The role of personality and behavioural plasticity in Common Blackbird (*Turdus merula*) reproductive success


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Thesis abstract

Behavioural biologists have focused on differences between species and populations in the past, while the importance of individuality in behavioural traits has been neglected for a long time. Within a population, behavioural phenotypic variation between individuals is common (Laland and Hoppitt, 2003). Recently the study of behavioural traits in individuals has attracted noticeable attention. This has resulted in behavioural ecology researchers developing a strong interest in the concept of *animal personality*, *plasticity,* and the role of individual variation in shaping behavioural traits. Additionally, behavioural ecologists have found different correlations between behavioural traits in terms of "*Behavioural syndromes"* (Garamszegi and Herczeg, 2012). Behavioural phenotypes may cause different lifestyles, influencing life-history strategies in populations (Cote et al., 2008; Edenbrow and Croft, 2011). I investigated in depth the breeding biology and behavioural traits of a population of common blackbirds (*Turdus merula*; hereafter blackbirds) in New Zealand during breeding and non-breeding seasons from 2017 to 2019. In addition, I studied behavioural variation in this species. The key objective was to focus on how personality and plasticity in traits contribute to reproductive success in this species. My study used field observations and experimental approaches to investigate blackbird behavioural variation and its consequences for reproductive success.

I presented breeding biology of blackbirds by investigating three key objectives: breeding biology and chronology, nest characteristics and parental provisioning in blackbirds. I found that blackbirds had a consistent number of eggs per clutch (mean= 2.9 eggs). I found a strong positive correlation between clutch size and latitude from blackbird breeding data around the world. Within breeding pairs that had more than one clutch, the number of fledged nestlings was significantly greater in the last clutches. Nests close to the road had a higher chance to be successful and fledged chicks. These results indicated evidence that predators strongly influenced the breeding success of blackbirds across the season. In addition, I found that the nest diameter increased across the breeding phases (from built to fledged chicks). In contrast, the nest thickness, internal nest depth, and external nest depth decreased. There was a positive correlation between the nest thickness/external nest depth and the number of eggs per clutch. Male and female blackbirds shared chick feeding equally.

Additionally, I investigated the variation of behavioural traits of blackbirds using two approaches: observational and experimental. In the observational approach, I recorded activity, vigilance, aggressiveness and shyness behavioural traits. The experimental tests aimed to measure risk-taking within individuals, neophobia, and antipredator behaviour within paired blackbirds. Here, I focused on four objectives: 1) determine explanatory factors that influence behavioural traits (e.g., weather conditions, sexes and age, human modification), 2) estimate repeatability and consistency of all behavioural traits over different time scales within individuals, 3) examine the correlation between behavioural traits, 4) evaluate the relationship between behavioural traits and reproductive success within individuals.

My results showed that activity, aggressiveness, and risk-taking behaviours increased significantly in the breeding season within individuals. Minimum temperature significantly affected the variation of behavioural traits. In addition, in the presence of a novel object, movement around the novel object and inspection time significantly increased in paired blackbirds. Inspection declined by increasing the number of trials. My results also demonstrated that the blackbird's movement around the novel object was influenced by age and the number of chicks. Pairs that had more chicks had a greater number of movements around the novel object. Nest visits by paired blackbirds declined in the presence of the novel object and a greater number of people. Furthermore, in the presence of a predator model, blackbirds showed aggressive (attack-alarm) and non-aggressive responses (they did not alarm and attacks and fed chicks) toward the predator model, with highly aggressive and less aggressive pairs. The aggressive responses of blackbirds were affected by the age and number of nestlings in the nest.

Repeatability analysis showed that the onset of egg-laying and the nest's thickness were moderately repeatable within females. Selected behavioural traits in the context of foraging were not repeatable (movement , aggressiveness, vigilant, shyness were highly flexible). However, I found that risk-taking behaviour was moderately repeatable within juvenile females and males (during breeding season) and tended to decrease in the non-breeding season. Neophobic response variables were moderately repeatable within paired blackbirds. Within pairs, antipredator responses were highly repeatable. In contrast, parental nest visits had a low repeatability estimation. Furthermore, the behavioural syndrome analysis revealed a positive correlation between activity and shyness. I also

discovered that risk-taker blackbirds were more vigilant. Regarding the consequences of behavioural traits on blackbird breeding, I found that shyer blackbirds had a greater number of fledged nestlings per season. In addition, blackbirds who were risk-takers (shorter FIDs, flight initiation distance) produced more eggs per season. Antipredator responses and neophobia in blackbirds were also influenced by breeding investments of blackbirds. Movement round the novel object (neophobic response) and aggressive response toward a predator increased in pairs with a greater number of chicks. In the post-stress situation (predator presentation), pairs with more chicks in their nests returned to their nests sooner (shorter latency) and had a greater number of post-stress nest visits.

Additionally, I investigated the response of male blackbirds to different conspecific songs by two playback experiments. In the first experiment, I investigated if blackbirds display different responses to playback songs from males of varying levels of aggressiveness. I also investigated the effect of anthropogenic disturbance, parental care and breeding success on the response of blackbirds to the playback. In the second playback experiment, I examined whether male blackbirds discriminated songs (a long-range signal) from neighbouring and stranger conspecifics. Results from my playback experiment revealed that there were no differences in the response of male blackbirds to the songs from aggressive and non-aggressive blackbirds. Interestingly, blackbirds that had their territories close to the road showed stronger responses toward the playback songs. In addition, there was a positive correlation between the response of male blackbirds and the number of nest visits during the chicks rearing. My results from the second playback experiment showed that a male blackbird responded equally to the dawn songs from his neighbours and strangers, while his response to the songs from far strangers (blackbird's songs recorded in Europe) was weaker than New Zealand blackbird songs. However, I also found that males respond to stranger blackbirds' daytime songs stronger than those from the neighbour, which confirmed the "Dear Enemy" theory in blackbirds.

My research is significant in that it is one of the first studies of breeding and behavioural traits of blackbirds in an urban population of New Zealand. It provides important highlights about intra-individual variation in behavioural traits, and its fitness consequences on the breeding success of blackbirds.

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My research was undertaken with permission from Massey University, Animal Ethics Committee (AEC/17 (Amended 01/14)) for all research carried out on Massey University, including sound recording, banding, bird monitoring and experiments.

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1.1 Breeding Biology

Empirical studies of the breeding characteristics of species contribute to our understanding of the patterns and processes of life-history evolution (Bennett and Owens, 2002; Covas, 2012; Crick, 2004; Dunn et al., 2001). Research on breeding biology within the context of evolution has been conducted by field ornithologists ever since Charles Darwin (Darwin, 1871). Breeding strategies vary between and within both species and populations (Mourocq, 2017). This information provides valuable insights into coping mechanisms, reproductive adaptations and factors that drive the distribution of bird species under different environmental conditions (Auer et al., 2007; Gross, 1994; Mainwaring et al., 2014a; Slagsvold, 1982a; Sutherland et al., 2004; Weatherhead, 2005). Specifically, breeding characteristics can inform how populations of a species decline or thrive in different habitats (Crick, 2004; Van Allen et al., 2012). Bird species vary in the timing of breeding, nest characteristics, clutch size, egg size, incubation period, nestling period, parental care, and nestling growth and breeding success (Creighton, 2000; Cresswell, 1997; Faivre et al., 2001a; Kentish et al., 1995a; Kucherenko and Ivanovskaya, 2020; Lack, 1947; Lu, 2005). These characteristics are driven by natural selection processes and with growing numbers of breeding studies in the last few decades, novel, and productive new directions for this research, such as the role of behavioural plasticity, are developing.

Clutch size and number of broods are two breeding parameters that significantly vary within and among species. Genetics, body condition, diet, and the degree of predation have been suggested as the most common factors influencing clutch size and number of broods (Dunn et al., 2000; Eldrigde and Krapu, 1988; Postma and Noordwijk, 2005; Rowe et al., 1994; Slagsvold, 1982b, 1984). Some species have genetically predetermined clutch sizes (e.g., wandering albatrosses*, Diomedea exulans*) and cannot replace lost eggs (Croxall et al., 1992). While, other species are indeterminant layers and can produce several clutches to and replace lost eggs (e.g., blue tits, *Parus caeruleus*) (Amininasab et al., 2016). In addition, other factors such as body condition can influence the clutch size, for example female common eiders, *Somateria mollissima*, that have good body condition (determined from mass at hatching) lay larger clutches than females with small body reserves (Erikstad et al., 1993). A study on mallard, *Anas platyrhynchos*, showed that a lower protein wheat diet results in reduced clutch size, egg size, laying rate, number of nesting attempts, and total

eggs laid (Eldrigde and Krapu, 1988). In bluebird, *Sialia sialis,* clutch sizes decline continuously throughout the breeding season and the short overall season results in birds producing just a single clutch because of food limitation (Dhondt et al., 2002).

Two sets of factors have been suggested to influence the breeding characteristics of species. First, environmental (ultimate) factors influence processes that increase the reproductive fitness of adults and the survival of the offspring (Golabek et al., 2012; Pakanen et al., 2016). These factors include food availability and competition for food resources within and between species, avoiding or limiting predator pressure and responses to latitude (Ungerfeld and Bielli, 2012). For example, in pied flycatchers, *Ficedula hypoleuca*, breeding success is lower in late season and influenced by food availability, as availability of food declines in late season (Siikamäki, 1998). Pair breeding and colonial species have different strategies to reduce predator pressure. Solitary bird species (e.g., European roller, *Coracias garrulus*) have widely spaced placement of nests. While colonial species (e.g., Kittiwake, *Rissa tridactyla,* Skimmers, *Rynchops niger*) rely on safe sites or colonies where many pairs build their nests (Schreiber and Burger, 2001; Ungerfeld and Bielli, 2012; Wiklund and Andersson, 1994, 1994). Hence, ultimate factors are important in the long term and shape reproductive behaviour from an evolutionary view.

Secondly, proximate factors stimulate gonad development, regulate the reproductive cycle, and influence breeding activity (Jones, 1986). Proximate factors include changes in daylength (photoperiodic variation), weather-related factors, social factors, age and physiological factors (Burger, 1982; Meijer, 1989; Pinaud and Weimerskirch, 2002). For example, older birds generally have higher breeding success than younger birds (Forslund and Pärt, 1995; Nol and Smith, 1987; Ollason and Dunnet, 1978). These factors can vary widely and have significant immediate effects on breeding activities. For instance, bird species occurring at similar latitudes, regardless of hemisphere show similar egg-laying patterns, such as introduced birds and native birds in New Zealand and other Southern Hemisphere birds (Cockrem, 1995). Proximate factors can influence patterns of breeding and reproductive success in a variable way in any given year. For example, social interactions in the Kentish plover, *Charadrius alexandrinus*, at localised scales influence patterns of reproductive pairing (McDonald et al., 2020).

Comparative evolutionary biologists constantly attempt to consider the maximum number of species from broad geographical ranges or habitats to analyse and increase the universality of life-history theories (Clarke, 1997; Pienaar et al., 2013). Identifying and investigating the key factors influencing breeding strategies of different populations will provide insights into how individuals cope with different environments (Jetz et al., 2008, BirdLife International 2015). For example, the global diversity of clutch size in half of all bird species has been investigated (Jetz et al., 2008; Williams, 1994). Unfortunately, the current knowledge of breeding parameters of birds is concentrated in northern temperate regions; breeding of birds in tropical and Southern Hemisphere regions has been poorly quantified (Myers et al., 2000; Stattersfield, 1998). Filling these information gaps will effectively improve comparative analyses (Xiao et al., 2017).

