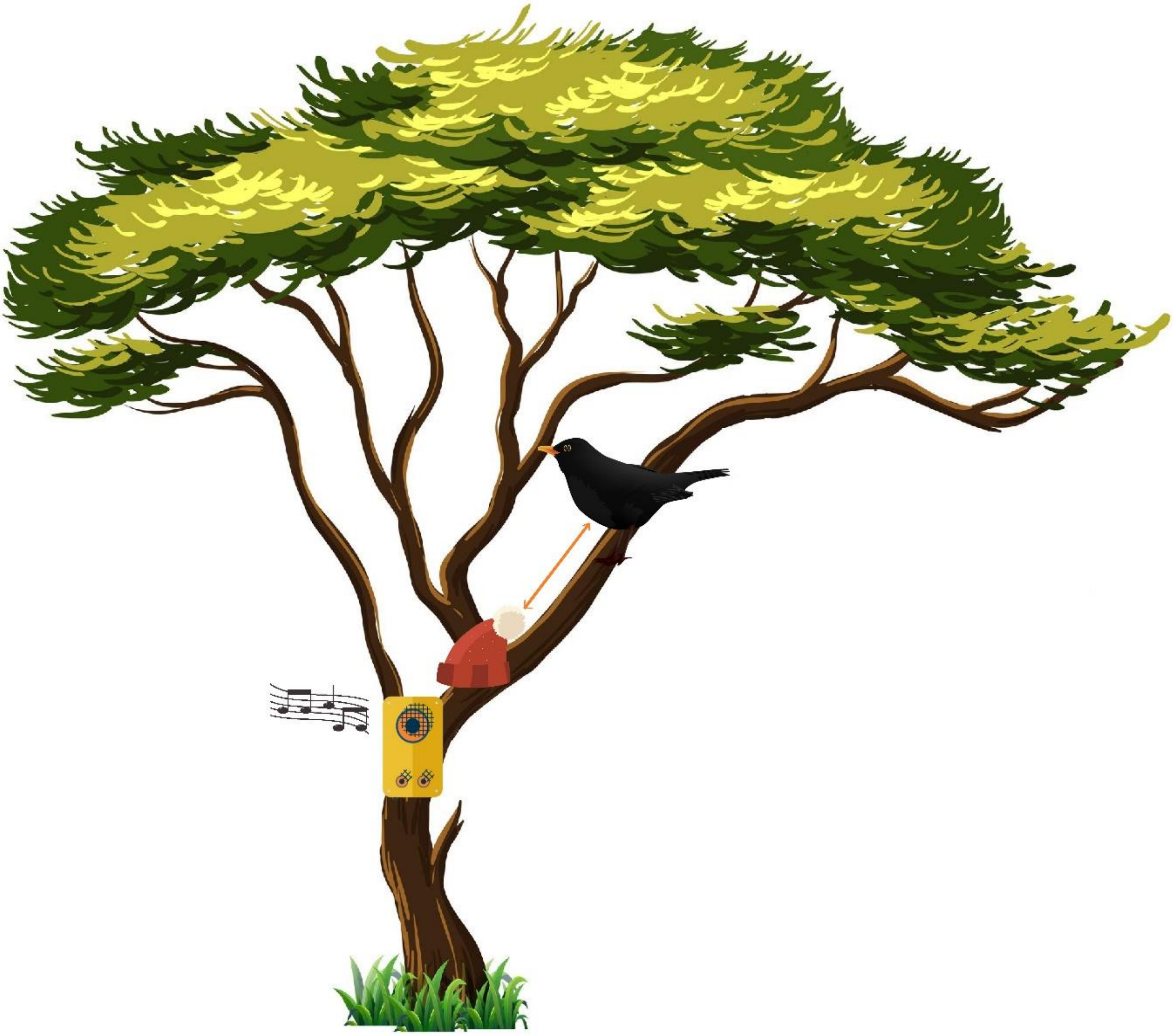

Figure 5.1 Exploratory behaviour was measured by recording the closest distance that the bird approached the novel object (red hat) by conspecific songs (played from the yellow speaker).

5.3 Results

5.3.1 Novelty-seeking response toward the novel object

Individuals that approached the speaker playing a conspecific song closely also approached the novel object closely. Birds did not approach the novel object without playback songs. Based on the Spearman rank test, there was a strong, positive, significant relationship between the closest distance to the novel object and the closest distance to the speaker in the absence of the novel object based on the aggressive measurement trial (refer to chapter 4), in both blackbird or song thrush populations (See Table 5.3).

All birds approached the speaker in the first trial playing the conspecific song. In the second trial, where the conspecific song was played with the novel object next to the speaker, some birds, even those that owned the territory, did not approach.

The novel object was approached by 73.53% of blackbirds. In rural sites, blackbirds showed a higer percentage of avoidance of the novel object. The percentage of avoiding approaching novel objects by urban blackbirds was significantly lower compared to rural and peri-urban river individuals (Table 5.4). There were significant effects of habitat types on approach responses in blackbirds (Table 5.5). Urban individuals had an opposite response compared to peri-urban river and rural conspecifics (Table 5.6). There were no differences between rural and peri-urban river habitats in approach response by blackbirds (Table 5.6). At the intra-specific level, blackbirds were more likely than song thrushes to approach the novel object in the second trial (p < 0.001, Tukey's HSD test for both pairwise comparisons (Table 5.4).

The novel object was approached by 68.23% of song thrushes. There were no relationships between the approach response and the peri-urban river and rural habitats (Table 5.4). The percentage of song thrushes avoid to approach the novel object was smaller for urban inhabitants. Neigther habitats nor regions show significant effect on approach responses in song thrushes, I did not run post-hoc test for them (Table 5.5).

There were no differences in distance to the novel object between those settled in rural and peri-urban river sites (Table 5.6, *p* = 0.44, Tukey's HSD test). The approach distance to the novel object for song thrushes was related to the habitat type (Table 5.6). The approach response in urban song thrushes did not vary among habitats. The probability of approaching the novel object and speaker was higher for rural and peri-urban river blackbirds compared to rural and peri-urban river song thrushes (approach response differences between the two species to the novel object= 5.3%, Tukey's p = 0.00167 in blackbird, Tukey's p = 0.00161 for song thrush).

The closest distance to the novel object varied with the different habitats (Tables 5.7). The birds from the Wellington and Christchurch regions showed similar responses toward the novel object and variable responses were related to different habitats. Urban individuals approached more than twice as close to the novel object compared to rural and peri-urban river individuals (Table 5.8). The approach distances to the novel object were longer than the approach distance to the speaker without novel objects. Few urban blackbirds sat on the speaker or touched the novel object directly. Peri-urban river song thrushes approached significantly closer to the novel object than rural individuals (Figure 5-2), while this pattern was not found with blackbirds (Table 5.9, Figure 5.2).

Table 5.3 Approach distances to the speaker playing a conspecific song by blackbirds and song thrushes in the Wellington and Christchurch regions, compared with approach distances by the same birds to the novel object, tested using Spearman's rank correlation. The mean and standard deviation are for the approach distance to speaker with and without the novel object.

	Blackbird		Song thrush	
Region	Wellington	Canterbury	Wellington	Canterbury
distance to the speaker with the novel object	*Rho* = 0.53, *p* = 0.0002***	*Rho* = 0.73, *p* < 0.00001***	*Rho* = 0.51, *p* = 0.0003***	*Rho* = 0.55, *p* = 0.0001***
	Mean = 4.61 m SD = 1.43 Range = 0.6 – 9.50 m	Mean = 5.25 m SD = 2.91 Range = 0.85 – 8.50 m	Mean = 6.11 m SD = 2.54 Range = 1.5 – 9.00 m	Mean = 6.10 m SD = 2.91 Range = 1.12 – 9.50 m
Distance to the speaker without the novel object	Mean = 3.75 m SD = 1.68 Range = 0.1– 8.50 m	Mean = 3.82 m SD = 1.58 Range = 0.2 – 7.52 m	Mean = 2.55 m SD = 1.83 Range = 0.4– 5.1 m	Mean = 2.21 m SD = 1.18 Range = 0.25 – 4.8 m

Significant independent variables are depicted with: <0.00001 '***'.

Table 5.4 Effect of habitat types and regions on approach response to the novel object and the playback speaker using GLM.

Interaction	Species	Mean (%) avoid to approached	Estimate	Std. Error	t value	*P*-value
Intercept	Blackbird	9.60	2.07	0.50	4.14	<0.00001***
	Song thrush	25.00	1.04	0.51	2.011	0.04*
Peri-urban river habitat	Blackbird	41.60	-1.91	0.55	-3.44	0.0005***
	Song thrush	42.85	-0.83	0.61	-1.36	0.17
Rural habitat	Blackbird	29.78	-1.38	0.56	-2.43	0.01*
	Song thrush	27.27	-0.11	0.61	-0.19	0.84
Region	Blackbird	Wellington: 23.28 Canterbury: 29.72	0.36	0.39	0.92	0.35
	Song thrush	Wellington: 31.81 Canterbury: 31.70	0.12	0.48	0.26	0.78

Significant independent variables are depicted with: <0.00001 '***', ≤ 0.01, '*'.

Table 5.5 Approach response to the novel object and the playback speaker by blackbirds and song thrushes in each habitat using ANOVA for GLMs.

	Blackbird	Song thrush
Region	*Chi*= 169.31, *df* = 1, *p* = 0.37	*Chi*=103.84, *df* = 1, *p* = 0.78
Habitat type	*Chi*=154.52, *df* = 2, *p* = 0.0006***	*Chi*=103.91, *df* = 2, *p* = 0.30

Significant independent variables are depicted with: <0.00001 '***'.

Table 5.6 Approach response differences toward the novel object and the speaker in each type of habitat for blackbirds using post-hoc (Tukey).

Linear Hypotheses	Estimate	Std. Error	t value	*P*-value
Peri-urban river – City =0	-1.91	0.55	-3.44	0.001**
Rural – City = 0	-1.38	0.56	-2.43	0.039*
Rural – Peri-urban river = 0	0.52	0.43	1.21	0.44

Significant independent variables are depicted with: ≤0.001 '**' ≤0.01, '*' .

Table 5.7 Effect of habitat types and region on approach distance to novel objects for blackbirds and song thrushes using LMER and the closest approach distance to the speaker as a random factor.

Interaction	Species	Mean±SD m	Estimate	Std. Error	p value
Intercept	Blackbird	2.83±0.63	276.7	26.32	10.51
	Song thrush	2.38±0.88	222.82	35.61	6.25
Peri-urban river habitat	Blackbird	5.89±1.70	280.88	35.03	8.01
	Song thrush	4.96±1.50	315.20	41.32	7.63
Rural habitat	Blackbird	5.31±1.44	233.09	33.27	7.006
	Song thrush	6.17±1.29	380.16	39.4	9.65
Region Wellington	Blackbird		21.95	28.61	0.76
	Song thrush		-4.15	25.35	-0.16

Table 5.8 Approach distance to novel object related to habitat types and regions using ANOVA.

	Species	Chisq	Df	*Pr(>Chisq)*
Habitat type	Blackbird	79.46	2	< 0.00001***
	Song thrush	100.72	2	< 0.00001***
Region	Blackbird	0.58	1	0.44
	Song thrush	0.03	1	0.87

Significant independent variables are depicted with: <0.00001 '***'.

Table 5.9 The approach distance differences toward the novel object for blackbirds among habitats using GLHT.