Currently, human modification of the planet is an important proximate factor that is impacting the natural world at an extraordinary pace. By 2030, around 60% of the world's human population will occur in urbanised environments (Montgomery, 2007). As the world becomes increasingly urbanised, wildlife faces new challenges, such as the loss of habitat and associated resources such as food, anthropogenic disturbance (pedestrian and vehicle traffic), noise and light pollution (Altermatt and Ebert, 2016; Giraudeau et al., 2014; Liu et al., 2016; Santos et al., 2010; Scherl, 2018; Schoeman, 2016; Slabbekoorn, 2013; Trombulak and Frissell, 2000). Although many studies have shown limitations for wildlife inhabiting urban environments, some species have successfully adapted to urban challenges, for example, the great tit, *Parus major*, and the blackbird, *Turdus merula* (Møller, 2010a; Rutz, 2008; Sol et al., 2012). Such species often prosper in urban areas as "urban adapted species" (Albery et al., 2021).

Bird species are useful biodiversity indicators (Buckland et al. 2008; Catterall 2004). The behaviour of many urban bird species is modified in response to urban challenges, particularly with respect to breeding and breeding site selection and foraging (Catterall, 2004; Fuller et al., 2008; White et al., 2005). Research of urban parks shows that the diversity of birds that use modified habitats for breeding depends on park structure and size and the surrounding landscape structure (Jokimäki, 1999). Rutz (2008) reviewed 26 threatened bird species and found that by adding artificial nest boxes, saving old trees, and using 'bird friendly' building design, these species are more broadly protected. Not all human modifications of environments have negative impacts. For example, artificial

illumination of feeding areas for wader species increases their foraging effort, and these behavioural shifts enhance prey intake rates (Santos et al., 2010). Finally, studies show that birds that establish in urban habitats have certain behavioural traits that potentially underpin their success. Urban populations can be comprised of more risk-averse, bolder and more aggressive individuals than rural populations (Clucas and Marzluff, 2012; Evans et al., 2010a; Møller, 2010b). Exploring reasons for the success and failure of species in urban areas will help the conservation of biodiversity in urban environments.

1.2 Behavioural variation

How do different individuals recognise and respond to environmental stimuli? Why do individuals of a population behave differently to the same stimulus? Are behavioural variations specific to individuals and are they stable during individual lifetimes? These questions have encouraged ethologists to carry out research into various aspects of individual behaviour for more than a century. Darwin made many observations about animal behaviour; not long after the publication of the Origin of Species (Darwin, 1852), the science of behaviour separated into two fields of study: ethology, primarily in Europe, and comparative psychology, primarily in North America (Armstrong, 1947). However, in the 1980's, the field of behavioural ecology emerged as an approach that combined elements from both factions but with an implicitly evolutionary approach. Although the study of animal behaviour has been approached using different methodologies by ethologists, comparative psychologists, and behavioural ecologists, all these approaches have found that animals have specific temperaments or behavioural patterns that are sources of variation in the behaviour of individuals (van Oers and Naguib, 2013a).

Behavioural variations in a population occur at both the inter-and intra-individual levels. Scientists have often regarded behavioural differences at the level of intra-individual as "plasticity" (Ogden, 2012). Behavioural plasticity occurs in response to environmental challenges such as food availability, predators, competition and mate choice; which consequently influence an individual's growth and survival (Mathot et al., 2012). In more heterogeneous environments, individuals must adjust their behaviour to match environmental and social conditions (Krebs & Davies 1997). For example, birds modify their level of aggressiveness based on the costs and benefits of an aggressive interaction (Dingemanse and Araya-Ajoy, 2015).

Recently, the significance of intra-individual variation in behaviour has been recognised by scientists (Dall et al., 2004; Réale et al., 2007). In the past, the general assumption was that individuals show variable behavioural responses so as to maximise fitness in different environmental contexts (Réale et al., 2007). Recently, a number of researchers have argued that individuals do not show complete plasticity in their responses and the term 'personality' has arisen to explain both the consistency and repeatability of an individual's behavioural response across distinct contexts and over time (Pennisi, 2016; Roche et al., 2016). Personality is, by definition, a heritable characteristic (Patrick et al., 2013), for example, a study of captive great tits over four generations demonstrated that exploratory behaviour is heritable and provides a foundation for predicting significant amounts of genetic variation for personality types in a wild bird (Fidler et al., 2007).

Animal personality studies have been conducted on a wide diversity of taxa, from invertebrates to vertebrates (Massen et al., 2013; McCowan et al., 2015). The most common measured behavioural traits in personality studies among different taxa include exploration tendency, shyness-boldness, aggressiveness, parental care or offspring provisioning, anti-predator behaviour and neophobia (Jones and Godin, 2010; Nettle, 2006; Ogden, 2012; Rockwell et al., 2012; Szasz et al., 2014). In personality studies, it is essential to provide an accurate definition and measurement of behavioural traits. However, measurable parameters of each behavioural trait are not universal and they depend on the context and situation in which the experiment is taking place (Roche et al., 2016a). For example, depending on the objective and context of the study, 'boldness' can be measured by different parameters such as average velocity, distance from a certain point or structure, or total traveled distance (Beekman and Jordan, 2017).

Ultimate and proximate perspectives are two general views that can illustrate mechanisms of personality causation (Nettle, 2006).

Ultimate (evolutionary) perspective: Several evolutionary models (mechanisms) demonstrate why personality types can arise and be consistent (Figueredo et al., 2009). Ultimate explanations include:

1) *Specialisation* where an adaptation to a special function or environment can reduce the level of conflict between conspecifics (Bergmüller and Taborsky, 2007). Individuals use a

specific tactic or behaviour to respond to a social challenge such as competing for food, space or mating partner when adopting a social niche (Bergmüller and Taborsky, 2010b).

2) *Positive feedback mechanisms* that describe an individual's ability to be proficient at a certain task and respond to environmental stimuli (Wolf et al., 2008). This mechanism can lead to consistency and divergence in behavioural traits. Therefore, individuals may reduce costs of responsiveness (e.g. reduce conspecific conflicts) from switching tasks, or they can improve performance at a task by learning (Bergmüller and Taborsky, 2010). Positive feedback describes the consistency of an individuals' responsiveness over time across various situations (Rosenzweig and Bennett, 1996). They either consistently respond or neglect environmental stimuli in all kinds of contexts. For example, some great tits alter their foraging behaviour toward a change in the feeding condition, whereas others stick to previously successful behaviours (Verbeek et al., 1994).

3) *Sexual selection* defines consistency in behaviour that can be a result of competition for, and attraction of mates, where individuals with consistent behaviour are favoured over conspecifics with inconsistent behaviour (Schuett et al., 2010). For example, consistency in male behavioural traits may indicate parental care abilities or genetic quality. If all females assess such benefits gained by choosing a certain male, then consistency in female preferences is expected. This results in inter-individual agreement in choice and consistent selection of behaviours (Blanckenhorn, 2005).

4) *Balancing selection* occurs when genetic variation is maintained by selection, so that different levels of a trait dimension are adapted to the same degree in different environmental contexts (Penke et al., 2007). The two most relevant balancing selection types for personality are frequency-dependent selection and environmental heterogeneity in fitness optima (Penke et al., 2007). Frequency-dependent selection refers to selection in which the fitness of a specific phenotype drops if the occurrence of that phenotype becomes too high (Buss and Duntley, 2008). Environmental heterogeneity in fitness optima refers to a situation when different phenotypes are preferred under different conditions (Buss, 2009), for example, urban versus non-urban environments.

Proximate perspective (mechanistic): On a proximate level, personality differences are explained in the context of genetic, physiological, and environmental factors that determine the expression of a behaviour (Réale et al., 2010a). For example, personality

differences can be related to differences in metabolism, stress physiology, and neuro-endocrinological traits (Stamps and Groothuis, 2010). Some proximate mechanistic examples include:

1) *Pleiotropy, antagonistic pleiotropy and linkage disequilibrium* (refer to glossary) present the functional architecture of personality traits. These mechanisms are responsible for the resulting genetic correlation (van Oers and Mueller, 2010). Antagonistic pleiotropy generates evolutionary trade-offs in relation to fitness advantages and disadvantages of related traits (Bergmüller, 2010; Verweij et al., 2012). Exploration, neophobia and risk-taking traits in great tits are correlated phenotypically and have a genetic basis that likely results from pleiotropic effects (Oers et al., 2004). A review on a few vertebrates considered antagonistic pleiotropic effects of the genes regulating the synthesis of brown to black melanin and revealed that lighter individuals are less aggressive and sexually active than darker individuals (Ducrest et al., 2008).

2) *Hormonal impact* can shape personality throughout an animal's life, but particularly during prenatal and postnatal ontogenesis (Biro and Stamps, 2008; Careau et al., 2008). Often multiple traits are influenced by the physiological state and associated with variation in hormone levels (Sih et al., 2015). For example, boldness and activity traits in fish are related to cortisol levels (Kappeler and Kraus, 2010).

3) *Neuro-endocrinological pathways*: Observations of rats show that more aggressive males perform a higher level of burying behaviour and have higher plasma noradrenaline levels after exposure to stressful situations Furthermore, more competitive proactive male rats had higher blood pressure, catecholamines and baseline levels of noradrenaline (Koolhaas et al., 2010; Réale et al., 2010b). Thus, individual variation of neuro-endocrinological pathways can influence the expression of behavioural traits (Carere et al., 2003; Groothuis and Carere, 2005a).

4) *Social and environmental factors*: Social factors such as conspecific interactions and parental behaviour and environmental factors such as food availability can influence individual personality development (Dingemanse et al., 2010). Studies of mother-offspring interactions have shown that various levels of maternal behaviour, such as stress, anxiety and exploratory behaviour, affect neurobiological and endocrine levels once offspring reach adulthood (Francis et al., 2002). Social factors as well as environmental factors can

influence the expression of individual personalities. For example, food restriction results in greater aggressiveness of young great tits (Carere and Eens, 2005).

1.3 Repeatability and heritability

In many taxa, individuals show heritable variation and consistent responses along behavioural axes such as shyness, aggression, neophobia or exploration (Wolak et al., 2012). Although heritability is difficult to assess in field studies (Findlay and Cooke, 1983), researchers can measure the repeatability of behaviour within the context of personality to determine its heritability. By consistently observing the behaviour of marked individuals, researchers can assess repeatability and measure the reliability of inter-observer and internal consistency of a trait (Bell et al., 2009).

For genetic purposes, repeatability explains a proportion of the overall phenotypic variation described by inter-individual differences (Falconer, 1996). Repeatability as a measure of the consistency of behavioural traits in personality studies is vital for the characterisation of inter-individual behavioural differences and the understanding of their ecological and evolutionary consequences (Archard and Braithwaite, 2010; Bell et al., 2009). Several parameters can influence the repeatability of a behavioural trait and affect the recorded measurements. For example, repeatability may vary between sexes or across different populations (Hedrick and Kortet, 2012; While et al., 2010). Clearly, behaviours least influenced by the environment are more repeatable than those with significant environmental input. The basic formula for calculating repeatability (interclass correlation coefficient) is r (ICC) = S^2_A /(S^2_w + S^2_A); where S^2_w is within-individual variance and S^2_A is between- individual variance over time (Dohm, 2002) . High S^2_A and low S^2 mean greater repeatability (Wolak et al., 2012).

An assumption of animal personality is that behavioural traits are repeatable over a period of time and across various environmental contexts (Biro and Stamps, 2010; Briffa and Greenaway, 2011a; Nakagawa and Schielzeth, 2010). Bell et al. (2009) performed a meta-analysis to discover factors and features that could explain to what extent behavioural traits are repeatable. They found that some behaviours were more repeatable over a short period of time than others and concluded that changes in gene expression during ontogeny and/or individual physiological state are likely factors (Bell et al., 2009; While et al., 2010). For example, larvae of the pit-building antlion, *Cueta lineosaforaging,* were studied by

measuring the movement pattern of individuals in different environmental contexts. This experiment demonstrated repeatable behaviour over a few days and across various environmental scenarios relating to sand depth and soil type (Alcalay et al., 2014).