Linear Hypotheses	Species	Estimate	Std. Error	z value	Pr(<|z|)
Peri-urban river – City = 0	Blackbird	280.88	35.03	8.02	< 0.00001***
	Song thrush	315.21	41.32	7.63	< 0.00001***
Rural – City = 0	Blackbird	233.1	33.27	7.006	< 0.00001***
	Song thrush	380.16	39.40	9.65	< 0.00001***
Rural – Peri-urban river = 0	Blackbird	-47.8	36.27	-1.32	0.18
	Song thrush	64.95	38.22	1.7	0.09

Significant independent variables are depicted with: <0.00001 '***',.

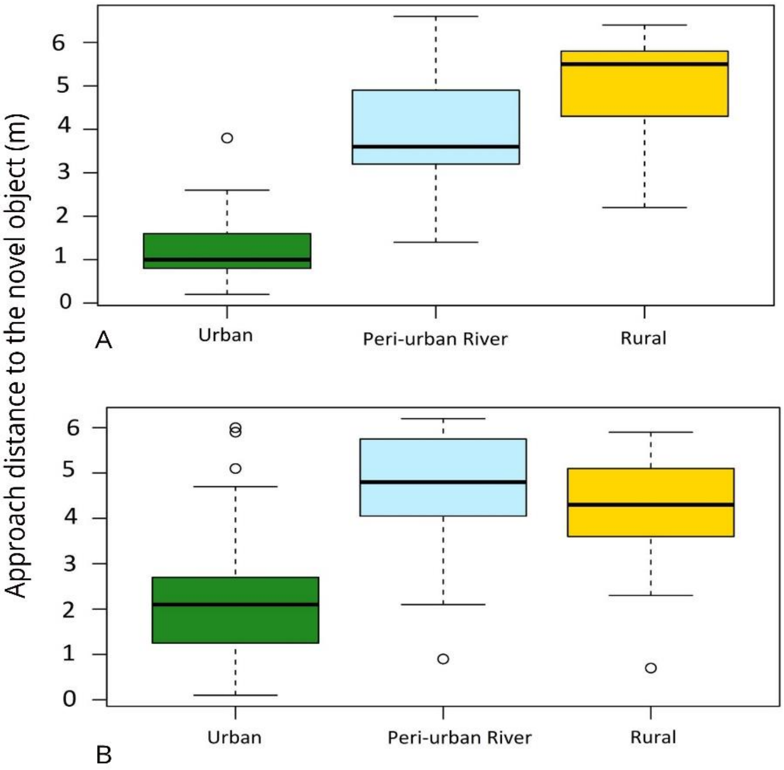

Figure 5.2 Approach distance in the presence of a novel object for blackbirds (A) and song thrushes (B) in each habitat for both regions. The y-axis indicates the distance to the novel object (m).

5.4 Discussion

The experimental method in the study included a combination of two behavioural tests to examine aggressive and exploratory responses of birds toward conspecific songs with a two-phase of broadcasting playback songs within the natural home range of birds (Evans et al., 2010; Hyman & Hughes, 2006; Hyman et al., 2004; Jacobs et al., 2014; Nowicki et al., 2002). The closest approach distance to the speaker was used to identify aggressively (for more information see chapter four)

(Searcy et al., 2006) and exploratory responses (Dingle et al., 2010; Nelson & Soha, 2004). Some birds did not respond after the second playback song and stayed in the same spot.

Identifying the variation in behavioural responses toward novel challenges within different habitats may enrich our knowledge of which animal traits allow them to thrive in urban habitats. I examined the hypothesis that urban birds show closer exploratory behaviour to novel objects. This may be due to living in high disturbance environments that cause individuals to respond more boldly to new resources compared to non-urban birds. My two measures of exploration (the approach distance to the novel object and the approach response in the presence of a novel object next to the speaker) showed different responses within populations of blackbirds and song thrushes but no differences between Wellington and Canterbury populations. Habituation usually occurs in urban areas where there is a high rate of anthropogenic disturbances, predators and competitors. The results are similar to Coleman et al. (2008) and Kittendorf and Dantzer (2021) who suggested that animals living in non-urban areas showed less vigilance and exploratory behaviour whereas urban birds displayed bolder, more vigilant and faster exploratory responses to predator and conspecific playbacks. However, showing a high level of exploratory behaviour towards a novel object could bring more risk to the bolder individuals in the presence of a predator which leads to reduced survival and a reduction in fitness (Dugatkin, 1992; Godin & Davis, 1995).

There was a significant positive relationship between urban habitats and neophilia responses toward the novel object. Urban birds showed more exploratory behaviour by approaching closer to the novel object and approaching sooner the second time at a higher rate compared to the peri-urban river and rural individuals. There were no significant correlations between regions and exploratory behaviour in the two species. The results were consistent with the assumptions that urban animals show more novelty-seeking and neophilia responses compared to non-urban individuals.

Urban birds displayed more neophilia and were faster explorers compared to the peri-urban river and rural birds in approaching the speaker in the presence of a novel object. At the intraspecific level, blackbirds showed faster responses by approaching the novel object for the second time and were less neophobic toward the novel object compared to the peri-urban river and rural individuals. Similar to some studies (Bokony et al., 2012; Cavalli et al., 2016; Labra & Leonard, 1999; Seress et al., 2011; Vincze et al., 2019; Weaver et al., 2018), both bird species approached the broadcasting speaker closer at the first than on the second attempt while there was the novel object next to the speaker. There are at least two possible explanations. At the first playback song test, birds were stimulated by a conspecific song in their possible territory and approached as closely as possible to gain more information on the intruder, as there were no visual objects. After placing the novel object and broadcasting the playback song, birds may have been disturbed by the presence of the novel object or have already gathered enough information about the playback song to reduce their exploratory behaviour.

My findings were in line with similar studies (Atwell et al., 2012; Greggor et al., 2016b; Kozlovsky et al., 2020; Lapiedra et al., 2018; Thompson et al., 2018) that have found urban blackbirds and song thrushes were bolder and faster explorers of novel objects compared to their peri-urban river and rural conspecifics. Animals should optimise accessing resources, such as food, space, and mates while minimising risk (Brown, 1999; Lima & Dill, 1990). Animals in urban environments are exposed to repeated stimuli and may have increased habituation to these stimuli (Botsch et al., 2018; Cavalli et al., 2018; Coleman et al., 2008; Dingemanse et al., 2012; Metcalf et al., 2000; Rankin et al., 2009; Shen et al., 2020; Solaro & Sarasola, 2019). Habituated animals will generally show a reduced response to a second novel stimulus compared to a more neophobic group (Kittendorf & Dantzer, 2021) due to cross-habituation (Cavalli et al., 2018; Curio, 1993; Dingemanse et al., 2012; McCleery, 2009). Testing exploratory behaviour with novel objects may cause disturbances with personality responses and measurements (Hannebaum et al., 2019).

There is no common agreement on how to examine exploratory behaviour, whether by conducting trials in a natural environment of species or within a novel and controlled environment (Hannebaum et al., 2019). Studies often try to record novel responses in unfamiliar versus familiar environments, which fit into avoidance-exploratory ranges (Kurvers et al., 2009; Réale et al., 2007; Stöwe & Kotrschal, 2007) or show personality variation across the shy-bold spectrum (Blaszczyk, 2017; Burns, 2008; Carter et al., 2012). For example, coyotes explored stimuli sooner within unfamiliar environments compared to the same novel object within familiar environments (Harris & Knowlton, 2001).

Along with the spectrum of avoidance to exploratory behaviour, birds have to estimate the risk of approaching a novel object. The approach distance to the novel object may also reflect defensive aggressive behaviour. The results indicate that the peri-urban river and rural birds exhibit relatively cautious responses to the novel object in their territories. The difference whether to approach or avoid the novel object in urban song thrushes compared to urban blackbirds might show species differences in the way they learn how to gather information about novel objects as a result of different experiences (Greggor et al., 2016). Neophobic behaviour might be modified by the shape of a novel object and its colour (Gamberale-Stille et al., 2007). However, if urban song thrushes approached the novel object, they approached closer to the novel object than blackbirds.

5.5 Conclusions

Urban blackbirds and thrushes showed novelty-seeking behaviour in the presence of novel objects compared to their rural and peri-urban river conspecifics. Other environmental factors may affect neophobia and neophilia responses. I highlighted the uncertain situation for wildlife while there was a potential risk. Most empirical studies have only focused on the response of one focal individual toward novel objects. Future work should identify and examine the effect of social networking, such as group size, and morphological traits on exploratory and neophobia behaviours.

There have been few New Zealand studies on urban-rural differences of native or introduced birds in neophobic responses to modified land use, noise, light and chemical pollution, habitat fragmentation, parasite, predators. For future research, I suggest examining the exploratory behaviour through multiple measurements, such as the differences in neophobia responses between natural and novel environments, the differences between latency to respond and the closest approach to a novel object, and the number of flights over novel objects.

I conclude that the use of the novel object and conspecific songs to attract birds is associated with less neophobic blackbirds and song thrushes. To my knowledge, this study is the first to relate neophobia and the use of conspecific songs as attracting and alerting birds about the presence of the novel object to habitat types. My findings allow us to link anthropogenic impact to the novelty avoidance-seeking behaviours in urban habitats compared to rural areas, contributing to modifying wildlife personality traits within different habitats.

Chapter 6 Morphological differences in two passerine species along an urban to rural habitat gradient.

6.1 Introduction

Introduction to a new environment can create novel opportunities and challenges for species (Zenni et al., 2014). Examining the response of introduced species to a new environment allows us to understand rapid micro-evolutionary changes (Lee, 2002; Lindström et al., 2013), and the adaptive mechanisms available through phenotypic variation (Moloney et al., 2009). Species introduction and colonisation may induce negative outcomes for native abiotic and biotic factors (Mooney & Cleland, 2001). Managing possible invasive species requires identifying traits that allow successful colonisation (Ruiz & Carlton, 2003), particularly in urban and rural areas (Sepp et al., 2018; Shochat, 2004). Anthropogenically influenced habitats, especially due to urbanisation, impact biotic factors, such as population size, age structure, population density, and affect abiotic factors, including spatial and geographical features and socioeconomic production (Seto et al., 2010). Urban areas are the remains of natural environments that are now fragmented, invaded by exotic species, and have low population diversity within native species (Johnson & Munshi-South, 2017; La Sorte et al., 2018). Due to the impact of these novel environmental conditions, urban-dwelling animals should show morphological differences compared to their conspecifics living in less urbanised areas (Marzluff, 2017).

6.1.1 Urbanisation shapes bird morphotypes

Structures, composition, and spatial distribution of vegetation are major factors limiting urban biodiversity. Availability of food resources throughout seasons, particularly for insectivorous species may determine body conditions (Naef ‐ Daenzer et al., 2001). The abundance and timing of insects are associated with vegetation densities and richness in urban habitats (Jones & Leather, 2013; Seress et al., 2018). Food availability of high-quality resources is limited by anthropogenic activities, such as chemical, noise and heat pollution (Aronson et al., 2017; Moretto & Francis, 2017; Williams et al., 2009). The food limitation hypothesis suggests that the reproductive success of urban populations decreases as the availability of high-quality food resources is reduced (Jones & Leather, 2013; New, 2015).

Although urban habitats offer limited high-quality food resources, there may be a large amount of anthropogenic food with lower nutritional quality that affects animals behaviour (Murray et al., 2015; Murray et al., 2016), body mass (Zhao et al., 2021), physiology (Schulte-Hostedde et al., 2018), and reproductive success (Mennechez & Clergeau, 2006; Plummer et al., 2018). The combination of limited high-quality food and abundance of anthropogenic foods may lead to lower reproductive success, such as fewer and smaller offspring in urban avian populations, compared to non-urban dwelling populations (Chamberlain et al., 2009; Sepp et al., 2018). Metabolism could change in response to urban conditions with decreased food quality, higher predation risk decreased foraging time and the urban-heat-island effect (Merckx et al., 2018b). Lower body conditions or smaller size of birds could act as an adaptive response to urban conditions (Salleh Hudin et al., 2016; Witter & Cuthill, 1993) to escalate their escape and flush ability of birds in high-risk environments. Based on Shochat's 'credit card' hypothesis differences in body mass condition between urban and rural populations may be affected by environmental factors, influencing the development of off-spring and leading to lower body mass in urban individuals (Liker et al., 2008). Some urban populations have access to higher quantities but lower quality food supplements (Shochat, 2004).

These particular variations may be an adaptation to higher temperatures and food availability in urban areas and may lead to lower fat reserves following Bergmann's rule (Cuthill et al., 2000; Liker et al., 2008; McDonnell & Hahs, 2015; Sepp et al., 2018; Seress & Liker, 2015). Bergmann's rule suggests that animals in colder conditions have a reduced surface-area-to-volume ratio, which helps decrease heat loss (Meiri & Dayan, 2003). Urban environments may favour birds with smaller body mass and size to optimally react and respond to novel threats by being bolder and faster.

Human activities have fragmented and isolated natural habitats into new anthropogenic habitats that are often hostile to the local native species (Fahrig, 2003; Haddad et al., 2015). Both introduced and native animal species must choose to either stay and survive in a newly modified habitat or disperse to other areas (Avilla et al., 2021). Each decision comes with consequences. Animal species that leave an area have to conduct potentially dangerous dispersal in an unfamiliar environment (Fahrig, 2007). Animals that stay may face a greater chance of death and reduced reproductive output (Fagan & Holmes, 2006). For some species, living in urban habitats may require changes in their behavioural and morphological traits (Cheptou et al., 2017; Corsini et al., 2019).

Studying animal phenotypic variation across a gradient from urban to rural environments can help us to understand the responses to different kinds of human activities (Avilla et al., 2021). European blackbirds and thrushes display different responses and behaviours in relation to their habitat (see the previous chapters). Urban and rural populations often diverge in morphology, as they do in behaviour, genetics, song, physiology and life history (Caizergues et al., 2022; Liker et al., 2008; Meillere et al., 2015; Sepp et al., 2018; Seress & Liker, 2015). For example, reduced body size of urban birds compared to rural individuals has sometimes been found (McDonnell & Hahs, 2015) although other studies have found no trend or significantly larger body size in urban individuals (Liker et al., 2008; Sepp et al., 2018; Seress & Liker, 2015).

6.1.2 The role of novel environment on phenotypes

Organism phenotypes are partially shaped according to food availability and abundance (Caizergues et al., 2021). Forest insectivorous birds rely on the abundance and timing of food resources for their body condition (Naef ‐ Daenzer et al., 2001). Low biodiversity of green spaces in highly urbanised areas may be due to the homogeneity of plants and insect diversity (Seress et al., 2018). The scarcity of insects could impact urban bird morphology (Seress et al., 2020) by not providing enough nutritional food resources and may lead to a reduction in body mass, despite the accessibility of novel food resources within urban areas (Chamberlain et al., 2009). A low level of insect abundance and availability of anthropogenic food could affect birds life stages (Caizergues et al., 2021), such as early egg-laying in urban birds. For example, anthropogenic seed feeders could benefit seed-eating birds but would not benefit those who depend on invertebrate resources (Pagani-Núñez et al., 2017).

The starvation-predation risk trade-off may explain body weight changes in birds as they balance the risk of predation and starvation (Bruun & Smith, 2003; Mitchell & Powell, 2004). In good foraging habitats, body mass will increase due to more time spent foraging to store more energy for winter (Bednekoff & Houston, 1994; Houston & McNamara, 1993; MacLeod et al., 2007; Thomas, 2000). However, in habitats with a high level of predation pressure, decreased body mass may be a result of less time spent foraging to maintain a higher escape ability (Brodin, 2000; Krams, 2002; Kullberg et al., 2002; Macleod et al., 2005; MacLeod et al., 2007).

There are anthropogenic factors other than the abundance of food resources that might affect birds morphological developments in urban areas. These factors might act directly or indirectly on phenotype variation, such as light, noise and chemical pollution, heat island effects, road disturbances and domestic or urban wildlife predator pressure (Hargitai et al., 2016; Longcore, 2010; Ruiz et al., 2016; Warren et al., 2006). For example, oxidative pollutants and anthropogenic stress may cause malnutrition (Dauwe et al., 2005; Koivula et al., 2011; Müller et al., 2006) and disrupt growth and energy storage that leads to reduced body size and mass (Koivula et al., 2011; Müller et al., 2006). Artificial lights at night may impact morphological and physiological traits, such as changes in reproduction activities, advanced laying, leading to a mismatch between the abundance of food resources and nestling period causing restricted and limited nestling development (Kempenaers et al., 2010; McMunn et al., 2019; Thawley & Kolbe, 2020; Touzot et al., 2020). Human-related activities can bring chronic stress to both adults and offspring. Urban wildlife in novel environments are confronted with two responses; either to be flexible and respond to changes or be removed by evolutionary selection (Caizergues et al., 2021).

6.1.3 Modified morphological phenotype

Modifying morphological traits to cope with new challenges created by anthropogenic conditions allows some species to thrive in urban habitats. For example, those traits that are responsible for species dispersal often allow pre-adaptation to fragmented patches in species distribution (Cheptou et al., 2017). Fragmented patches surrounded by anthropogenic activities hinder animal dispersion, due to the often hostile and harsh environment, or matrix, between liveable patches (Avilla et al., 2021). Morphological changes in urban animals may be an allometric response to avoid conflicts with anthropogenic structures (Brown & Brown, 2013b). Changes in body size and mass (Lowe et al., 2014; Merckx et al., 2018b) may occur as a response to heat-island, urbanisation, predator pressure, neophobic behaviour (Sarno et al., 2015) or reproductive physiology (Boggie & Mannan, 2014). Urban bird populations are a suitable target for studying phenotypic divergence due to urban-related forces (Marzluff, 2017).

When individuals are unable to disperse effectively beyond their home range it could stop them from occurring within urban environments or may isolate populations in these areas (Cade & Bird, 1990; Martel et al., 2002). Morphological traits may be distinct between urban and rural populations, such as reduced body size and mass (Corsini et al., 2021). Urban birds may show reduced bill length due to the use of novel food resources and feeders with easier accessibility (Bosse et al., 2017). Urban blue tits with shorter tarsi cling and hang more, which aids them in accessing a wider range of foraging niches (Carrascal et al., 1995). In birds foraging vertically on tree trunks, the function of climbing the trunk impact the tarsus and tail length (Milá et al., 2009; Norberg, 1979; Tubaro et al., 2002; Zeffer & Norberg, 2003) allowing optimal manoeuvres for capturing insects that directly related to body mass and optimise climbing ability. Fragmented forest patches with a reduction in epiphyte cover on tree trunks will decrease humidity and habitat suitability for invertebrates and force birds to change their diet or adapt to capturing insects differently (Laurance et al., 2018; Parra-Sanchez & Banks-Leite, 2020).

European populations of urban blackbirds were more sedentary, had reduced corticosterone stress levels, lay eggs earlier (Partecke & Gwinner, 2007; Partecke et al., 2006; Partecke et al., 2005), had stubbier bills, shorter tarsi and wing length compared to rural populations (Grégoire, 2003). A study on partially migratory European blackbirds found no morphological divergence between sedentary and migratory populations (Fudickar & Partecke, 2012), although another study found wing pointedness was reduced in urban migratory blackbirds compared to rural populations (Saccavino et al., 2018). However, blackbirds across Europe did not reveal a constant pattern in morphological differences, such as wing size and body size across an urban-rural gradient (Evans et al., 2009).

A large-scale study on 132 North-American bird species found that natural-history traits, such as foraging, might explain which species were affected by urbanisation, but it did not show a correlation between species abundance and anthropogenic environments (Lepczyk et al., 2008). Other studies have found that decreased body size and mass was a response to increasing urban temperature related to climate change and that increased wing length was more common in North American migratory birds that allow them to fly long distances and manoeuvre through hard weather conditions (Weeks et al., 2020).

Several studies on common blackbirds, house sparrows, blue tits, and great tit have shown that urban individuals had lesser body conditions compared to forest populations (Bailly et al., 2016; Ibáñez-Álamo & Soler, 2010; Ibáñez ‐ Álamo & Soler, 2010; Liker et al., 2008; Perrins, 1965; Seress et al., 2012). While most morphological studies focus on tarsus length and body mass, other traits, such as wing and tail length, plumage characteristics and bill length may also provide useful information. For example, urban great tits showed shorter wing sizes compared to rural individuals (Seress et al., 2020), whereas, no divergence was found between urban and rural populations of mountain chickadee (*Poecile gambeli*) (Marini et al., 2017).

6.1.4 Objectives

Blackbird and song thrush are some of the most widespread introduced bird species throughout much of New Zealand that have been introduced for over 150 years and their populations, have likely begun to diverge from the ancestral European populations, especially in migratory related traits such as wing, tarsus and tail length.

Comparing morphological traits between European and New Zealand birds will identify differences in body size, such as shorter tarsus, wings and tail lengths due to being sedentary (Caizergues et al., 2021). Testing morphological traits differences between historical UK and New Zealand populations of blackbirds and song thrushes showed decreasing tarsus lengths trends toward contemporary New Zealand samples of blackbirds and no significant differences in song thrushes populations (Blackburn et al., 2013). Blackbird populations across Europe did not reveal a consistent pattern in morphological differences, such as wing size and body size across an urban-rural gradient (Evans et al., 2009).

Blackbirds and song thrushes are more sedentary in New Zealand and do not migrate like their European counterparts (Peter & Cowling, 2007). As such, the New Zealand populations would be expected to have shorter tarsus and wing lengths compared to European populations. Temperature differences between New Zealand urban and rural areas are not likely to be as great compared with North American or European areas (Caloiero, 2017; Salinger & Griffiths, 2001).

Are sex differences in blackbird samples indicated by morphological traits? There are behavioural differences between New Zealand urban and rural populations of blackbirds and song thrushes (see chapters 3, 4 and 5). Does the degree of urbanisation also play a role in shaping morphological traits between urban and rural areas, including length of wing, tarsus, tail, bill and body mass? Is there a morphological difference between introduced New Zealand and ancestral populations?

6.2 Methods

Fresh road-killed blackbirds and song thrushes, adults and juveniles, were collected from the Wellington and Canterbury regions from 2019 to 2021. The sites of their retrieval allowed us to categorise them as urban and rural dwellers. The birds were transferred to a freezer for storage. Later they were measured for (a) tarsus length (O'Connor, 1985), used as an indicator of overall body size due to high correlation with general bone size (Freeman & Jackson, 1990), (b) wing length, from the bend of the flattened wing to the end of the longest primary feather (Demongin, 2016), (c) bill (culmen) length, being the tip of the upper mandible to the first feathers, (d) head length, the distance from the tip of bill to the back of the skull (Figure 6.1), (e) weight (Demongin, 2016; Jenni & Winkler, 2020), sex (Demongin, 2016; Jenni & Winkler, 2020; O'Connor, 1985) in blackbirds (from plumage). Bill and tarsus length measurements were made with calliper at least 0.1 mm precision, wing and tail length measurement were recorded with to a 1 mm percision, and weight was measured with a digital scale to the nearest 0.01 g.