The number of experimental repetitions is a key factor in the reliability of repeatability estimates (Briffa and Greenaway, 2011a; Boulton et al., 2014). Some behavioural researchers applied two repetitions for each experiment, whereas others repeat experiments significantly more frequently to assess the consistency of a specific behaviour (Boake, 1989; Edwards et al., 2013). Although there is an assumption that increasing the number of repetitions reduces the measurement error of observations, it might also give false results as individuals may become accustomed or sensitive to the experiment (Adolph and Hardin, 2007). When assessing correlations among repetitions, the number and time periods between repeats and factors such as age, sex and context of the experiment need to be considered (Drent et al., 2003a; Hedrick and Kortet, 2012).

1.4 Behavioural syndromes

In ecological studies, the term ' Behavioural syndrome' refers to correlated traits and sets of correlated behaviours (Dingemanse et al., 2012, 2012; Garamszegi and Herczeg, 2012). Syndromes can occur at either the individual or species level (e.g. species that are bolder versus the shy ones)(Garamszegi and Herczeg, 2012a; Pintor et al., 2008). When behavioural traits are correlated, they must be studied together rather than as isolated units (Bergmüller, 2010; Monceau et al., 2015). The existence of behavioural correlations has been found in several species, e.g. freshwater fish, *Rivulus harttii*, where individuals with high dispersal ability are also bolder and more aggressive than low dispersal individuals (Conrad et al., 2011). Studies of great tit (Dingemanse et al., 2003), common mice *Mus musculus,* (Krackow, 2003) and two Hymenoptera species: *Vespa crabro* and *V. velutina*, (Monceau et al., 2015) have found similar correlates.

Studying correlated sets of behaviours across different contexts represents a significant change in the way that behavioural ecologists investigate about behaviour. For example, spiders exhibit positive correlations between aggressiveness in both the context of territorial defence and foraging behaviour (Reichert and Hedrick, 1993). Likewise, birds show a positive correlation between exploration and dispersal and fish demonstrate positive correlations between aggressiveness and boldness towards predators (Martins

and Bhat, 2014; Patrick and Weimerskirch, 2014; Winandy and Denoël, 2015). Studies show that behavioural syndromes can significantly influence individual fitness, speciation rates and species distributions (including species invasions) (Sih et al., 2004a). For example, when individuals encounter a new habitat, assessing an individual's behavioural syndrome can predict its likelihood of success in that novel environment; successful individuals are often bold, exploratory and aggressive (Malange et al., 2016; Wong and Candolin, 2015).

Different situations can influence individual success due to trade-offs between traits. For example, bolder individuals may be socially dominant but are more at risk of predation (Pintor et al., 2008; Sih et al., 2004a, 2004b). Likewise, for aggression, some individuals are consistently more aggressive than others in different contexts, although an individuals' overall aggression level may change with context (Cote et al., 2008; Edenbrow and Croft, 2011). A trade-off for aggression occurs if aggressive tendencies continue into circumstances where caution or care are more appropriate (e.g., in an anti-predator or parental care context). In contrast, less aggressive individuals might perform well in circumstances where low aggression is favoured, but they are unsuccessful in competitive circumstances (Bell and Sih, 2007; Dingemanse et al., 2007).

Behavioural syndromes may happen because of certain constraints on the evolution of behaviours or because natural selection favours certain correlations (Rosenthal and Stuart-Fox, 2012). For instance, in three-spined stickleback, *Gasterosteus aculeatus*, individuals show a strong correlation between aggressiveness and boldness only in populations where fish predators exist (Dingemanse et al., 2007). This diversity in behavioural syndromes across populations may be a result either of natural selection favouring correlated behaviours in a particular environment or because of processes such as drift, mutation, founder effects or gene flow (Bell, 2005). Thus, the structure of behavioural syndromes can vary depending on the evolutionary history of the population with respect to natural selection (Phillips and Suarez, 2012).

1.5 Singing behaviour

Bird song is a behaviour trait that plays a crucial role in social interactions and in sexual selection and is a well-studied field in many birdsong species (Catchpole, 1987; Price, 1998). Songs play a central role in reproductive success and mating decisions (Capp and

Searcy, 1991a; Naguib and Riebel, 2014). In addition, songs contain information such as quality and reproductive success and survival of signaller (Brunton et al., 2016). Furthermore, song can act as a proxy for age (Kipper and Kiefer, 2010; Nemeth et al., 2012), competitive ability (Price et al., 2009), interactions among individuals (Rosvall, 2011), personality (Naguib et al., 2010, 2016) and social behaviours (Todt and Naguib, 2000). Thus, understanding different aspects of vocalisation in songbirds enhances our knowledge regarding the mechanisms that correspond to individual signalling within populations and species.

Song features have been found to vary among individuals and provide information on the signal sender's condition, quality, and motivation (Naguib et al., 2011; Nowicki and Searcy, 2004). In addition, these elaborated signals participate in long-range advertisement among individuals and create social networks (Amy et al., 2010; Beecher, 1989; Liu, 2004). Moreover, there is evidence of a link between songs and fitness consequences when used in mate attraction and resource defence (Baptista and Morton, 1982; Petrinovich and Baptista, 1984). For example, song rate is correlated to early mating in male snow bunting, *Plectrophenax nivalis* (Hofstad et al., 2002). Song complexity in European robins, *Erithacus rubecula*, transfers sender aggression and influences receiver response (Kareklas et al., 2019). Song matching in indigo buntings, *Passerina cyanea*, influences mating, nesting, and fledging success (Payne, 1982). Hence, bird song is a behavioural trait that provides an excellent research model for the study of plasticity and repeatability.

Additionally, there has been considerable research on the ability of birds to discriminate between individuals on the basis of vocal signals (Dabelsteen and Pedersen, 1992; Guillette and Sturdy, 2011). Individual vocal recognition has benefits for the territorial owners; it can prevent wasting time, energy, and risk of injury by applying an appropriate territorial defence level (Brunton et al., 2008; Lovell and Lein, 2004; McArthur et al., 1981). Song playback experiments nicely demonstrate avian song discrimination. Neighbour versus stranger song discrimination is well-known in many bird species, e.g., Audubon's shearwater, *Puffinus lherminieri*, common chaffinch, *Fringilla coelebs*, corn crake, *Crex crex*, and yellow-bellied tit, *Parus venustulus* (Budka and Osiejuk, 2013; Hansen, 1984; Mackin, 2005; Skierczynski et al., 2007; Wei et al., 2011). Neighbour–stranger discrimination to playbacks has been used to test the “Dear enemy hypothesis”. In this hypothesis, a territorial holder may avoid unnecessary aggressive conflicts with a familiar individual

(neighbour) while aggressively reacting to a stranger or unfamiliar conspecific because of the unknown territorial status and potentially greater threat of the stranger (Brunton et al., 2008).

Many male songbirds react aggressively to songs of conspecific males in their territory, while some males do not respond. Song signals can be an indicator of the quality of individuals, fighting ability and aggressive intent (Panhuis and Wilkinson, 1999). A territorial male may assess the intent of an intrusion and evaluates how his reproduction and territory are at risk (Ripmeester et al., 2007). For example, greater song overlap, and song matching can motivate and escalate fighting between males (Vehrencamp 2001, Naguib & Kipper 2006). In addition, temporal and spectral characteristics of the song at the level of intra-individuals may indicate motivational state (Capp and Searcy, 1991b). In Eurasian hoopoe, *Upupa epops*, specific song elements can elicit more aggressive responses in the receivers of these signals (Martín-Vivaldi et al., 2004). Blackbirds use a range of song types in their territorial defence and in aggressive encounters with territorial intruders. 'Strangled song' is a short-distance, aggressive signal, that often precedes a physical attack. It consists of low amplitude, high frequency elements, of uneven duration. In contrast, the 'regular advertisement song' are loud and have a more stereotypical structure. Both of these blackbird song types indicate a motivation for an aggressive response (Dabelsteen, 1984; Dabelsteen and Pedersen, 1985; Ripmeester et al., 2007).

1.6 Influence of different behavioural traits on life-history strategies

A number of evolutionary studies propose that personality traits are related to the fitness of individuals (Adriaenssens and Johnsson, 2016; Koolhaas and Van Reenen, 2016). For example, personality research on a long-lived seabird shows that both boldness and foraging personalities are correlated with fitness consequences, depending on sex and food availability. Data reveal that bolder females and shyer males have higher fitness, but the power of this relationship depends on food availability (Cote et al., 2008; Edenbrow and Croft, 2011). Also, depending on the context in which an individual exhibits its behaviour, fitness can change (Edenbrow and Croft, 2011, 2011; Patrick and Weimerskirch, 2014). For instance, more aggressive individuals in the context of competition, have higher

reproductive success, while these same individuals who are in an anti-predator context have a low survival rate (Sih et al., 2004a; Smith and Blumstein, 2008).

The view that an individual's behavioural traits are linked to life-history strategies has resulted in the concept of the Pace-Of-Life Syndrome (POLS). POLS predicts that specific ecological conditions favour specific life-history strategies, which lead to a set of traits (Careau et al., 2010; Galliard et al., 2013). Environmental conditions include different factors such as resource fluctuation and distribution predictability, environmental stability, predators, diseases, population density and parasites (Reznick et al., 2002). For example, research on tropical birds reveals that these birds have a slow POLS with a lower metabolic rate, lower growth rate, longer lifespan, fewer offspring and relatively late maturation than fast POLS (Bennettand and Harvey, 1987; White et al., 2007; Wiersma et al., 2007a). The POLS concept can explain the relationship between the behavioural type, physiology and life history of an individual (Réale et al., 2010c; Urszan et al., 2015). This theory assumes that different individual personalities have different lifestyles (Cote et al., 2008; Edenbrow and Croft, 2011).

There are two common strategies that explain individual variation: fast POLS and slow POLS. Slow PLOS refers to individuals who are less active, avoid taking risks, less aggressive and exhibit cautious exploratory behaviour. It is predicted that they have a slow rate of growth and metabolism. They mature later with a low rate of early reproduction, a more efficient immune system and a longer life span (Montiglio et al., n.d.; Urszan et al., 2015). While fast-paced individuals are more competitive, active and bolder, these proactive individuals often have a higher reproductive success and perform better in predictable and stable environments but have lower survival rate (Biro and Stamps, 2008). Research has supported this hypothesis in different taxa, e.g. mangrove brown trout, *Salmo trutta,* (boldness and exploration-growth) (Adriaenssens and Johnsson, 2010), killifish, *Kryptolebias marmoratus,* (exploration and boldness- growth rate) (Edenbrow and Croft, 2011), field cricket, *Gryllus intege,* (exploration- metabolic rate) (Niemelä et al., 2012), zebra finches, *Taeniopygia guttata*, (feeding motivation –activity) (Brust et al., 2013), agile frog tadpole, *Rana dalmatina,* (predator-conspecific; native tadpoles) (Urszan et al., 2015). Interestingly, animals may have fast or slow strategies. Each will trade-off current reproductive output with survival, but both strategies may lead to the same fitness level in individuals within the same population (Edenbrow and Croft, 2011, 2011; Gyuris et al.,

2012). Thus, overall lifetime reproductive output/fitness might be in equilibrium (Urszan et al., 2015).

1.7 Avian Studies

Studies of avian species have included breeding, genetics, hormones, physiology and neurology mechanisms, vocal analysis, communication, migration, distribution and the impact of environmental conditions (Burtt and Giltz, 1973). Because of their visibility, distribution and diversity of species, birds are ideal models for the study of complex behaviour. The concept of personality or behavioural consistency and behavioural syndromes has been advanced by multiple avian studies on great tits (Carere et al., 2005a; Dingemanse et al., 2003; Verbeek et al., 1994). Great tit behaviour has been well studied and behavioural profiles of individuals fit well with the published animal personality patterns of other species (Baugh et al., 2013; Cote et al., 2010). Great tits have also been studied in captivity, where individual behaviour can be easily observed (Martin et al., 2007). Studies of personality in captive situations complement the interpretation of results in the natural context (Carere et al., 2005b; Greenberg and Mettke-Hofmann, 2001). In this study, I have focused on the common blackbird, which is now globally widespread. Although significant studies on different aspects of blackbirds have been done, many aspects of behavioural variation are still a new field of study for this species.