There were 44 blackbirds (21 urban and 23 rural) and 14 song thrushes (3 urban and 11 rural) collected from the Canterbury region. Due to severe wind and cold weather in winter and Covid-19 lockdowns from March to mid-August 2020, fewer dead birds could be collected in the Wellington region: 9 blackbirds (3 urban, 6 rural samples) and 5 song thrushes (3 from urban and 2 from rural, Figure 6.2).

The English data were obtained from Peter and Cowling (2007). These specimens were collected from across England, but the names of the locations were not mentioned. Birds were dead or alive and were found by the public or members of the British Trust for Ornithology and biometric measurements were recorded and submitted. For England and New Zealand comparisons, I used wing and tail length as a measure of aerodynamic structure and tarsus length. This measurement is invariant across seasons and available on all the samples for the present study.

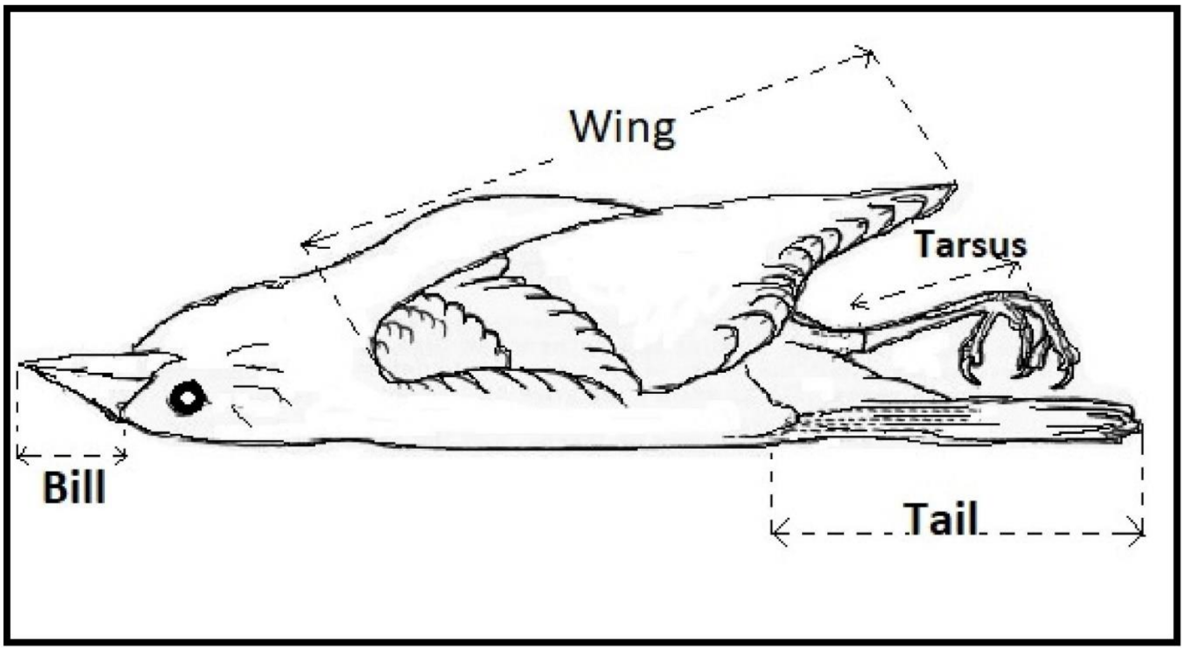

Figure 6.1 Morphological measurements of blackbirds and song thrushes.

6.2.1 Statistical analysis

To test the differences in the morphological measurements, a paired t-test was run to compare tail length (mm) in blackbirds and song thrushes. A General Linear Model (GLM) was run with R 3.6.3 packages lme4 and lmerTest (Bates et al., 2014; Kuznetsova et al., 2017), with Gaussian error distribution for all morphological measurements, tarsus, culmen, wing and tail length and weight taken from urban and rural individuals in the Wellington and Canterbury regions.

A GLM was run to examine the differences between tail, wing and tarsus length of the England (21 blackbirds and 21 song thrushes) and New Zealand samples. In the models, habitats were fixed factors and regions were an explanatory factor. ANOVA was run to test the significant differences between groups.

A GLM was used to test the effect of sex (male and female) in blackbirds on morphological measurements with binomial error distribution. I was unable to determine the sex in song thrushes. As tarsus length is not different between post-juveniles, they undergo a partial moult in their first autumn (Svensson et al., 2009), and adults (Blackburn et al., 2013), therefore I added juvenile samples in the data related to tarsus length (Welch's test: t: 1.508, *p* = 0.145).

6.3 Results

6.3.1 Morphological variation between urban and rural individuals

Sex-related morphological traits were not correlated with habitats. There were significant differences in wing and tail length between male and female blackbirds. The sex-related morphological triats showed that females had smaller wings and longer tail lengths than male’s (Table 6.1). Female-related morphological traits showed trends toward shorter tarsus and bill length and lighter weight compared to males but it was not significant (Table 6.2).

Table 6.1 Effect of sex differences on morphological traits in blackbirds using GLM, habitat types as an explanatory factor.

Measurements	Sex	Range	Mean ± SD mm	Estimate	Std. Error	z value	Pr (>|z|)
Tarsus (mm)	Males	90 - 120	91.70 ± 2.37	-0.002	0.32	-0.008	0.99
	Females	91 - 130	91.10 ± 3.25				
Wing (mm)	Males	120 - 135	127.40 ± 3.77	0.50	0.21	2.36	0.01*
	Females	113 - 129	123.50 ± 4.6				
Tail (mm)	Males	90 - 120	108.30 ± 7.18	-0.28	0.13	-2.17	0.03*
	Females	91 - 130	115.60 ± 9.17				
Bill (mm)	Males	18 - 25	21.766 ± 1.81	-0.07	0.45	-0.17	0.86
	Females	18 - 26	20.70 ± 2.00				
Weight (g)	Males	44.8 – 103.6	80.43 ±11.7	-0.03	0.06	-0.47	0.63
	Females	58.2 – 92.2	75.51 ± 11.7				
Habitat Rural				0.36	1.18	0.30	0.76

Significant independent variables are depicted with: 0 ‘***’, 0.001 ‘**’ 0.01, ‘*’ 0.05 ‘•’.

Table 6.2 Effect of sex differences on morphological traits in blackbirds (ANOVA for GLM).

Measurements	Chisq	Df	Pr(>|z|)
Tarsus (mm)	0.0001	1	0.99
Wing (mm)	12.58	1	0.0004***
Tail (mm)	11.28	1	0.0008***
Bill (mm)	0.03	1	0.86
Weight (g)	0.24	1	0.62
Habitat Rural	0.09	1	0.76

Significant independent variables are depicted with: 0 ‘***’, 0.001 ‘**’ 0.01, ‘*’ 0.05 ‘•’.

The linear model conducted across all habitats showed no significant effect of habitat and region on tarsus, wing and tail length but bill length and weight showed weak correlations with region and habitats, respectively. Blackbirds in the Wellington region displayed a trend towards shorter bill length compared to individuals in the Canterbury region (Figure 6.3). Rural blackbirds were on average heavier than urban individuals (Table 6.3). The effect of habitats on weight was slightly significant. The mean wing length decreased toward urban to rural habitats but the results did not find a significant effect of habitats on wing length (Table 6-3, Figure 6.3). There were trends toward shorter tarsus and tail from urban to rural habitat but they were insignificant (Table 6.4, 6.5). Two out of three rural carcasses had missing tails, I discarded them from the tail length and weight analysis.

The model did not show any significant effect of habitats and regions on morphological traits of song thrushes. The only measurement was the tail length that was affected by regions. There was a trend towards shorter tail length from the Wellington to the Canterbury region. Rural song thrushes showed on average longer tail length than urban individuals but it did not show a significant relationship with habitats (Table 6.3, 6.6). There were trends toward shorter tarsus, wing and bill length in urban song thrushes to rural samples but the results did not show any significant effect of habitats (Table 6.7, Figure 6.4). I suggest that the results related to song thrushes may be confounded by sex due to the small sample size.

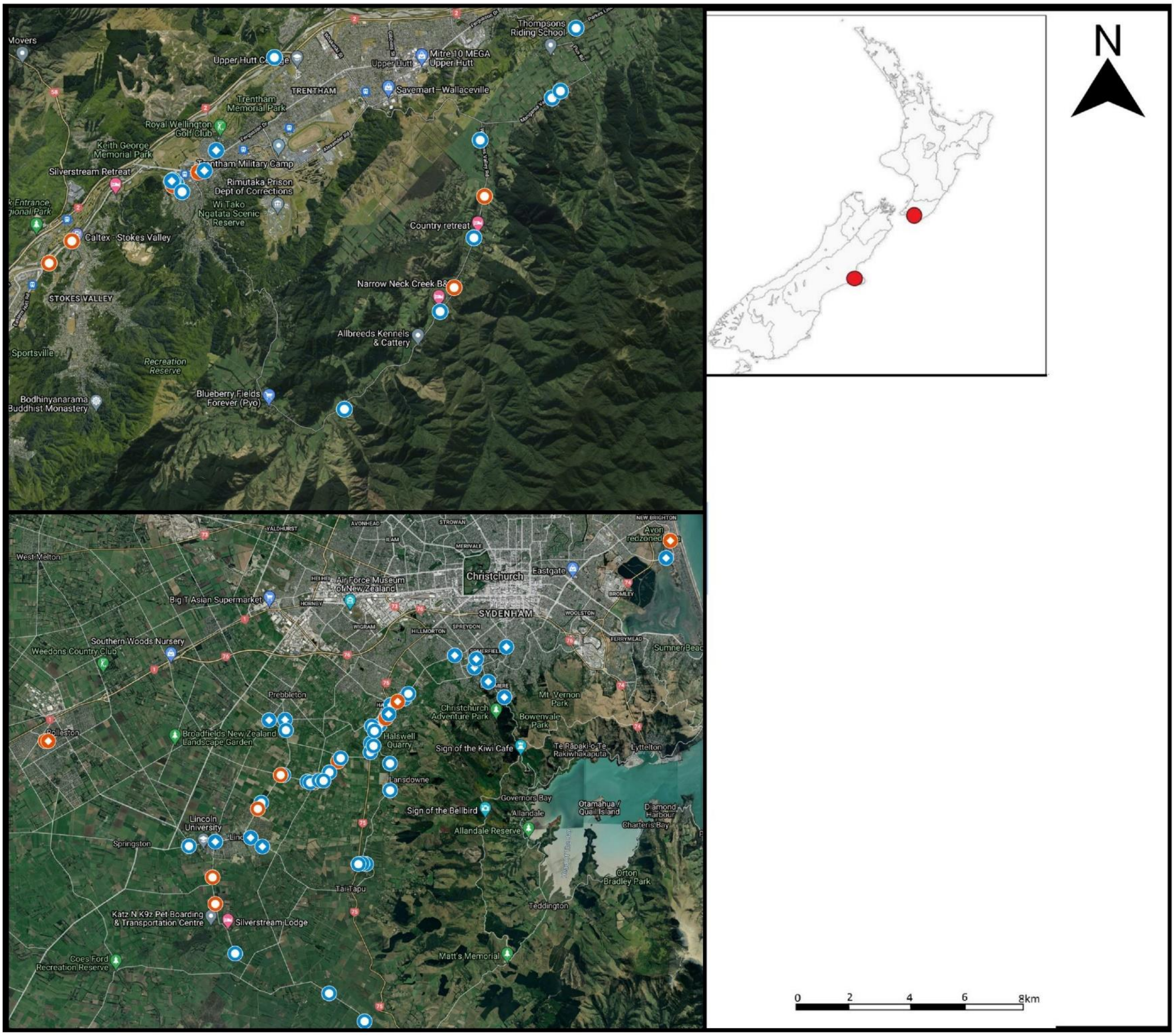

Figure 6.2 Locations of blackbird (blue circles) and song thrushes (orange circles) collected in the Wellington (upper left) and Canterbury regions (lower left). Urban and rural samples were indicated with diamond and circle shapes, respectively.

Table 6.3 The mean and standard deviation of morphological traits in blackbirds and song thrushes across urban and rural habitats in New Zealand.

Measurements	Habitat	Blackbirds	Song thrushes
		Mean ± SD	Mean ± SD
Tarsus (mm)	Urban	20.44 ± 2.12 mm	30.09 ± 2.05
	Rural	20.04 ± 2.03 mm	29.46 ± 2.89
Wing (mm)	Urban	125.83 ± 4.90 mm	118.33 ± 2.94
	Rural	126.94 ± 3.76 mm	116.27 ± 5.38
Tail (mm)	Urban	110.11 ± 9.80 mm	77.50 ± 1.12
	Rural	110.13 ± 6.90 mm	92.86 ± 11.65
Bill (mm)	Urban	21.33 ± 1.90 mm	16.4 ± 2.60
	Rural	21.63 ± 1.91 mm	16.16 ± 5.82
Weight (g)	Urban	75.37 ± 15.21 g	67.52 ± 8.89
	Rural	82.63 ± 6.08 g	68.22 ± 11.71

Table 6.4 Effect of habitat types on morphometric variation in blackbirds using GLM, regions as an explanatory factor.

Measurements	Habitat/Region	Estimate	Std. Error	t value	Pr (>|t|)
Tarsus (mm)	Intercept	3.01	0.02	121.70	< 0.00001 ***
	Rural habitat	-0.02	0.03	-0.68	0.5
	Region Wellington	0.02	0.04	0.58	0.56
Wing (mm)	Intercept	4.83	0.008	587.08	< 0.00001 ***
	Rural habitat	0.007	0.01	0.66	0.51
	Region Wellington	0.01	0.01	0.93	0.35
Tail (mm)	Intercept	4.69	0.01	262.59	< 0.00001 ***
	Rural habitat	-0.005	0.02	-0.22	0.82
	Region Wellington	0.04	0.03	1.55	0.13
Bill (mm)	Intercept	3.06	0.02	147.51	< 0.00001 ***
	Rural habitat	0.02	0.02	0.77	0.44
	Region Wellington	-0.06	0.03	-1.77	0.08 •
Weight (g)	Intercept	4.33	0.03	119.54	< 0.00001 ***
	Rural habitat	0.09	0.04	2.09	0.05 •
	Region Wellington	-0.10	0.07	-1.52	0.13

Significant independent variables are depicted with: 0 '***', 0.001 '**' 0.01, '*' 0.05 '•'

Table 6.5 Effect of habitat types and regions on morphometric variation in blackbirds using ANOVA for GLM.

Measurements	Habitat/Region	Chisq	Df	Pr (>|Chisq |)
Tarsus (mm)	Habitat	0.46	1	0.49
	Region	0.33	1	0.56
Wing (mm)	Habitat	0.44	1	0.50
	Region	0.86	1	0.35
Tail (mm)	Habitat	0.05	1	0.82
	Region	2.37	1	0.12
Bill (mm)	Habitat	0.6	1	0.43
	Region	3.20	1	0.07 •
Weight (g)	Habitat	4.04	1	0.04 *
	Region	2.38	1	0.12

Significant independent variables are depicted with: 0 '***', 0.001 '**' 0.01, '*' 0.05 '•'

Table 6.6 Effect of habitat types on morphometric variation in song thrushes using GLM, regions as an explanatory factor.

Measurements	Habitat/Region	Estimate	Std. Error	t value	Pr (>|t|)
Tarsus (mm)	Intercept	2.94	0.08	36.92	< 0.0001 ***
	Rural habitat	-0.06	0.08	-0.76	0.45
	Region Wellington	-0.05	0.09	-0.51	0.61
Wing (mm)	Intercept	4.75	0.05	84.50	< 0.0001 ***
	Rural habitat	-0.05	0.06	-0.84	0.41
	Region Wellington	0.03	0.06	0.60	0.55
Tail (mm)	Intercept	4.41	0.07	63.52	< 0.0001 ***
	Rural habitat	0.11	0.07	1.43	0.18
	Region Wellington	-0.30	0.15	-1.96	0.07 •
Bill (mm)	Intercept	2.90	0.15	18.31	< 0.0001 ***
	Rural habitat	-0.09	0.17	-0.54	0.60
	Region Wellington	-0.28	0.22	-1.21	0.24
Weight (g)	Intercept	4.25	0.09	46.02	< 0.0001 ***
	Rural habitat	-0.03	0.10	-0.33	0.74
	Region Wellington	-0.11	0.15	-0.77	0.45

Significant independent variables are depicted with: 0 '***', 0.001 '**' 0.01, '*' 0.05 '•'

Table 6.7 Effect of habitat types and regions on morphometric variation in song thrushes using ANOVA for GLM.

Measurements	Habitat/Region	Chisq	Df	Pr (>|Chisq |)
Tarsus (mm)	Habitat	0.57	1	0.44
	Region	0.27	1	0.60
Wing (mm)	Habitat	0.70	1	0.40
	Region	0.35	1	0.55
Tail (mm)	Habitat	2.10	1	0.14
	Region	4.10	1	0.04 *
Bill (mm)	Habitat	0.30	1	0.58
	Region	1.54	1	0.21
Weight (g)	Habitat	0.11	1	0.73
	Region	0.61	1	0.43

Significant independent variables are depicted with: 0 ‘***’, 0.001 ‘**’ 0.01, ‘*’ 0.05 ‘•’

6.3.2 Morphological variations between New Zealand and English populations

The model showed a significant effect of location on tail length between England and New Zealand populations of blackbirds and song thrushes. On average, tarsus length decreased and tail lengths, increased significantly in New Zealand blackbirds (Table 6.8, Figure 6.6, A and C). The model showed non-significant trends toward increased tarsus and wing length in New Zealand blackbirds compared to English samples (Table 6.9, Figure 6.6, B).

As in the full model, song thrushes showed decreasing tail length in New Zealand compared to England (Table 6.10), and the mean tail lengths for English samples were longer than the mean tail length of New Zealand song thrushes (Figure 6.6, F). Tarsus length was smaller on average in New Zealand samples than English individuals (Figure 6.6, D) but the results did not find a significant effect of location on tarsus and wing length in song thrushes (Table 6.11). The wing length of English song thrushes was slightly longer on average than New Zealand samples.

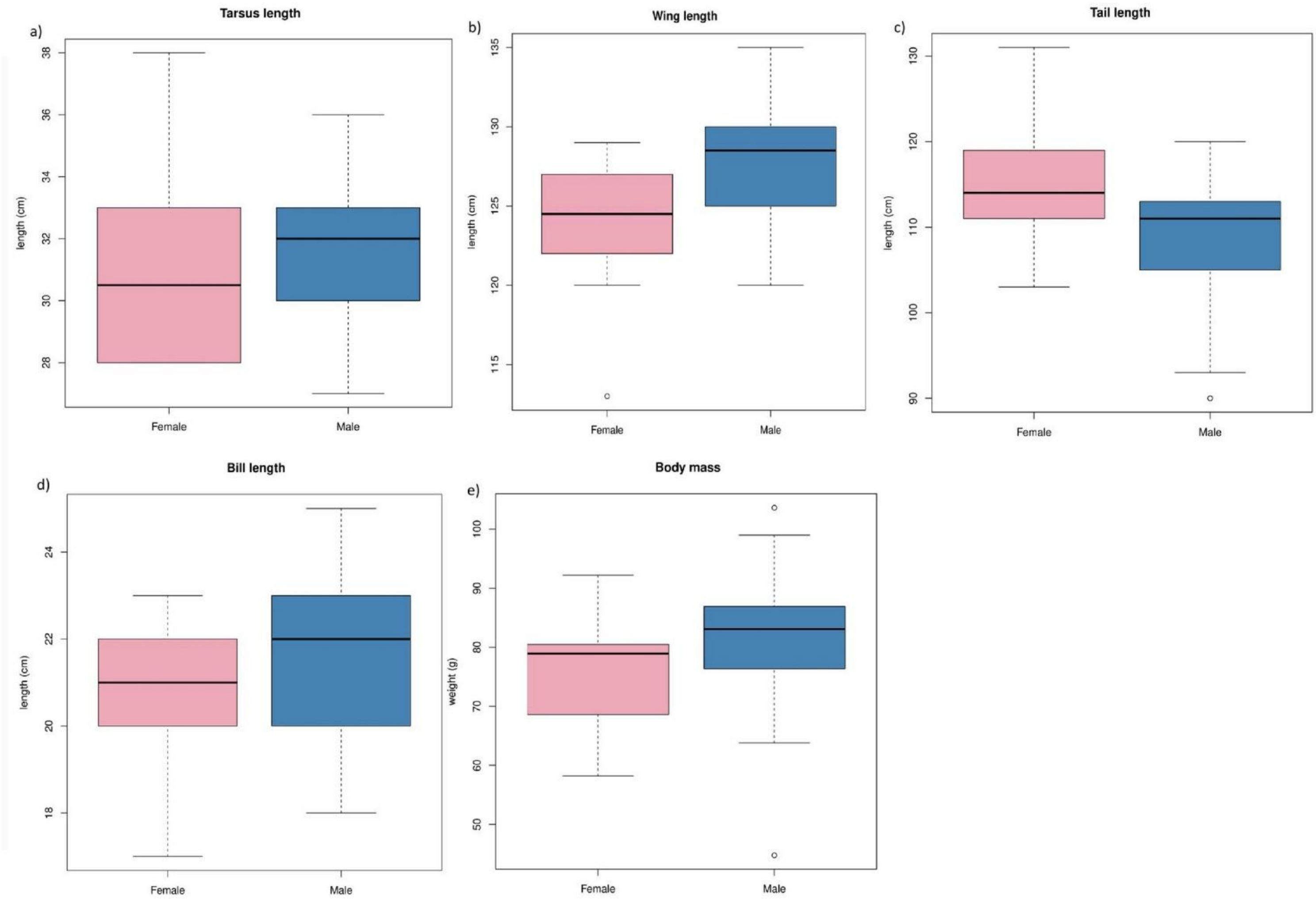

Figure 6.3 Morphological differences between female and male blackbirds in New Zealand for (a) tarsus length, (b) wing length, (c) tail length, (d) bill length and (e) body mass. Box plots show the median (bar in the middle of rectangles), upper and lower quartiles, maximum and minimum values (vertical lines), and outliers (white dots). Wing and tail lengths were significantly varied between males and females.