1.8 Species and history

The common blackbird, *Turdus merula,* is a medium-sized thrush. Blackbirds (also known as Eurasian blackbird) are sexually dimorphic in plumage; male blackbirds have entirely black plumage with an orange-yellow bill, while females have dark brown plumage with brown-black wings, tail, and bill (Myers, 1955a; Snow, 1956, 1958a). They mainly feed on invertebrates (earthworms, insects). They regularly forage on the short grass; hence, it is easy to monitor their foraging behaviour (Shukshina, 2019). They usually forage on the ground in pastures and lawns. Their foraging behaviour depends on rainfall, which influences the soil moisture and food availability in the soil (Greenwood and Harvey, 1978).

Blackbirds in Europe have developed from a previous forest species to urban-adapted birds in less than two centuries (Partecke et al., 2006a). With this range expansion, urban populations of European blackbirds have adapted to new urban environments by a higher breeding density, an extended breeding season, greater longevity and a reduced propensity

to migrate compared with non-urban populations (Greenwood and Harvey, 1976a, 1978; Vliet et al., 2009; Wysocki et al., 2004). The European blackbird population has gone through a sustained period of decline from 1970 to the 1990s, followed by a recovery period between 1995 and 2008 (British Trust for Ornithology, https://www.bto.org/, 2012). Populations in Germany, France, and Italy are stable, but there is a trend of increasing numbers across the rest of Europe. Consequently, the species is evaluated as secure and has been listed in the green category since 2002. This species is now globally widespread, with an estimated population of 0.9 to 1.2 million breeding pairs (Husting & Vergeer 2002).

Blackbirds have successfully been established throughout Europe (except for northern Scandinavia) and in North Africa, eastern Asia and Australia and New Zealand. They inhabit a diverse range of ecological niches including, urban, suburban, wetland, forests and farmland (Ibáñez-Álamo and Soler, 2010a; Kentish et al., 1995a; Myers, 1955b; Partecke et al., 2005; Snow, 1958a; Venables, 1952; Wysocki, 2004; Zeraoula et al., 2016), but they avoid the high plateaus (Lu, 2005). Blackbirds are socially monogamous and partially settle on their territory year-round (Hatchwell et al., 1996a). They prefer to forage within 100-200 meters of vegetation cover.

Blackbirds were introduced to New Zealand between 1867 and 1879 and have settled throughout the country. Although they are originally a forest species, blackbirds are common in New Zealand in urban and suburban areas, parkland, farmlands, woodland, orchards, bush edges, and native forest (Luniak et al., 1990). Blackbirds are often considered as a pest because they damage many fruit products in orchards and spread unwanted plant seeds like blackberry and elderberry (Williams, 2006a). Nonetheless, blackbirds are a valuable disperser of native plant seeds and consume pest species such as slugs, snails, and other invertebrates (Biddle et al., 2015).

Blackbird studies have broadly addressed distribution and abundance (Selmi, 2007), territory (Jackson, 1954; Snow, 1956; Weatherhead and Robertson, 1977; Wysocki et al., 2004), breeding biology (Faivre et al., 2001a; Lu, 2005; Ludvig et al., 1995; Zeraoula et al., 2016), nest characteristics (Biddle et al., 2015; Bull, 1946; Karakaya and Arikan, 2015; Mikula et al., 2014a; Taberner et al., 2012; Weatherhead and Robertson, 1977; Wysocki, 2005) and factors influencing their reproductive success (Faivre et al., 2001a; Grégoire et al., 2003; Ibáñez-Álamo and Soler, 2010a; Kurucz et al., 2010a; Ludvig et al., 1995).

Additionally, data recorded from behavioural studies reveal additional information regarding blackbird foraging strategies and success (Greenwood and Harvey, 1978; Post and Götmark, 2006a; Shukshina, 2019; Støstad et al., 2017; Török and Ludvig, 1988), adaptation to urban areas (Fernández-Juricic and Tellería, 2000a; Partecke et al., 2006b; Wysocki et al., 2004), and altering migratory behaviour (Greenwood and Harvey, 1976b; Miranda, 2017; Van Vliet et al., 2009; Vliet et al., 2009). Recent studies on blackbirds confirm neophilia and neophobia behaviour as personality traits (Miranda et al., 2013a). Researchers find that differences in personality traits result from microevolutionary fluctuations in genetic polymorphisms (refer to glossary) (Miranda et al., 2013a). Thus, the presence of behavioural traits relating to harm avoidance are associated with particular genetic polymorphisms in the serotonin transporter protein gene (SERT, refer to glossary).

1.9 Significance of research and gap knowledge

Although many studies have been conducted on blackbirds, little is known about the ecology of the common blackbirds in New Zealand. There are few studies that investigate blackbird breeding and dispersal in New Zealand (Bull, 1946; Gurr, 1954; Snow, 1958a). In New Zealand, blackbird population trends, behavioural variations (regarding personality and plasticity), song characteristics, breeding ecology and nest characteristic are poorly described. Therefore, I used blackbirds as a model for my research for the following reasons:

- They are easy to observe year-round on their territories.
- Detailed behavioural data can be matched with life history data for individuals over varying temporal scales.
- Blackbirds have well-described morphology, physiology, ecology, and genetics, which give me detailed background and comparative information.
- Personality and plasticity of behavioural traits in blackbirds in New Zealand has not been previously studied.
- Studies of blackbirds in their native and expanded ranges provide background information on variations and differences of the behaviour of the population.
- Experiments can be carried out on individuals both in the wild and in semi-captive conditions.

- The Massey University population is colour banded and individual birds are easy to identify and monitor.

My Ph.D. research is the first study in New Zealand to assess the association between the personality, behavioural plasticity, and song of the urban population of free-living blackbirds and their reproductive success. This study provides quantitative results on how individual blackbirds within a population react to potential risks, explore their environment and what factors influence their reproductive success. Learning about the behavioural variation of blackbirds will enhance our knowledge about their behaviour and increase our understanding of urban blackbird populations in New Zealand.

1.10 Thesis aim

The central aim of my thesis is to investigate variation in behavioural traits of a free-living model species, the common blackbird, by comparing the effect of a range of ultimate and proximate factors. I also investigate the concept of personality its consequence on breeding investment and success. My thesis is comprised of six chapters. Data were collected during breeding and non-breeding seasons between 2017 and 2019.

I assessed the different behavioural traits and breeding biology of this species to answer the following research questions:

1) Are there significant differences between the sexes, and across different age classes of blackbirds, in shared behavioural traits?
2) How do sex-specific traits vary in blackbirds?
3) What external factors influence the variation of behavioural traits in blackbirds?
4) How do behavioural traits associated with foraging vary between breeding and non-breeding seasons?
5) How consistent are individual blackbirds across a repertoire of behavioural traits?
6) Do different behavioural traits correlate within individuals, i.e., form a behavioural syndrome?
7) How does variation in behaviour correlate with fitness, e.g., breeding success?

1.11 Thesis Outline

Chapter 1 provides the general context for my research and reviews current literature on the topics covered by my study. I state the significance of my research, the current gaps in knowledge and the thesis outline.

Chapter 2 describes a general perspective of the breeding biology of blackbirds, such as the timing of breeding, clutch/brood size and breeding success of a blackbird population in New Zealand. I present data I collected on breeding failure, parental care, and nest-site selection of a blackbird population over three consecutive breeding seasons. Additionally, I examine the impact of weather (rainfall and temperature), habitat, human modification on breeding parameters and nest survival of this population. I also investigated variation of nest characteristics in female blackbirds. Overall, results from this chapter provide a new update on blackbird breeding biology in New Zealand ,and explore the link between behavioural traits and reproductive success.

Chapters 3 and 4 examine the variations of blackbird behaviours both inter-individually and intra-individually. The behavioural traits of blackbirds were studied using a) observational (Chapter 3) and b) experimental (Chapter 4) study designs. In the observational approach, I record the daily activities of individual blackbirds to quantify the behavioural traits of blackbirds. Behavioural traits include activity, vigilance, aggressiveness, and shyness. In Chapter 4, I applied experimental tests to measure selected behavioural traits such as risk-taking, neophobia, and antipredator behaviour. I assess behavioural repeatability and behavioural syndromes and the correlation of behavioural traits on an individual's breeding success. I also investigate factors that influence behavioural traits, such as sex, weather parameters, human habitat modifications, and intraspecific species. Finally, I evaluate the links between behavioural traits and breeding parameters (investment and success) in blackbirds.

In Chapter 5, I investigate the response of male blackbirds to songs from males with varying levels of aggressiveness. I also assess the impact of human modifications on the response of male blackbirds to song playbacks. Moreover, I search for the links between the response of males and parental care and breeding success. In the second playback experiment, I evaluate the response of the male blackbirds to the songs from neighbours and strangers regarding the song's complexity (daytime and dawn songs). I also explore

how male blackbirds vary in response to the song (a long-range signal) of neighbours and strangers using an experimental playback.

Chapter 6 provides a summary of my key findings. Here, I offer a new outlook on blackbird behavioural variation and suggest future research directions to enhance current knowledge in the field of the animal behaviour (personality and plasticity).

Common Glossary

Antagonistic pleiotropy explains that two traits are associated genetically and phenotypically so that one trait corresponds with fitness costs while the other trait corresponds with fitness benefits, which ends up to generating evolutionary trade-offs (Roff and Fairbairn, 2007).

Behavioural syndrome: a suite of correlated behaviour which is consistent across contexts or situations (Conrad et al., 2011).

Consistency: refers to stability and maintenance of inter-individual differences in behavioural scores across repeated measurements of the same individuals whether in the same context (at different time points), or else repeated the measurements in different contexts (Harvey and Freeberg, 2007).

Life history is the pattern of survival and reproduction in an organism, along with the traits that directly affect this pattern across age classes, or across different stages in an organism's complex life cycle (Western and Ssemakula, 1982).

Linkage disequilibrium refers to a situation when a gene involved in the expression of one behavioural trait is present on the chromosome near a gene involved in expressing another trait (non-random association between alleles at different loci)(Bouchard and Loehlin, 2001).

Personality is consistent inter-individual differences in their behaviour across contexts and time (Roche et al., 2016a).

Pleiotropy refers to the state when one gene expresses two or more different behavioural traits (multiple effects of individual genes)(Van Oers et al., 2005).

Plasticity: Plasticity is an intra-individual variability that expresses different behavioural phenotypes and aspects of the variability within one individual under distinct environments or behavioural domains (Frost et al., 2007a).

Repeatability is a standardised measure of behavioural variability that is caused by inter-individual differences in a sample (David et al., 2012).

SERT: serotonin transporter protein gene is recognized as a candidate gene for aggression, harm avoidance and behavioural syndromes in human and birds (Riyahi et al., 2015).

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Chapter 2:

Blackbird breeding biology

Blackbird chicks (photo: Louise Vermorken)

2.1 Abstract

Detailed breeding biology information is essential for improving our understanding of avian life-history theory and conservation of many bird species. I studied the breeding biology of an introduced bird species, common blackbirds from 2017 to 2019 in an urban area in Auckland New Zealand. I had three key objectives: quantify breeding activities and their chronology, measure nest characteristics, and quantify the parental provisioning in blackbirds.

The blackbird breeding season in my population was New Zealand is typically from August to mid-December. The average clutch size was 2.9 eggs, the average brood size was 2.6 chicks, and the number of fledglings per successful nest was 2.5. Just over half of all nests were successful (54.7%, N = 214). Within pairs who had more than one breeding attempt, clutch size did not vary over several breeding attempts. While the number of fledged chicks was significantly higher for clutches laid in the late season, it seems that predation had a strong impact on breeding success and the number of fledged chicks per nest, specifically early in the breeding season. I found a significant positive link between clutch size and latitude from global blackbird data (Pearson's r = 0.8, p = 0.001).