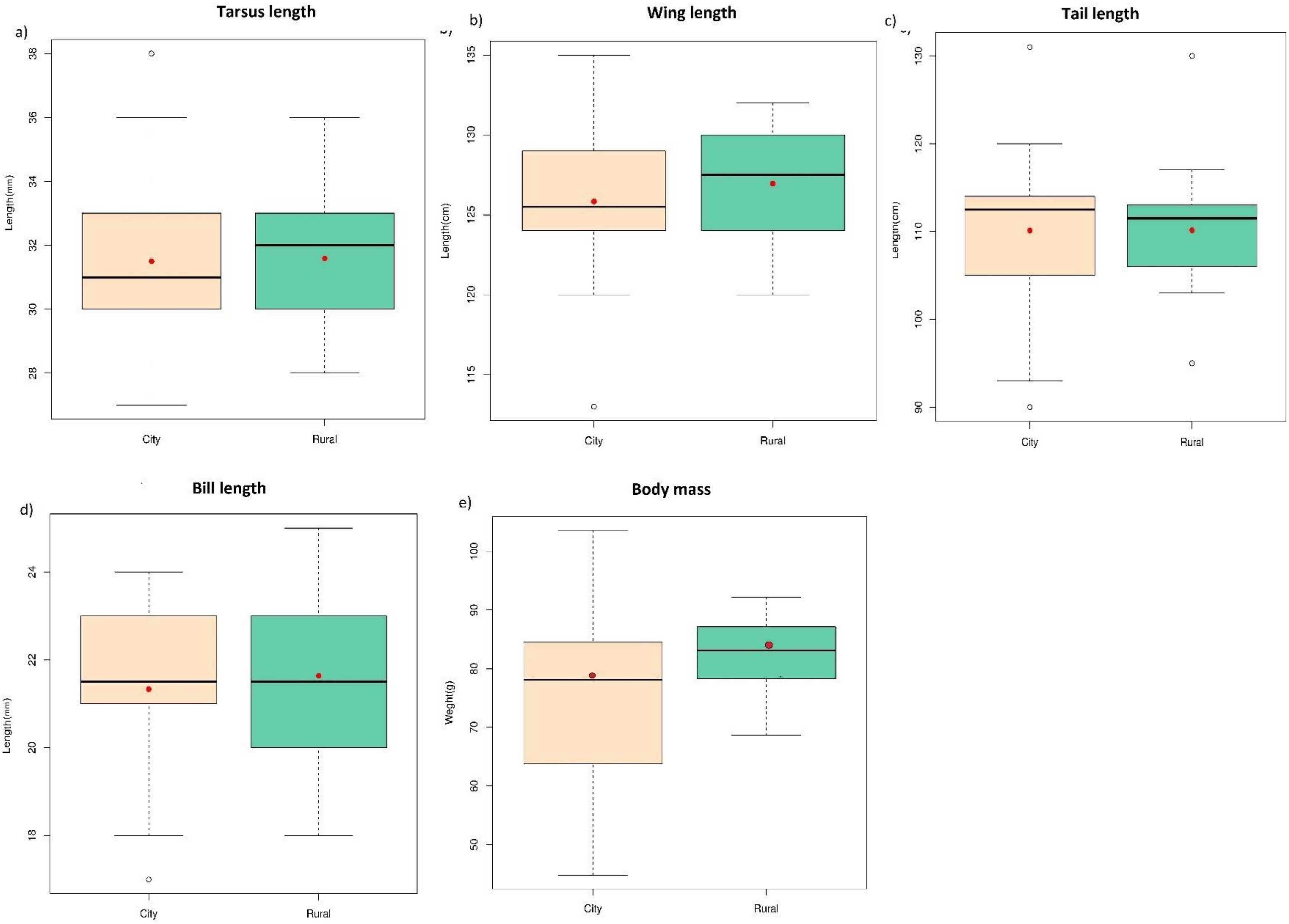

Figure 6.4 Morphological variations in New Zealand blackbirds from rural and urban habitats (a) tarsus length, (b) wing length, (c) tail length, (d) bill length and (e) body mass. The y-axis represents the length (cm) and weight (g) for body mass. Box plots show the median (bar in the middle of rectangles), mean (red circle), upper and lower quartiles, maximum and minimum values (vertical lines), and outliers (white dots). Body mass was significantly different between urban and rural individuals.

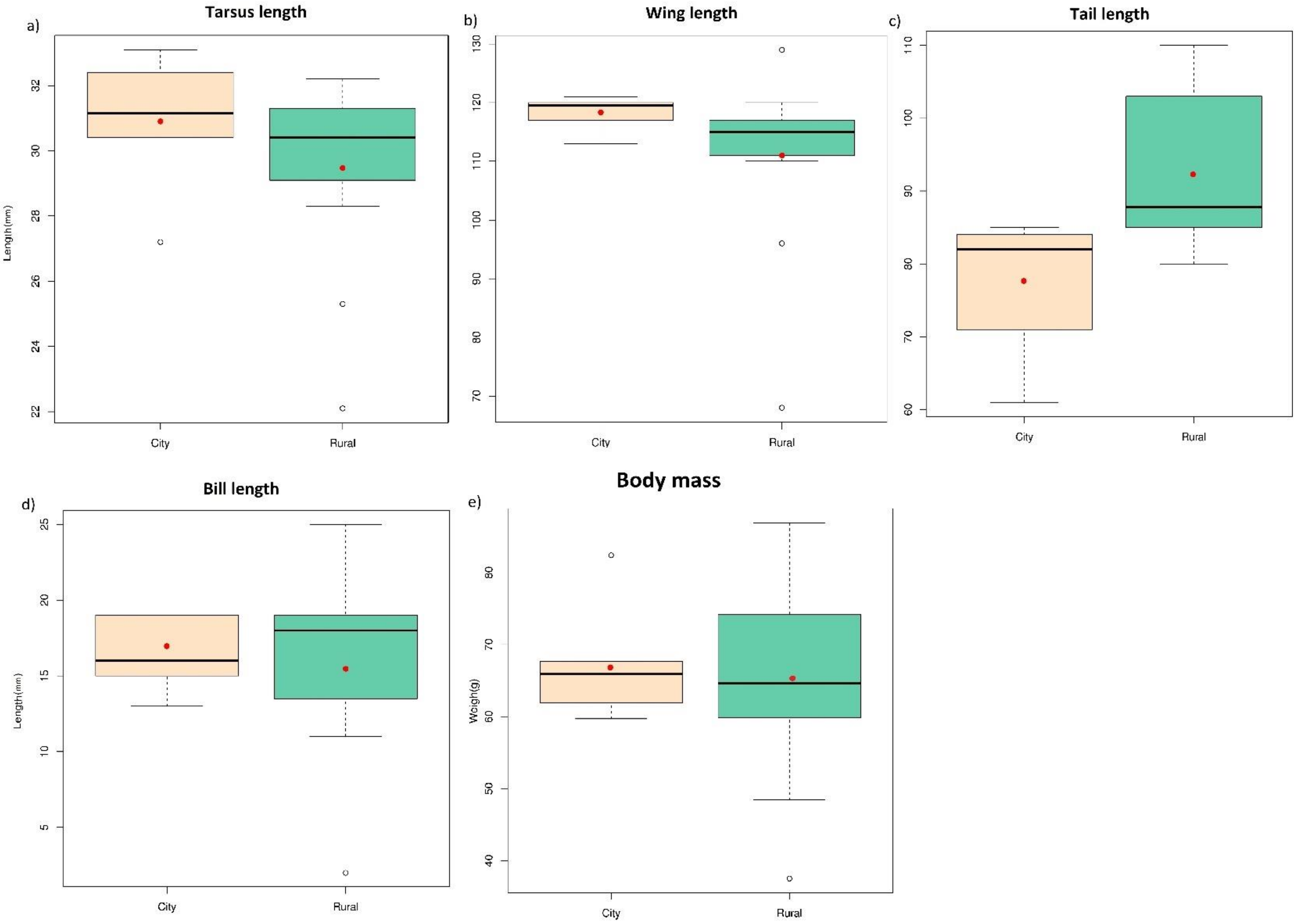

Figure 6.5 Morphological variations in New Zealand song thrushes rural and urban habitats (a) tarsus length, (b) wing length, (c) tail length, (d) bill length and (e) body mass. Box plots show the median (bar in the middle of rectangles), mean (red circle), upper and lower quartiles, maximum and minimum. No significant differences between habitats.

Table 6.8 Morphological variations between NZ and UK populations of blackbirds (GLM).

Measurements	Population	Estimate	Std. Error	t value	P-value
Tarsus (mm)	England	3.48	0.025	138.00	< 0.00001***
	New Zealand	-0.038	0.02	-1.41	0.16
Wing (mm)	England	125.23	1.11	112.62	< 0.00001***
	New Zealand	-0.05	1.31	-0.03	0.97
Tail (mm)	England	99.07	3.09	31.99	< 0.00001***
	New Zealand	9.34	3.63	2.56	0.01*

Significant independent variables are depicted with: 0 ‘***’, 0.001 ‘**’ 0.01, ‘*’ 0.05 ‘•’

Table 6.9 Morphological variations between NZ and UK populations of blackbirds (ANOVA for GLM).

Measurements	Mean ± SD mm		F value	P-value
	NZ	EN		
Tarsus (mm)	31.26 ± 2.5	32.5 ± 1.07	1.98	0.16
Wing (mm)	126.38±4.33	125.86±3.32	0.001	0.970
Tail (mm)	110.128 ± 1.7	108.42 ± 7.05	6.59	0.012*

Significant independent variables are depicted with: ≤ 0.01, ‘*’ .

Table 6.10 Morphological variations between NZ and UK populations of song thrushes (GLM).

Measurements	Population	Estimate	Std. Error	t value	P-value
Tarsus (mm)	England	32.37	0.41	77.71	< 0.00001***
	New Zealand	1.27	0.97	1.30	0.22
Wing (mm)	England	124.51	6.03	20.65	< 0.00001***
	New Zealand	4.29	8.25	0.52	0.60
Tail (mm)	England	104.18	2.23	46.59	< 0.00001***
	New Zealand	-12.11	3.20	-3.77	0.0006***

Significant independent variables are depicted with: <0.00001 ‘***’.’

Table 6.11 Morphological variations within NZ and UK populations of song thrushes (ANOVA for GLM).

Measurements	Mean ± SD mm		F value	P-value
	NZ	EN		
Tarsus (mm)	29.77±2.47	32.37±1.30	1.695	0.225
Wing (mm)	124.62 ± 4.04	125.18 ± 5.61	0.2703	0.6058
Tail (mm)	92.07 ± 13.51	104.18 ± 3.4	14.272	0.0006***

Significant independent variables are depicted with: <0.00001 ‘***’.

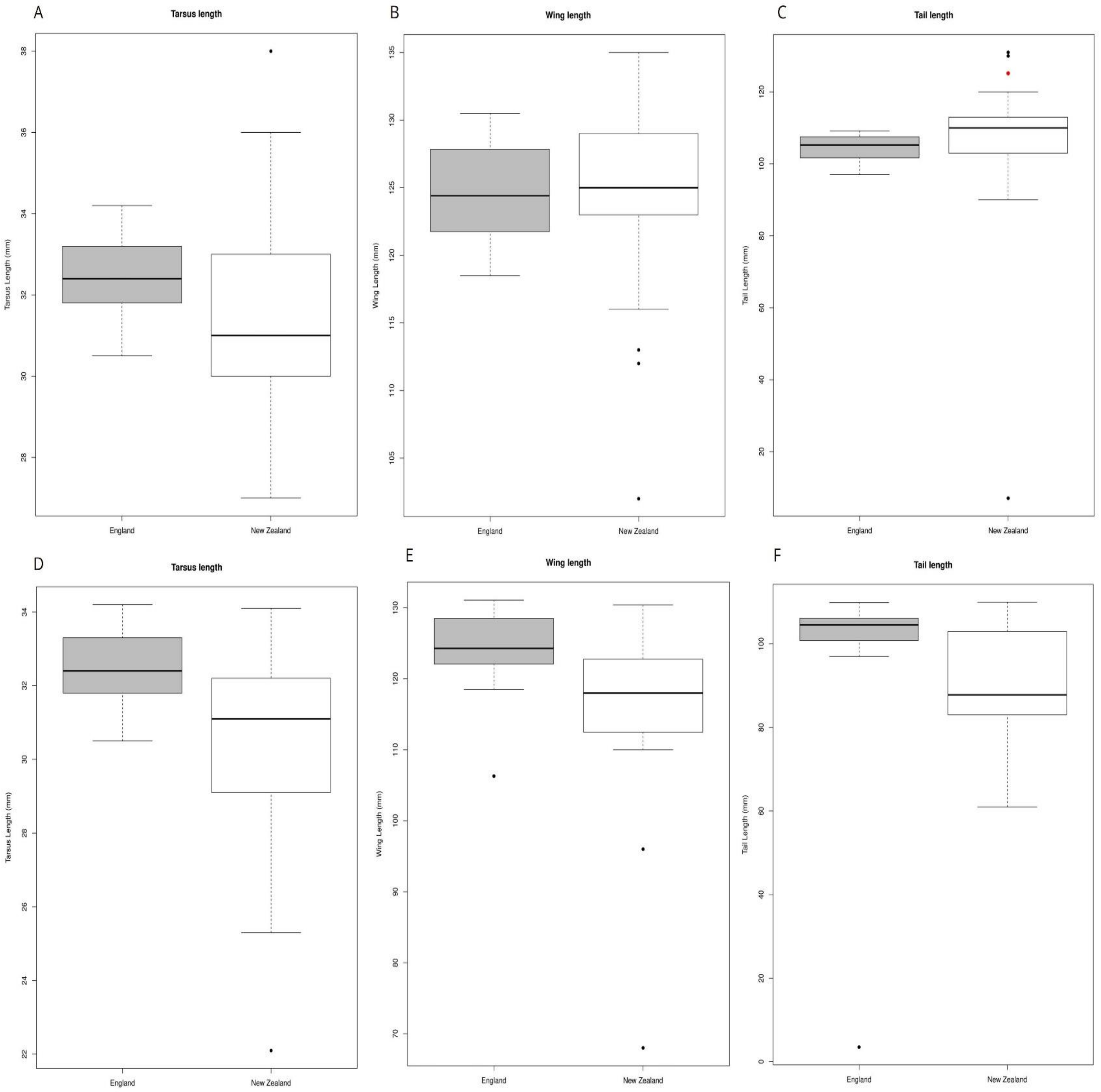

Figure 6.6 The boxplot of differences in morphological traits including tail, tarsus and wing length between England and New Zealand populations of blackbirds (A, B, C) and song thrushes (D, E, F). Box plots show the median (bar in the middle of rectangles), mean (red circle), upper and lower quartiles, maximum and minimum values (vertical lines), and outliers (white dots). Tail length in

blackbirds in song thrushes were significantly different between England and New Zealand samples.

6.4 Discussion

The study assessed the impact of habitats and regions on morphological traits in blackbirds and song thrushes from the Wellington and Canterbury regions and the potential morphological divergence between New Zealand's exotic populations and England's native populations. The results showed that morphological variations may respond to different regions rather than different habitats.

Female blackbirds generally had shorter wings (3.06%), longer tail lengths (6.7%) and lighter body mass (6.1%) than males. Body mass is related to wing and tail length directly to optimise and manage flight skills (Dulisz et al., 2016). Sexual selection may favour males with larger wing lengths due to territory defence behaviour, mating activities and opponents' competition. The length and shape of the wing help birds to manoeuvre (Tittler et al., 2009), travel long distances and affects dispersion (Dawideit et al., 2009). Longer and pointed wings are useful for flying long distances typical of dispersal and migration (Lockwood et al., 1998; Mönkkönen, 1995). Sedentary birds have rounded and shorter wings that are better able to manoeuvre (Dawideit et al., 2009).

Tail length was a sex-related trait in blackbirds. Females had longer tail lengths than males, which might be related to their different parental roles. There was no significant correlation in tail length between urban and rural blackbirds. Tail length was affected by regions in song thrushes where tail length was longer in the Canterbury region compared to individuals in the Wellington region (differed by 31.5%). Most findings suggested that longer tail length allows birds to have better manoeuvring in more disturbed environments, such as urban areas. The tail length differences may be a pre-adaptation response towards local conditions. I speculate that perhaps this is due to an artifact of uneven sample sizes between habitats and regions.

The only morphological trait that differed between urban and rural populations was body mass in blackbirds. Urban body mass in blackbirds was decreased by 8.7% than their rural counterparts. Body mass and condition could reflect habitat suitability and food availability. Similarly, rural song thrushes were heavier on average than urban individuals but it was not affected significantly by habitats. The mean body mass for song thrushes ranged the same weight for urban and rural individuals but body weight rural song thrushes showed wide dispersion. Foraging might also be influenced by predator presence, external disturbances, such as human activities. Inter-specific competitions may be another factor that heavier and dominant birds compete with smaller birds to push them into lesser-quality habitats.

Body mass variations between urban and rural blackbirds may be explained by a combination of Shochat's 'credit card' hypothesis and the theory of starvation-predation risk. Rural blackbirds may have access to higher-quality food resources and are disturbed less by human presence compared to urban individuals. A reduction in daily intake of energy in less suitable environments may be an adaptive response (Bruun & Smith, 2003; Mitchell & Powell, 2004). Even the presence of anthropogenic food sources and heavy-metal pollutants could be unsuitable for the blackbird digestive system.

The significant differences in bill length between the Wellington and Canterbury blackbirds could reflect the differences in diet composition between habitats of these regions. Bill length for blackbirds in the Canterbury region was slightly longer (6.3%) than for the Wellington samples. Variation in food resources may cause changes in foraging related traits, such as bill size and shapes in birds (Badyaev et al., 2008; Bosse et al., 2017; Giraudeau et al., 2014). Magory Cohen et al. (2021) suggested that living in different environments require certain foraging phenotypes. For example, changes in seed size availability in European goldfinches (*Carduelis carduelis*) influenced bill size (Domínguez et al., 2010). Blackbirds are omnivorous, also taking fruit and seeds but mainly feeding on ground-dwelling invertebrates, especially earthworms, snails and insects (Peter & Cowling, 2007). It is assumed that longer bill length could help with better feeding with less time spent scratching for food (Cresswell, 1998; Wysocki, 2002) and digging deeper into the soil would facilitate them to forage optimally. Bill growth is heritable and affects an individual's efficiency of foraging (Boogert et al., 2006; Djemadi et al., 2019; Senar & Björklund, 2020). I assume that different geographical conditions, such as different types of soils provide birds with various abundance and availability of food resources. A longer bill may be favourable in Canterbury regions where soils are of high fertility and have adequate drainage (https://soils-maps.landcareresearch.co.nz) so that birds with the longer bill have greater benefit from probing deeper into the soil for plant seeds and worms.

There were no significant differences in wing length between blackbird and song thrush populations from England and New Zealand but it increased by 0.41% in blackbirds and decreased by 0.44% in song thrushes over a relatively short time (at most 160 years) and that may be related to dispersal ability. A similar study on European starling (*Sturnus vulgaris*) in New Zealand did not find an increased wing length after colonisation but did show that wing length had decreased by 3.8% over 120 years (Bitton & Graham, 2015). Migratory English populations have longer and more pointed wings. Introduced populations in New Zealand are sedentary and travel shorter distances.

The morphological measurements from England and New Zealand blackbirds showed that morphological divergence has likely occurred between native and exotic populations. The significant differences in tail length between native and introduced populations of blackbirds and song thrushes suggest divergence related to the environment. This tail length varaition may be related to climate change effect where birds responded with decreased body sizes. Tarsus length was significantly shorter in New Zealand blackbirds compared to English samples. In the 160 years since blackbirds were introduced from the UK to New Zealand, the population mean tarsus length now decreased by 38.9%. This aligns with a similar study that compared UK native and NZ introduced populations of blackbird (Blackburn et al., 2013) that showed a similar reduction in tarsus length by 16.3% in their New Zealand blackbird samples and no tarsus changes between the UK and New Zealand song thrushes. My results found tail length differences between England and New Zealand populations of blackbirds and song thrushes, while (Blackburn et al., 2013) did not find significant differences. The other explanation might be the island rule where body size tends to increase with island area (Meiri et al., 2011), but most studies found that exotic species that were introduced to New Zealand have smaller body sizes than their native populations (Blackburn et al., 2013; Fountain et al., 2018; Mackinven & Briskie, 2014; Sol & Lefebvre, 2000; Sorci et al., 1998; van Heezik et al., 2008; Veltman et al., 1996).

Differences in collecting samples and measuring morphological traits may impact final results. English samples were taken from live birds, while New Zealand samples were taken from roadkill birds where the exact time of death was unknown but should not be more than one or two days before collection. A dead bird’s body may shrink in size and body mass that causing bias in data analyses. Defrosting frozen carcasses can cause shrinking in body size if not done correctly. I did not freeze all the samples, Roadkill birds from the Wellington region were measured on the same day. There may be bias in morphological measurements of England samples done by different people but there is no evidence for that, I assume the samples are unbiased measurements of morphological traits.

The other possible consideration about data is that small sample sizes may not give support to determine significant effects and differences if they are any.

6.5 Conclusion

In this study, significant differences between female and male blackbirds might be in response to different parenting role. As I found no sex-related escape behaviour between blackbird females and males in Chapter 3. Females showed less tolerance toward potential predators and fled at longer distances compared to males. Female blackbirds may suffer higher predation pressure combined with starvation risk, decreased foraging time to escape sooner from predators. I could not identify the sex differences in song thrushes to investigate the possible body mass sex-related. I speculate that increased predation pressure on females and suitable adaptation response, such as shorter wings and longer tail length may directly affect their morphological traits related to the aerodynamics or locomotory performance in flushing faster from predators. Phenotypic variation should be investigated for native species as a response to environmental changes and habitat fragmentation.

The body mass variations between urban and rural blackbirds may reflect the impact of diet on body conditions. Bill length differences between the Wellington and Canterbury regions may be related to catching food functions that are affected by environmental conditions, such as the type of soil. The results suggest the possible correlation between bill length and body mass in response to food resources and foraging behaviours. I suggest that future works may focus on the effect of soils on the foraging behaviour of ground-foraging species. It would be helpful to understand the cause of body mass variations by investigating the diet of urban and rural populations using molecular analysis of the digestion systems of roadkill birds.

The divergence between New Zealand and England populations appears to be happening slowly. The results showed that New Zealand populations have generally smaller locomotion-related traits (shorter tail length in blackbirds and song thrushes) than their English counterpart. This could result from different environmental conditions and predator pressure that leads to different ecological processes present in England and New Zealand. The predator pressure in New Zealand may be decreased compared to England due to the presence of cats in urbanised landscapes and mustelids as the only terrestrial predator, while birds in England have to face foxes and predator birds as aerial predators, such as sparrowhawks and kestrel (*Falco tinnunculus*).

However, the effect of sample size on the results should not be neglected. Collecting dead birds could bias sampling, as higher sick or parasite-infected and unfit individuals have higher mortality rates. Urban samples were mostly collected on the margin of urban boundaries and may not be under severe conditions of urbanisation, such as the heat-island effect, noise and air pollution. Studying the response of introduced species to new environments would help us to understand the adaptive forces of phenotypic variation (Moloney et al., 2009), and the rate of micro-evolutionary changes (Lee, 2002; Lindström et al., 2013). Introducing exotic species can lead to a destructive impact on native ecosystems and species (Mooney & Cleland, 2001), thus identifying the traits that help exotic species to thrive and colonise in new habitats would provide knowledge about preventing future invasion (Ruiz & Carlton, 2003).