I found that successful nests were closer to the road (mean ± SE = 25.1 ± 1.0 m, N = 111 nests), while more predated nests were located further from the road (mean ± SE = 38.2 ± 4.0 m, N = 46 nests). Nest characteristics varied with nest age. Specifically, I found that the nest diameter increased across the breeding phases (from built to fledged chicks). In contrast, the nest thickness, internal nest depth, and external nest depth decreased. In addition, there was a positive correlation between the nest thickness/external nest depth and the number of eggs per clutch. I conclude that females build thicker and stronger nests prior to laying large clutch sizes.

Repeatability analysis showed that the timing of breeding onset for females was moderately consistent (R = 0.45, p = 0.01). The location of nests (distance from the trunk) and nest thickness were also moderately repeatable (R = 0.3, ≤ 0.001) in females. In addition, the nest distance from the road was highly repeatable within females (R = 0.7, ≤ 0.001). I suggest that there may be a genetic component to nest site selection in female blackbirds and the repeatability of nest thickness and location of nests was also related to the number of eggs per clutch. Finally, male and female blackbirds share chick feeding

equally. I found that parent nest visitation rates were only slightly influenced by the number of nestlings and the nest height from the ground. I also conclude that predators influenced the breeding success in blackbirds across the breeding season. In general, data presented in this research provided a broad view of the success of the blackbirds in breeding activities in an urban area.

2.2 Introduction

One of the major goals of avian life history studies is to better understand the causes and consequences of breeding strategies in avian populations. Studies of the breeding biology of many bird species vary from simple records to more detailed information based on monitoring of nests, nestlings and juveniles (Both et al., 2004; Roper; Schaefer et al., 2006). Research has shown that avian species display a huge diversity in the timing of breeding, clutch size, number of fledgling per nest, incubation and nestling period, parental care, and reproductive success (Anderson; Roodbergen and Klok, 2008; Siriwardena et al., 2000; Slagsvold, 1982; Wysocki et al., 2004). Breeding strategies are also generally influenced by photoperiod (Jones, 1986), latitude (Lu, 2005) and climate change (Jamriška et al., 2008; Jankowiak et al., 2014). In addition, researchers show that foraging behaviour (Rytkönen and Krams, 2003), personality and behavioural plasticity of parents and offspring (Barros et al., 2016; Semlitsch et al., 1993; Walsh et al., 2010) appear to shape different breeding strategies. Moreover, environmental variables, such as habitat (Hatchwell et al., 1996b), food availability (Fernández-Juricic and Tellería, 2000b), predation pressure (Kurucz et al., 2010b) and urbanisation (Ibáñez-Álamo and Soler, 2010a), have significant impacts on different breeding strategies. Studding these elements provides a range of critical natural history data that not only contributes to our understanding of nature but also helps to formulate general theories about patterns of life-history evolution.

Reproductive strategies of many northern hemisphere avian species are well known and have contributed significantly to the development of the life-history theory (Auer et al., 2007; Both et al., 2004b; Sutherland et al., 2004; Xiao et al., 2017). Although tropical and southern hemisphere birds include a large portion of the world's total avian diversity, the knowledge of their reproductive biology is still incomplete. In temperate regions with seasonal and predictable environmental conditions, breeding synchrony is common and breeding generally occurs in spring (Gilsenan et al., 2020; Jones, 1986; Wiersma et al., 2007b). In spring, longer days are required to initiate a cascade of neuroendocrine and endocrine processes in photoperiodic birds that lead to the development of gonads and the activation of breeding behaviours (Partecke et al., 2005). A study of free-living common blackbird populations, *Turdus merula* (hereafter, blackbird) proposes that blackbird urban populations have adapted to the rise of novel urban environments by developing their

gonads three weeks earlier in spring when compare to blackbirds that inhabit in forest areas (Partecke Jesko et al., 2004).

There is now substantial evidence from the last few decades that many songbirds respond to climate change by shifting their breeding synchrony (Møller et al., 2010). Climate change is also an important factor that influences nesting in bird species. It influences food availability and nest survival mediated by changing rainfall and temperature patterns (Fletcher and Koford, 2004; Ludvig et al., 1995; Meijer et al., 1999). In addition, other aspects of reproduction such as clutch size (Fletcher et al., 2013), incubation behaviour (DuRant et al., 2019) and parental investment (Wiley and Ridley, 2016) may be affected by climate change. Recent climate change leads to the mismatch between the timing of peak food supply and chick's demand in small insectivorous passerines. These small insectivores, parents expend more energy searching for food and this is reflected in their lower reproductive lifetime and reduction of nestling growth and survival of fledged chicks (Sanz et al., 2003). However, in some species reproductive timing can be flexible and, for these species, adapting to climate changes and anthropogenic modifications of environments is less problematic. Understanding species plasticity in life history and behavioural responses to changing environments is critical for assessing future impacts.

Scientists have often regarded behavioural variation at the level of intra-individual as "plasticity" (Ogden, 2012). Behavioural plasticity occurs in response to environmental challenges such as food availability, predators, competition, and mate choice. The above-mentioned factors influence an individual's growth and survival (Dingemanse et al., 2010; Mathot et al., 2012). Individuals adjust their behaviour to match environmental conditions (Gross, 1994). For example, black redstarts, *Phoenicurus ochruros*, recognise human disturbance as a predation risk. In response, they exhibit adaptive behavioural plasticity in nest-site selection associated with concealment (Chen et al., 2011). Researchers have argued that individuals do not show complete plasticity in their responses, and the term "personality" has arisen to explain both the consistency and repeatability of an individual's behavioural response across distinct contexts and over time (Burtt and Giltz, 1973; Pennisi, 2016; Roche et al., 2016). For example, male Southern masked weavers, *Ploceus velatus*, show a repeatable behaviour performance during building ring-nest phase (Walsh et al., 2011). In chestnut thrush, *Turdus rubrocanus*, bolder females may select nest sites with lower nest density, positively affecting the number of nestlings (Zhao et al., 2016).

Therefore, it is possible that personality and plasticity affect nest site-selection and may also indirectly affect reproductive success.

Habitat characteristics are another important set of factors (size, complexity, vegetation and patch type) that strongly impact the fitness of individual birds through varying resource quality and availability and breeding success (Møller, 1989). Some species select different patch types as their home range during their life as functional territories (Rotenberry and Wiens, 1980). In many bird species, size, shape, vegetation type and isolation of individual patch territories play important roles in nest-site selection (Gjerdrum et al., 2005; Kelleher and O'Halloran, 2006; Møller, 1989). Vegetation structure and type of habitat influence the availability of safe nesting sites and successful foraging for birds during their reproductive process (Holt et al., 2011). A study on nesting success in sharp-tailed, *Ammodramus caudacutus*, and seaside sparrows, *A*. *maritimus*, explains that successful nests occur in taller vegetation and species used a range of breeding strategies and nest-site selection to increase their reproductive success, for example, in response to habitat impacts like flooding (Gjerdrum et al., 2005). Understanding the characteristics of habitat is of critical importance for guiding the management of both invasive and vulnerable species.

Nest-site selection is a type of parental care characteristic of natural selection that is often driven by predation risk. This may play an important role in the breeding success of individuals (Ghalambor et al., 2013). In altricial birds, during the incubation and chick raising stages, parental activities are exposed for a long period (Gloutney and Clark, 1997). Several research studies on nest-site selection have demonstrated the impacts of height (Assandri et al., 2017), habitat complexity (coverage) (Tieleman et al., 2008; Wysocki, 2005), female age (Wysocki et al., 2015a) and environmental factors (James Reynolds et al., 2019) on nest placement. These factors are related to higher hatching success and reducing nest predation rate (Burton, 2006; Gjerdrum et al., 2005). Overall, selecting suitable nest placements may help pairs find food sources within territories and provide safe places to raise their chicks, leading to their breeding success (Liebezeit and George, 2002).

The design, shape and dimension of nests are specific in many bird species, from small elaborate nest cups constructed by passerines to the large mound nests built by megapods (Hansell, 2000). Hansell (2000) argued that there are specific genes whose phenotypic

expression leads to the specific architecture of nests. For example, studies on nest-building behaviour in sticklebacks, penduline tits, *Remiz pendulinus*, and barn swallows, *Hirundo rustica*, demonstrate significant potential for genetic control over nest building (Møller, 2006; Rushbrook et al., 2008; Schleicher et al., 2021a). Additionally, nest characteristics may be influenced by environmental factors. long-tailed tits, *Aegithalos caudatus*, adjust the mass of feathers incorporated into their nest materials with the nest's thermal environment (McGowan et al., 2004). Therefore, nest characteristics may reveal facts about the individual's ability under genetic control and can impact mate acquisition and nestling survival (Raventos, 2006; Rushbrook et al., 2008).

Predator pressure is one of the most significant selective factors in the evolution of fast growth rates in altricial bird species and it is also one of the primary causes of mortality in incubation and nestling states (Bosque and Bosque, 1995; Soler et al., 2015). Predators may identify nests either through visual signals (conspicuous nest) or auditory signals (chick calls) during the chick raising stage (Abudayah and Mathis, 2016; Ibáñez-Álamo et al., 2014; Kullberg and Lind, 2002; Rodriguez-Prieto et al., 2009). Although many species cover their nests, visual concealment may be insufficient because of chick noise (Haskell, 1994). A study on altricial birds in oceanic islands shows that open-nesting native birds take longer to hatch and fledge when compared to related species from continents, which is thought to be due to a relaxation of predation pressure (Bosque and Bosque, 1995). Studies suggest that there may be two strategies that individuals can apply in response to a high probability of nest predation. First, individuals increase their investment to protect the nesting attempt (Barash, 1975, 1980). Secondly, individuals reduce their investment (fewer eggs per clutch) in any one breeding attempt and use these resources for further nesting attempts (Lundberg, 1985). A reduction in clutch size may lead to decreasing nest dimensions; the time spent on building nests, and shortening of incubation and nestling periods (Cresswell, 1997).

Urbanisation represent a variety of fragmented natural areas exposed to urban pressures and provide novel environments, such as, parklands (Fernandez-Juricic and Jokimaki, 2001; Satge et al., 2019). Fragmentation, colonisation and growing novel areas have given rise to ”urban-positive” species (Stracey, 2011). This phenomenon has been observed for a variety of taxa and is particularly well documented in house sparrows (*Passe domesticus*), rock doves (*Columba livia domestica*), common starlings (*Sturnus vulgaris*) and common

blackbirds, all of which thrive in urban habitats (Ebenman and Karlsson, 1984; Kurucz; Mikula et al., 2014b). These urban "adapted birds" differ from urban "avoider birds" in many biological traits, such as, migratory behaviour (Bonnet-Lebrun et al., 2020; Rodewald and Shustack, 2008), nesting (James Reynolds et al., 2019), feeding habitat (e.g. feeding-table species; Croci et al., Galbraith et al., 2017), diet (Murray et al., 2018; Seress and Liker, 2015) and behavioural flexibility (Rodewald and Shustack, 2008; Sol et al., 2002). Urbanisation increases the frequency of occurrence of non-native birds that invade and successfully breed in cities by using food resources and occupying new ecological niches and survive in these environments (Davies et al., 2015; Ibáñez-Álamo and Soler, 2010b; Jokimäki et al., 2016, 2001).

The common blackbird, Linnaeus 1758, is one of the most common nesting birds now found throughout large parts of the world (Partecke et al., 2005; Wysocki, 2004). English colonists introduced this species to New Zealand between 1867 and 1879 (Hale and Briskie, 2007; Hatchwell et al., 1996). The common blackbird is a medium-sized thrush, belonging to the Turdidae family. Blackbird pairs are socially monogamous and stay on their territory year-round. However, the population in northern Europe migrates south in winter (Myers, 1955b; Snow, 1958b). Breeding season in the northern hemisphere starts approximately between March and April (Faivre et al., 2001b; Havlin, 1963; Jamriška et al., 2008; Tomialojć, 1993a; Wysocki et al., 2004). In the southern hemisphere in New Zealand, the breeding season occurs from August until early February (peaking in September to November) (Gurr, 1954; Williams, 2006a). During the breeding season, females build a bowl-shaped nest with grass, plastic bags, tissue, dead leaves, small twigs, moss, roots and mud in the forks of trees and shrubs (Biddle et al., 2015; Wysocki et al., 2015a). The female is reported to lay 2-6 eggs that are bluish-green with reddish to brown spots. Incubation takes 13-14 days. Chicks are blind and naked when hatched. Both parents feed the chicks. Chicks are fledged at 13-15 days and become independent at 28-31 days (Lu, 2005; Zeraoula et al., 2016, 2016).

Studies of the breeding ecology of common blackbirds have mostly concentrated in the tropics and temperate areas of the northern hemisphere (Europe, America, and Asia) (Jankowiak et al., 2014; Lu, 2005; Myers, 1955b; Osborne and Osborne, 1980; Selmi, 2007; Snow, 1958b; Weatherhead and Robertson, 1977; Wysocki et al., 2004). There are few studies recorded from the southern hemisphere (Australia and New Zealand) that examine

breeding ecology traits (Bull, 1946; Gurr, 1954; Kentish et al., 1995a). As a successful species that has occupied different ecosystems, blackbirds are an excellent model to study life-history evolution and breeding biology. The extensive research available on blackbirds around the world provides a comprehensive comparison of breeding biology between New Zealand, Europe, Asia, North Africa, and Australia. It also explains breeding variation related to invasion and colonisation.

In this chapter, I completed an in-depth investigation of the breeding biology of a blackbird population in New Zealand from 2017 to 2019. I presented an analysis of breeding biology in blackbirds by investigating three key objectives: 1- breeding biology and chronology, 2- nest characteristics and 3-parental provisioning in blackbirds.

My key questions concerning breeding biology and chronology were: 1) How do breeding activities vary across breeding seasons in blackbirds? 2) Are there significant differences in clutch size and breeding success between early and late nests? 3) What are the main causes of nest failure in blackbirds? 4) How does breeding length vary for blackbird pairs across years? 5) Are there significant differences in clutch size and breeding success between first and second clutches in pairs with more than two clutches? 6) How consistent is the duration of breeding activities within pairs across the study years? 7) How do nest height and urban modifications influence the breeding success of blackbird pairs? 8) How do blackbirds 'breeding characteristics vary across the world ?

I described the timing of blackbird breeding activities including nest building, incubation, and rearing chicks. I predicted that the blackbird clutch size would not change across the study years due to the length of the breeding season. Females would lay multiple clutches through a long breeding season. I expected that the number of fledglings per nest might change between the early and late seasons driven by varying predation pressure, weather conditions, food availability, and parental body condition. I also predicted the length of the breeding season within pairs would be moderately repeatable due to the consistent start of the breeding season and female physiological characteristics. In addition, I expected that predation would be a main cause of nest failure in blackbirds in early breeding season, while nest abandonment would be higher in late breeding season due to the variation of food availability. As blackbirds have been recorded to be a successfully adapted urban species, I also predicted that urban characteristics like roads would positively affect the breeding success or at least would not have a negative effect on the blackbird breeding.

Areas around the road have lower predation risks, be warmer and have greater food availability for birds living in cities.

Data from this study provide a comparative case study with other blackbird studies around the world. Multiple reasons influence the timing of breeding, clutch size, fledged size, incubation, and nestling durations. These factors include food source and quality, latitude, photoperiodic, parental care, bird density, and predator pressure. In this study, I explained the variation of breeding characteristics of blackbirds around the world and explained possible reasons for the variation of blackbird breeding characteristics in my research. I expected that the timing of breeding activities and clutch size in blackbirds who were located in the same latitude would be similar. Clutch size in blackbirds would also increase across the latitude due to daylight hours and food availability. The length of the breeding season in blackbirds varied across different countries because of food availability across the breeding season and weather parameters, such as declining rainfall and rising temperature, which affect food availability in the late breeding season.

Second, I addressed questions regarding the nest-site selection and nest structure: 1) How do nest dimension and nest-site selection vary in blackbirds? 2) What factors influence nest dimensions? 3) Do nest dimensions relate to nest-site selection? 4) How repeatable are nest-site selection and nest dimensions in female blackbirds? 5) are there correlations between nest characteristics in blackbirds ?

I described general variation of nest dimensions and nest- site selection in blackbirds of my study. And I expected that the female blackbirds vary nest structure dependent on the number of eggs laid. I also predicted nest dimensions would vary across the different breeding phases (from building until nestlings leave nests) depending on factors such as the weight of eggs, weight of the chicks, weight of the female and the movements of female and chicks in the nest. Nest dimensions were also expected to vary across the breeding phase because egg/ chick weights and female/chick movements would stretch the dimensions of the nest. I predicted that blackbird nest dimensions would vary with nest placement (proximity to trunk and height from ground). Nest-building includes the energy costs of collecting materials and building (Mainwaring & Hartley 2013); therefore, I predicted that building nests higher in trees is energetically more costly. Moreover, I predicted that nests located close to the road were located lower on the tree than nests located far from the road, because near the road the presence of predators may be lower. I

also hypothesised that nest characteristics such as nest dimensions, nest height, the distance of the nest from the main road and the distance of the nest from the trunk would be repeatable within the female blackbird population throughout the study.

Third, for parental provisioning, I investigated the following questions 1) How do nest visits vary between males and females within pairs and with different brood sizes and ages of chicks? 2) How do weather parameters affect the number of nest visits in blackbirds? 3) Are nest visits in blackbirds influenced by urban modifications and nest-site characteristics? I predicted that pair visits would depend on the number of chicks and the age of chicks in the nests. Male blackbirds would increase their participation in feeding chicks when there were a greater number of chicks in the nest. Nest visits would increase because of rising chick demands following the chick's age in the nest. I also expected that pairs would visit their nests more frequently when nests were located higher from the ground and/or closer to roads because these nests higher were more protected from predators. Moreover, I expected nest visits would be more in weeks (times) that the weekly rainfall is higher, due to increasing soil moisture and food availability (earthworms) .

2.3 Methodology

The study area was located on the North Shore of New Zealand's largest city; Auckland, with a population of approximately 1.5 million in 2017. Auckland is in a sub-tropical climate zone. Summers are warm and humid, and winters are mild. Typical summer temperatures vary from 22°C to 26°C and rarely exceed 30°C. Winter temperatures vary from 12°C to 17°C. The average annual sunshine is about 2000 hours in most areas. Summers are often warm and breezy. Winters are the most unsettled time of the year and are subject to frequent rainfall. Storms of tropical origin in summer and autumn bring high winds and heavy rain from the east or northeast (Sturman and Tapper, 2006). The area has a low topology and open vegetation provide extensive suitable habitat for blackbirds (Williams, 2006a).

My study was conducted on 53 blackbird pairs (34 banded pairs and 19 un-banded pairs) over 15 ha of Massey University Campus (Figure 2.3.1), Auckland, New Zealand. Approximately 7 pairs per hectare were living in the study area. The area consists mainly of open lands (lawns), bushes, green walls, and buildings. The low vegetation surroundings provide a range of potential nesting and brood-rearing locations. The open pastures afford extensive foraging areas and year-round food resources. The fieldwork was carried out each year from late July to late January. Breeding territories were identified by the presence of a blackbird pair that was observed continuously occupying the area each year. Breeding territories were identified by the presence of a pair and not by the presence of singing males.

Figure 2.3.1 Study area includes the Massey University campus and some areas around the campus (taken from Google earth). Blackbird territories were shown in the picture

2.3.1 Data collection

Measurements that were part of this study included: breeding characteristics (timing of breeding activities, reproductive measurements), nest characteristics, and parental provisioning.

2.3.1.1 Breeding Characteristics

I collected common blackbird breeding data between 2017 and 2020. The blackbird breeding activities began at the first observation of nest building and egg-laying activities and spanned from late July to late December (141 days in 2017, 26 July – 13 December; 137 days in 2018, 1 August – 12 December; and 153 days in 2019, 19 July – 22 December). Nesting activities were recorded by observing the blackbird pair behaviour on their territories every second day, searching for active nests in dense vegetation, and checking old nests from the previous season. Commencement of activities, such as nest building, incubation, and brooding, were recorded as exact dates. When the exact date was unknown, I assessed incubation and brooding time by backdating from known hatching and fledging dates (13 days incubation and 14 days brooding; Mayer-Gross 1974; Simms 1978). I recorded the timing of nesting and the outcome of each nest (failed, successful),

number of eggs per clutch (hereafter clutch size), brood size, fledgling number and pair identity (if banded). Clutch size, brood size and the number of fledglings were calculated using the same criteria as Snow (1955), Mayer-Gross (1972) and Marchant (1974).

I recorded clutch and brood sizes as the number of eggs/chicks recorded on two or more nest checks. I recorded the maximum number of eggs and chicks observed during nest checks, which allowed detecting reductions in clutch or brood. The number of fledglings was recorded as the number of chicks that left the nest after 12 days. Breeding success was the proportion of eggs that produced fledged chicks successfully. As a measure of nest success, I calculated the proportion of nests that successfully fledged at least one chick (Mayer-Gross 1972). Moreover, I recorded nest failure by recording the causes of nest failure: predated and abandoned nests. Nests were checked regularly, when I found a ruined or broken nest, broken eggs, blood on the nest and killed chicks or body parts of chicks around the nest, I recorded the nest's destiny as a predated nest. Based on my regular nest checking, when the female rejects sitting on the eggs and eggs got cold, or the male and female didn't visit their nest to feed the chick, I recorded the nest destiny as an abandoned nest.

Additionally, I estimated the length of breeding for pairs who had one or more than one clutch. The length of breeding per pair per season was defined as the difference between the first egg-laying date of the first clutch and the last egg-laying date of the last clutch for each blackbird pair (Jankowiak et al., 2014). To adjust days of the month for each year across different seasons, I considered one season's length to be from July 10 to December 30 (173days) and dates were modified to days from the start of the breeding season. I also collected daily weather data from the nearest weather station, Auckland, North Shore Albany EWS station (obtained from Cliflow; https://cliflo.niwa.co.nz/). Weather data included maximum temperature (°C), minimum temperature (°C) and precipitation (mm). Finally, to compare breeding characteristics of blackbirds (timing of breeding, clutch size, brood size, and nest success) in this study with blackbirds around the world, I used the extracted related data from published papers around the world with the distinct location of study sites.

2.3.1.2 Nest characteristics

I measured blackbird nest characteristics in two categories: nest dimensions and nest-site parameters (Figure 2.3.2). Nest dimensions were measured in three phases: 1- when

female built a nest entirely before egg laying started (built phase), 2- before chicks hatched at the nest, the second week of incubation (Incubated phase), and 3- when nestlings left the nest (fledged phase). In each stage, the nest dimensions were measured (three times) using a ruler while parents were not around the nest and where they were forging far and not been seen near the nest . Nest dimensions included internal diameter (D), thickness, internal nest depth, and external nest depth (Table 2.3.1). Additionally, nest-site parameters included nest height, trunk to the nest's centre and the distance of the nest from the road (Table 2.3.1).

Figure 2.3.2. Measuring a blackbird nest after chicks fledged from the nest (taken by Enzo M R Reyes).

2.3.1.3 Parental care

As a part of the study, I observed parental provisioning by blackbird pairs attending nestlings aged 3-10 days. The observation time was 30 minutes between 7 am and 4 pm.

Sample size per nest was per nest was 2 to 6 records. The observer positioned 15 m distance away from the nest and recorded the number of nest visits by paired blackbirds.