Chapter 7 General discussion and suggestions

7.1 Overview

Populations appear to accumulate or exhibit behavioural and morphological phenotypic differences in response to novel environments along urban to rural gradients. I hypothesised that anthropogenic environments frequently confront wildlife with unfamiliar and novel stimuli and potential predators and that their responses will vary between populations.

I examined three different behavioural traits and a set of morphological measurements in response to anthropogenic alterations and disturbances. These results are consistent with the hypothesis that animal populations respond to anthropogenic challenges with plasticity.

The causes, consequences and patterns of within-population ecological variation have been missing in explaining the source of intraspecific trait variation, implying that the viability of ecological communities may result from personality (Bolnick et al., 2011). These studies suggest the effect of intraspecific and interspecific differences on the ability of an individual or population to adapt to environmental changes (Sih et al., 2015). Causes and consequences of trait variation may be determined by analysing genetic and phenotypic patterns of ecological differences and examining them across multiple species and generations (Bolnick et al., 2011; Bolnick & Otto, 2013; Bolnick et al., 2002).

7.2Implication of findings

7.2.1 Should I go or should I stay? Blackbirds and thrushes respond to approaching potential predators and regulation of risk-taking behaviour (Chapter 3).

Most studies on impacts of the urban environment rely on FID, alone or combined with SD. If we only consider FID as a proxy for risk-taking behaviour, we neglect other factors related to FID, such as AD, SD, DF, escape and response strategy, group size and sexual dimorphism. All of these shape risk-taking behaviours in birds living within different anthropogenic habitats. I found that risk-taking behaviour, response and escape strategies are related to habitats. For example, there was a positive relationship between FID and SD, but this correlation might be confounded with habitat impacts. Starting distance is often constrained by terrain. In open rural habitats, SD can be at a greater distance from target individuals than in more cluttered urban habitats.

I found that there was a higher probability of escaping by walking to open spaces at shorter distances for urban and peri-urban river blackbirds and song thrushes as FID increased compared with flying to cover at longer distances when the observer was closer. I assumed that landscape structure and composition in urban areas are more compact with buildings and tall vegetation, which predicts a longer distance between green patches. Urban birds may be more likely to flee to anthropogenic cover resulting in shorter FID. I suggest examining other risk-taking traits, such as age differences, dimorphisms, clothing colour of the approaching observer, human density, landscape configuration, structure and composition, and vegetation cover. How birds regulate their escape behaviour in response to aerial and terrestrial predators may help us to identify the risk and threats, especially for endangered species.

After the world pandemic hit and lockdown happened nationwide across New Zealand, I noticed that urban birds behaved differently and expanded their foraging boundaries. I observed that urban birds increased their FID with a decreasing level of human presence. This suggests that the response of birds toward human presence is a temporary attitude, fitting to current conditions. If individuals were transferred from highly disturbed habitats to less urbanised areas or vice versa, how long would take until they adapt to the new environment?

Animal behaviours are species-specific responses and my results should not be interpreted as an overall pattern in response to human-caused environmental changes. The escape response of birds could be influenced by body mass. Generally, larger birds showed shorter FID than smaller birds (Møller et al., 2016). However, escape behaviour in birds may vary with the kind of predator, including terrestrial or flying avian predators (Alexandrino et al., 2019). I suggest that future research should consider body mass differences when assessing the possible interaction of morphological conditions on risk-taking behaviour and to what extent risk-taking behaviour might change according to the abundance of terrestrial and aerial predators.

7.2.2 Where do angry birds live? Analysing aggressive behaviour in response to an intruder (Chapter 4).

I investigated the aggressive and signalling behaviour of blackbirds and song thrushes to a conspecific playback song in their territories in the Wellington and Canterbury regions. Aggressive and signalling behaviours were affected by habitat types and regions. Urban birds were more likely to use aggressive responses, while rural and peri-urban river birds were more likely to use signalling behaviour. The behavioural responses varied between regions, which may be due to local adaptation. The inter-species differences in response to playback songs indicated that studying urban ecology needs to consider each species separately. I used a combination of responses toward playback songs to understand adaptive responses to urbanisation.

This study only measured male blackbirds. It would be useful to investigate inter-sexual aggression behaviour variation among dimorphic species in their territory and their response to urbanisation. Aggression behaviours in urban birds appeared to be associated with environmental factors, such as patch connectivity, food availability and predation risk. Future studies may identify the level of predation pressure on life-histories traits, especially aggression and signalling behaviour during breeding and nonbreeding seasons. The level of urbanisation may be a variable factor to examine the role of urbanisation on wildlife and conservation programs.

Differences in aggressive and signalling behaviour between habitats and regions show that behavioural syndromes and phenotypic plasticity may be a useful index to develop more sustainable solutions for conservation programs for native and exotic wildlife. Identifying personality traits without having to capture birds to observe in controlled conditions would be particularly useful. The observations may be closer to reality and allow us to understand aggressive behaviour in passerines.

By testing the behavioural responses of two closely related species across an anthropogenic gradient, we can measure the strength and direction of urbanisation impacts on animal populations. The relationship between the level of urbanisation and physiological factors, such as stress hormones concentrations (e.g., corticotrophin), could be measured in wildlife (Angelier et al., 2018; Badyaev, 2005). I assume that chronic stress levels may vary at intra and inter-specific levels and individuals and assist landscape planners to quantify anthropogenic effects on free-ranging bird populations (Strubbe et al., 2020).

7.2.3 Hide or seek? How birds deal with novel objects (Chapter 5).

I investigated exploratory behaviour and the approach initiation response in response to a novel object mounted in a bird’s territory. I designed two assays including the closest approach distance to a novel object and the frequency of approach response by broadcasting conspecific songs. The level of urbanisation predicted the neophobic responses and exploratory behaviours in animals toward the novel object.

One of the adaptive responses resulting from the cost of living in urbanised areas is dealing with novel challenges, instead of flying and escaping, despite the high level of risk (Breck et al., 2019; Johnson et al., 2020; Nacarova et al., 2018). I found that exploratory behaviour could be investigated at inter and intra-species levels within the different levels of urbanisation and human presence.

The exploratory behaviour assay allowed me to examine the aggressive behaviour of birds in their territory with their second approach to the novel object. I speculated that birds would respond to the second round of playback songs and the novel object based on their first experience and habituation. Accordingly, I suggest examining novelty-seeking responses to a different set of novel objects to reduce the chance of habituation without using conspecific songs.

I identified that exploratory behaviour in response to stimuli objects varied significantly between species. I identified that when birds approached closer to the novel object (explorer) with a higher rate of approach response (faster), they displayed increased exploratory behaviour. Population differences (urban, peri-urban river and rural) in novelty-seeking behaviour were explained by habitat. Taken together, my findings suggest a synergy between ecology and evolutionary components to behavioural variation in understanding the biological basis of exploratory behaviour.

7.2.4 Morphological differences in two passerine species along an urban to rural habitat gradient (Chapter 6).

I compared New Zealand introduced species with their England source populations. The results suggested phenotypic change over the last hundred or so generations. Differences were found in locomotor morphology, such as tarsus and tail lengths. Different phenotypic divergence patterns in intraspecific-level interactions with anthropogenic habitats after the introduction may lead to cascading effects on ecological factors (Auer & Martin, 2013; Thompson, 1998).

My findings were not in line with some studies that have found urban individuals had shorter wing, tail and tarsus lengths compared to rural populations (Caizergues et al., 2021; Caizergues et al., 2018; Dulisz et al., 2016; Liker et al., 2008). I found only bill and tail length differences at the regional level between Wellington and Canterbury regions. I suggest that bill length variation may be related to differences in food resources or soil types. However, future studies should measure bill depth, skull size and food diversity and availability of individuals. My results only found significant morphological differences in body mass between urban and rural blackbirds where there were trends toward increasing body mass from urban to rural habitats. I assume that testing the intensity level of pollution, predator pressures, inter-and intra-specific competitions, connectivity and composition of landscape patches may highlight the intrinsic factors important to variation between populations.

There were morphological differences in tarsus and tail lengths between the study’s introduced and source populations. New Zealand populations had shorter tails and tarsus length compared to English individuals. This morphological difference may ultimately lead to speciation between two populations.

Further morphological studies are needed to inspect live captured birds, assessing anthropogenic changes in food resources and their relationship with bill shape in birds. I found sexual-specific morphological traits between male and female blackbirds and I encourage future research to focus on dimorphic species to examine the effect of mating-related traits, dispersal-related phenotypes of birds between urban and non-urban habitats. Studying morphological and genetic differences would help us to understand isolation forces processes that eventually lead to reinforcement and speciation between habitats.

7.3 Conclusion

Future work could investigate whether phenotypic traits linked to urbanisation, such as body mass, tail, wing, tarsus and bill lengths, are also common in other invasive populations in New Zealand. It would be informative to explore whether these patterns are also present in the native source populations of these species, or whether these responses are specific to the exotic populations as adaptive responses to new environments. The mechanisms of dispersion and the establishment of populations could be examined along with population-level and nationwide studies of traits leading to reintroduction success. These phenotypic divergences suggest a combined adaptive phenotype caused by the introduction process might favour traits that facilitate individuals to thrive, colonise and spread across new habitats.

My study found that sex-specific life-histories might account for intersexual differences in predation risk, wing and tail length, independent of habitat differences. Meta-analysis investigations of behavioural and phenotypic variation in passerines and their association with related genes may allow us to understand selection pressure and life-history syndromes (Merilä & Sheldon, 2001; Rivkin et al., 2019; Santangelo et al., 2020).

I was unable to conduct genetic analyses of behavioural and morphological variation due to time limitations. Ideally, I would examine the extent to which genetic diversity and genome polymorphism, such as the genes DRD4 or SERT, are partially responsible for aggressive and boldness behaviours between urban and rural populations (Korsten et al., 2010; Riyahi et al., 2016; Riyahi et al., 2015{; Timm et al., 2015). I suggest long-term studies of genetic and environmental factors of behavioural and phenotypic traits across landscapes and over generations.

Understanding the response of individuals and populations to anthropogenic habitat changes could help us to decipher ecological, evolutionary and conservation enigmas. Most examples of behavioural and morphological traits variation across levels of anthropogenic landscape changes result from the plasticity process rather than from natural selection. In my study, I chose two widespread and cosmopolitan species because one can compare and generalise the findings to the European populations. For example, escape responses were in line with most similar studies that showed bolder and shorter FID of urban populations in response to potential predators compared to rural individuals. The escape response of blackbirds and song thrushes in my study met the assumptions as FID reflects the level of fearfulness responses in passerines and is related to habitat types and escape and response strategies were affected by DF, habitats. Therefore, if landscape variation can shape the risk-taking behaviour, other antipredator behaviour-related factors, such as SD, AD, flock size and sex-related responses need to be examined with the same species in Europe to identify whether the correlations are related to interspecific differences or geographical variations. I assume that the responses toward human presence may be similar.

Differences in behavioural and morphological variation between urban and rural populations may be associated with genotype frequencies of polymorphism, gene regions related to personality variation. I expect that future studies might use genetic markers to examine the magnitude of genetic variation in particular responses across landscape matrices. I assume that passerine genetic structure across different levels of anthropogenic landscapes would be influenced by the level of habitat fragmentation and connectivity between subpopulations. In this study, I indicate that the deliberate introduction of passerines may act as selective forces, leading exotic populations to exhibit different behavioural and morphological traits from source populations.

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