Table 2.3.1. Description of nest characteristics measured for determining nest features in the common blackbird.

Nest characteristics	Definition
Nest dimension	
Inner diameter	The average length and width of the inner nest-cup diameter (cm)
Thickness	The average thickness of the nest edges measured from four different sites of nest (cm)
Internal nest cup-depth	Internal nest-cup depth (cm)
External nest cup-depth	External nest-cup depth (cm)
Nest-site	
Nest height	The height of the nest (from the bottom of the nest) from the ground (m)
Trunk to the nest (TNC)	The distance between the main trunk to the nest centre (cm)
Distance from road	The closest distance of the nest to the edge of the nearest road. (m)

2.4 Statistical analysis

All statistical analyses were performed using R software version 4. 0. 4 (R Development Core Team 2020). Before starting analysis, all variables were tested for normality (Shapiro test). Analyses were conducted depending on normal/non-normal distributed data.

2.4.1 Breeding characteristics

I reported the blackbird breeding activities such as nest building, egg-laying, hatching and fledgling of nests during the breeding seasons from 2017 to 2019. I determined the variation of breeding activities across the breeding season. I also calculated the duration of nest building, incubation and chick rearing activities. Additionally, I calculated clutch size (number of eggs per clutch), number of chicks (brood size), number of fledglings, and nest success (number of nests that had fledged chicks/ total number of nests) across three breeding seasons. A Kruskal Wallis test was applied to compare clutch size, brood size and number of fledglings across years. I tested variation in clutch size and breeding success between early and late clutches with a Mann-Whitney U test (non-parametric data). I used the median dates of egg-laying to determine whether nests were early or late. The time periods were created based on the earliest and latest egg-laying dates and categorised as: Early = 10 August-27 September; Late = 28 September-13 December. Moreover, the proportion of nest failure and success were calculated. I also explained the causes of breeding failure (predation, abandonment and unknown) in different breeding stages (from building nest to fledged chicks). I used a Pearson correlation coefficient to investigate the variation of clutch size across different latitudes around the world .

I estimated variation of breeding length in pairs who had more than one clutch with a Generalised Linear Mixed Model (GLMM) using package *lme4* (Bolker et al., 2009; Knudson). To answer how breeding length varies within pairs, I excluded pairs with one breeding attempt in further analysis. I tested if the breeding length, first clutch date, and last clutch date varied across years. So, I created five models for response variables, including the length of breeding (hereafter breeding length), first clutch date, last clutch date, clutch size (number of eggs per clutch) and number of fledglings. I ran a Poisson distribution function for all GLMM response variables. In these models, the year was a fixed factor, and the pair identification was a random factor. Then I tested whether clutch size (number of eggs) and number of fledglings per nest varied between first and last clutches

and across years in blackbird pairs. In these two models, the clutch time (first/last) and year were fixed factors, and the pair identification was a random variable. Additionally, I estimated the repeatability of breeding length, the first clutch date, and the last clutch date in pairs across years using a repeatability analysis, "*rptR*" package (Stoffel et al., 2017). The response variables included breeding length, first and last clutch dates, and pair identification as a random variable in the models. This package used a GLM model with a log link. A "*rpt. poisson GLMM. Multi*" function was applied for the response variables.

I ran a Spearman's rank correlation analysis to assess the correlation between nest distance from the road and the number of fledged chicks per nest. I also used Spearman's rank correlation to estimate the link between nest height and the number of fledged chicks per nest.

2.4.2 Nest characteristics

I calculated all nest characteristics and presented them as mean ± SD. To test whether the common blackbird had a significant variation in the selection of plant species used for nest placement, a chi-square test was applied. To find out what factors influenced nest dimensions and nest characteristics, I investigated several factors including breeding phase, number of eggs per clutch, nest site characteristics and habitat characteristics.

First, I assessed how nest dimensions changed during different breeding phases (building, incubation, and fledged stages) using a repeated measure correlation. I applied a repeated measure correlation using the package "*rmcorr*" (Bakdash and Marusich, 2017). This statistical technique evaluates the common within-individual association for paired measures assessed two or more times for multiple individuals. In fact, *rmcorr* estimates the standard regression slope, the association shared among individuals. Second, I applied a linear correlation test (Spearman's rank and Pearson's r) to investigate if a female built her nest based on the number of eggs, she would subsequently lay in that nest. Hence, I used measurements of the nest dimensions before the female started laying eggs (building phase) to make sure other parameters such as the weight of the female, eggs, and chicks, and female and chicks' movements on the nest did not alter nest dimensions. Third, I applied the linear correlation analysis (Spearman's rank correlation or Pearson's correlation) to assess the links among nest characteristics. I included nest measurements from the incubation phase in the test because more data of nest dimensions were collected

during this phase. Finally, I estimated the repeatability of nest characteristics to answer how consistent nest-site section and nest dimensions are in females across the years (at least two nests per female) . Repeatability of nest-site characteristics was also assessed by *rptR* package (Stoffel et al., 2017). I included dimensions of the nest that were measured in the building or incubated phases. Continuous nest characteristic variables were analysed as Gaussian data in the repeatability model. Female identification was a random factor in the model.

2.4.3 Parental provisioning

I estimated the variation in nest visits using 30-minute observations, across years and between sexes. I also calculated the visitation ratio (female/male). First, I investigated the relationship between the visitation ratio (female/male) and the number of chicks at the nest with a Spearman's rank correlation. To assess the impact of different factors on the number of nest visits by individuals and pairs, I used a GLMM analysis using package lme4 (Kuznetsova et al., 2017; Nakagawa et al., 2017). Individual and pair identifications were included in all models as the random variables and the nest visit was the response variable. First, I investigated the variation of nest visits across the year, which was the fixed factor in the GLM model. Then I tested if there was variation in the nest visits between males and females (sex was the fixed factor). Since there was no sex-based difference in nest visits, hence I pooled these data in further analyses. I designed three final models. In the first model, I tested the variation of nest visits in relation to clutch size and age of chicks. To answer the impact of urbanisation, I created the second model of nest visits in relation to anthropogenic impacts: number of people passing withing 10 meter around the nest, the distance of the nest from the road, and the nest height from the ground as fixed factors. Finally, I ran a model with weather parameters (daily weather parameters: maximum temperature, minimum temperature, and rainfall) as the fixed factors to investigate the variation of the nest visits in relation to local environmental conditions.

2.5 Results

2.5.1 Breeding biology

2.5.1.1 Breeding characteristics

I observed breeding activities of blackbirds from late July to late December. The earliest nest-building activity was observed in the last week of July and the latest in early November. Egg-laying was recorded from early August to mid–December (125 days in 2017, 10 August–13 December; 115 days in 2018, 12 August–5 December; 99 days in 2019, 15 August–22 December). Peak nesting activities occurred in August, with peak nest building in early August. The number of nests built per female each season averaged 2.1 ± 0.1 (± SD) with a range from 1 to 6, and a median of 2 nests (N = 189 nests built by 89 females over three seasons). This number was slightly smaller than a report from Snow (1958) in British Botanic Gardens (N = 2.6 nests per female).

First egg and commencement of incubation occurred in early August (Figure 2.5.1). Nests were built over 3-10 days (mean ± SD: 6.1 ± 2.6 days, N = 80 nests). There was a minimum one day and maximum one month interval between nest building and first egg-laying (mean ± SD: 9.3 ± 6.1 days, N = 80 nests). Depending on clutch size, egg laying took place over 1-4 days. The first peak of egg laying was observed in late August and there was a second, smaller peak in egg laying and incubation in early October (Figure 2.5.1). A total of 619 eggs from 214 nests were recorded (Table 2.5.1). The incubation period lasted from 11 to 16 days; the mean (± SD) was 13.5 ± 0.8, N = 113 nests and a mode of 14 days. The first nest to hatch was recorded in late August and the peak hatch frequency was observed in early September. Clutch size ranged between 1 and 4 eggs (mean ± SE = 2.9 ± 0.04; median = 3, Table 2.5.1). The clutch size measured over three years was not significantly different (Kruskal Wallis test, $\chi^2 = 1.2 \pm 6$, df = 2, $p = 0.5$, Table 2.5.1). Brood raising lasted between 12 and 17 days and a mode of 14 days; the mean (± SD) was 14.2 ± 1.1, N = 114 nests. The first fledglings were recorded in early September, with a peak in late September and a second peak in November (Figure 2.5.1). Only one nest had chicks who left the nest later than 19 days after hatching. Breeding activities ended in late December. Egg laying was only recorded from two nests in December.

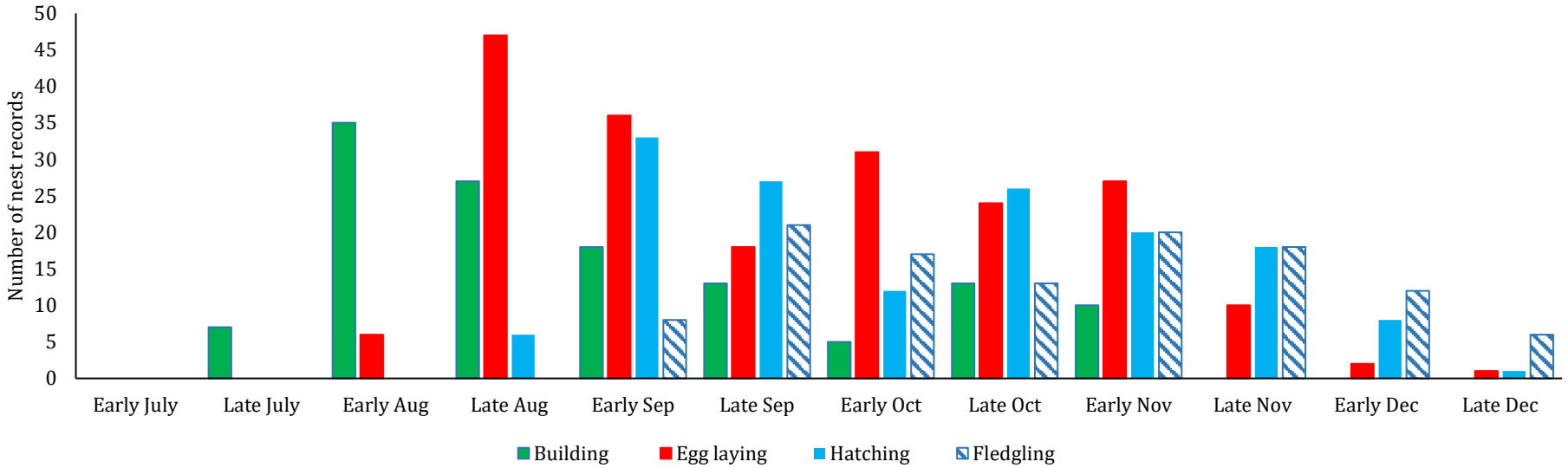

Figure 2.5.1. Breeding chronology of common blackbird in the area between 2017 and 2019. Presenting the number of nests in half- monthly periods.

Table 2.5.1. Mean clutch, brood, number of fledglings, and outcome of breeding success for common blackbird between 2017 and 2019.

Year	**Clutch size**			**Brood size**			**Fledgling number**			**Breeding success**	**Apparent nest success**	
	Total no. Egg/nest	Mean	SE	Chick/nest	Mean	SE	Fledgling/nest	Mean	SE	Fledgling/egg	n	%
2017	213/74	2.9	0.07	151/57	2.6	0.09	119/45	2.6	0.1	0.5	45	60.9
2018	226/75	3 0	0.04	133/51	2.6	0.09	93/39	2.4	0.1	0.4	39	52.0
2019	181/64	2.8	0.09	119/45	2.6	0.08	82/33	2.5	0.1	0.4	33	51.0
Total	619/214	2.9	0.04	403/153	2.6	0.05	294/117	2.5	0.07	0.4	117	54.7

The egg laying dates of 214 nests (619 eggs) were identified to estimate the variation of clutch sizes between early and late clutches. Clutch size did not differ between early (mean ± SE = 2.9 ± 0.06) and late (mean ± SE = 2.9 ± 0.07) seasons (Mann-Whitney U Test: W = 4826, $p = 0.3$). In addition, a total of 403 chicks hatched from 153 nests. The mean brood size (± SE) was 2.6 ± 0.05, (Mode = 3, range = 1-4, Table 2.5.1). Brood size did not vary across years (Kruskal Wallis test, $\chi^2 = 0.25$, df= 2, $p = 0.8$; Table 2.5.1). Moreover, 294 fledged chicks were recorded from 117 nests (mean ± SE = 2.50 ± 0.07, Mode = 3). Fledgling number did not significantly vary across years (Kruskal Wallis test, $\chi^2 = 3.31$, df = 2, $p = 0.19$).

2.5.1.2 Comparison with other studies

I compared the current study with data from different countries (Table 2.5.2). Records from the southern hemisphere (Bull, 1946; Gurr, 1954; Kentish et al., 1995, Niethammer, 1970) revealed a two-week shift in egg laying dates from late August (New Zealand and Australia) to early August in the current study. In addition, the breeding season in the Australia study ended later (from late August to late January), while the breeding season ends late December in New Zealand(Gurr, 1954; Bull, 1946 and current study). Reports from the northern hemisphere show that the breeding season generally starts in March and ends in July (Table 2.5.2). The longest breeding seasons were reported from South England and France (6 months, Table 2.5.2) (Grégoire et al., 2003; Myers, 1955b); whereas the shortest breeding seasons were reported from Tibet (3 months) and Scotland (3.5 months)(Cresswell, 1997; Lu, 2005).

In my study, nest building took approximately 6 days (3-10 days), similar to those reports from Slovakia (6.8 days) and China (7-9 days) (Wu and Li, 1984 in Lu, 2005). The incubation period in blackbirds from around the world was 13 to 14 days (Table 2.5.2). In addition, nestlings commonly stay in the nest for 14 days. Nestling period in Algeria (15.7 days; Zeraoula et al., 2016) and Tibet (16-18 days, Lu, 2005) was longer than in this study, while the report from Spain (10 days, Ibáñez-Álamo and Soler, 2010) was shorter than the current study (Table 2.5.2). The largest clutch sizes were recorded from Slovakia (Jamriška et al., 2008), Shetland in the UK (Venables & Venables, 1952) and Belgium (Verheyen in Snow, 1955) (Table 2.5.2). The mean clutch size in my study was similar to ones recorded from Tibet (Lu, 2005) and Algeria (Zeraoula et al., 2016), but slightly lower than one reported from Australia (Kentish et al., 1995) and other studies from New Zealand (Bull, 1946; Gurr 1954) (Table 2.5.2). There was a strong correlation between increasing latitude and clutch size in blackbirds (Pearson's r = 0.8, p = 0.001*, Figure 2.5.2). Brood size from the current study was smaller than those reported from

UK/Shetland (Venables & Venables, 1952), Australia (Kentish et al., 1995) and Czechoslovakia (Havlin, 1963) (Table 2.5.2). The brood size from my study was comparable to those reported from Spain (Ibáñez-Álamo and Soler, 2010).

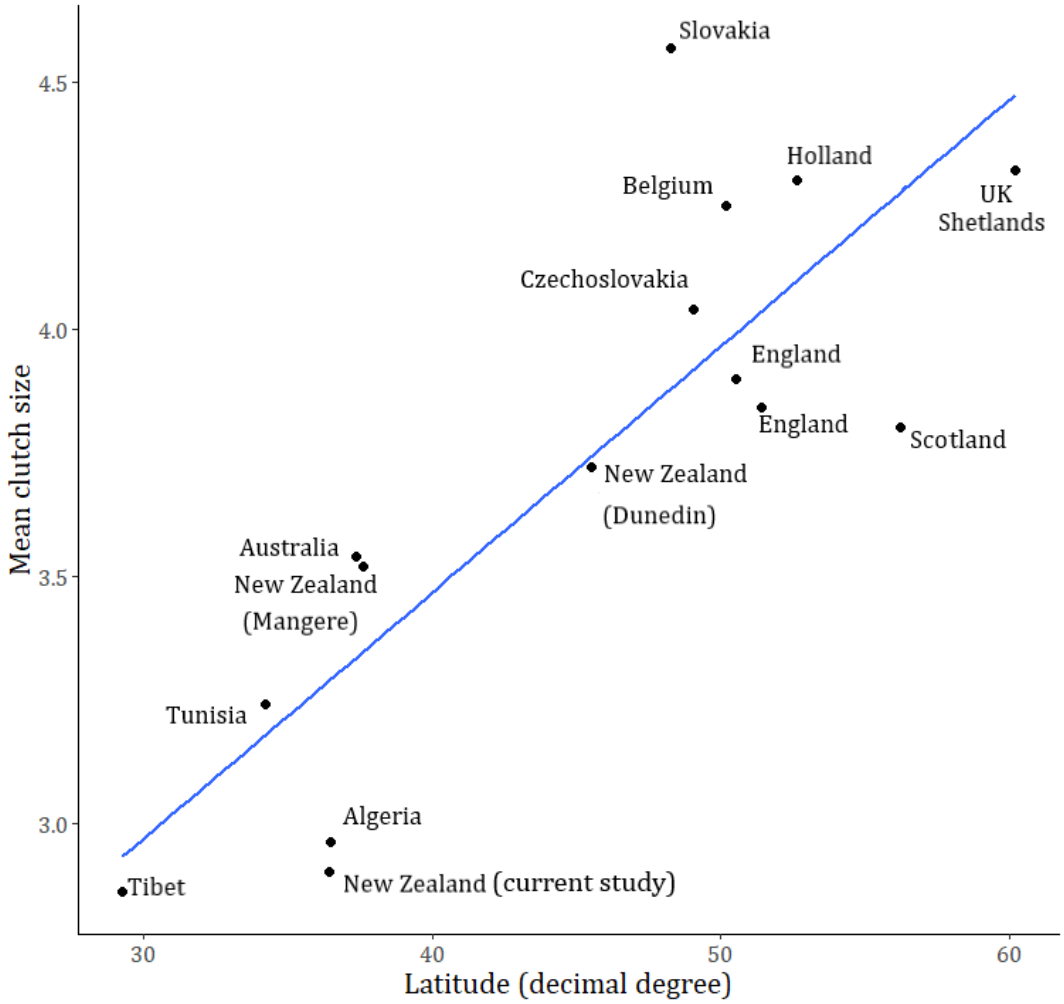

Figure 2.5.2. Correlation between blackbird clutch size and latitude (Pearson's r = 0.8, *p* = 0.001*) from 15 different studies around the world. A significance level of p ≤ 0.05 is shown by an asterisk (*).

Table 2.5.2. Comparison of breeding activates of blackbirds from different countries in endemic and introduced distribution.

Country	latitude	longitude	Nest (N)	Clutch size	Brood size	Nest success(%)	Breeding season	Reference
Algeria	36°49'N	7°45'E	130	3	-	65.4	Mid-March, Mi-Jun	Zeraoula et al., 2016
Australia	37°36'S	145°1'E	612	3.5	3.1	41.4	Late-Aug, Late-Jan	Kentish et al., 1995
Belgium	50°20'N	4°27'E	450	4.6	-	61	-	Verheyen, 1953 in Snow,1955
Czechoslovakia	49°06'N	17°70'W	-	4.0	3.7	65.7	-	Havlin, 1963 in Kentish et al., 1995
Slovakia	48°3'N	17°7'E	7	4.6	2-3	-	-	Jamriška et al., 2008
Holland	52°7'N	5°17'E	981	4.3	-	-	-	Lack 1949 in Venables 1952
New Zealand	37° 6'S	174°48'E	60	3.5	-	-	Late-Aug, Late-Dec	Bull, 1946
New Zealand	45°52'S	170°30'E	38	3.7	-	-	Late-Aug, Late-Dec	Gurr, 1954
New Zealand	36°44'S	174°41'E	214	2.9	2.6	54.7	Early-Aug, Late-Dec	Current study
Scotland	56°25'N	4°10'W	145	3.8	-	62	Mid-Mar, Late-Jun	(Cresswell, 1997)
Tibet	29°27'N	91°40'E	40	2.8	2.3	59	Early-May, Late-Jul	Lu, 2005
Tunisia	29°27'N	91°40'E	66	3.2	-	44	Mid-Mar	Selmi, 2007
England (South)	50°53'N	1°14'W	673	3.7	-	-	Late-Feb, Late-Jul	Myer, 1955
England (North)	51°45'N	1°15'W	347	3.9	3.3	-	Early-Mar, Late-Jun	Snow, 1958
UK/Shetlands	60°22'N	1°15'W	117	4.3	-	-	Late-Feb, late-July	Venables & Venables, 1 952
Spain	37°59'N	3°59'W	209	-	2.7	49.5	Early-Mar, Early-Jul	Ibáñez-Álamo and Soler, 2010

2.5.1.3 Breeding outcome (success/failure)

Nest success was reported as 54.7% (Table 2.5.1) in my study. Worldwide, the highest apparent nest success is reported from Czechoslovakia (forest: 69% and urban: 62.5%; Havlin; 1963 in Kentish et al., 1995), Algeria (orchard: 65.4%, N = 130 nests; Zeraoula et al., 2016), Scotland (park: 62%, N = 145; Venables & Venables, 1 952) and Belgium (unknown: 61%, N = 750 nests; Verheyen, 1953 in Snow,1955). Nest success report from my study (urban: 54.7%, N = 214 nests) was similar to the reports from Spain (urban: 53%, n= 58 nests; Ibáñez-Álamo and Soler, 2010) and England (garden: 50%, N = 222 nests; Snow, 1958). Australia (urban: 43.5%; woodland: 45 %; N = 612; Kentish et al., 1995), Hungary (urban park: 44 %, N = 136 nests; Moskat et al., 2003), Tunisia (oases, 44%, N = 66 nests; Selmi, 2007), North England (unknown: 41%, N = 1428 nests; Snow, 1955) and New Zealand (South Island: 33%, N = 96 nests; Niethammer, 1970; 37-41%; van Heezik et al. 2008) have a lower nest success compared with my study. The lowest percentage of nest success is reported from, Spain (woodland, 17%, N = 87 nests; Ibáñez-Álamo and Soler, 2010) and the United Kingdom (woodland: 14 %, N = unknown; Snow, 1958 in Kentish et al., 1995; urban, 13%, N = unknown; Groom, 1993).

In my study, most breeding failures occurred during incubation (23.5%, Table 2.5.3). 14.3% of nests failed before females laid eggs, and 15.1% of total nests failed during chick rearing (Table 2.5.3). In this population,36 nests failed before laying eggs and 97 breeding attempts failed after the female laid the egg. The most common cause of failure during incubation was abandonment (37.1%, Table 2.5.4), while during chick raising, the main cause of failure was predation (24.7%, Table 2.5.4).

Table 2.5.3. Overall breeding outcomes for the Albany blackbird population.

Nest fate	Stage	Number of nests	%
Failed	Pre egg laying	36	14.3
	incubation	59	23.5
	nestling	38	15.1
	Total	133	53.2
Successful		117	46.8
All nests		250	100

In total, 60.9% of failed nests happened during the incubation period and 39.1% during the nestling stage (exclude the number of nests failed in per egg laying stage, Table 2.5.4). Similar to a report from Algeria, 62.9% of nest failure was reported during the incubation period and 37.1% was recorded in the nestling stage (Zeraoula et al., 2016).

Table 2.5.4. Causes of reproductive failure in blackbirds in the study area 2017-2019

Nest stage	Cause of failure	No. of nests (%)	No. of nests per year			No. of eggs/chicks
			2017	2018	2019	
Incubation	Abandonment	36 (37.1)	12	13	11	94 eggs
	Predation	21 (21.6)	4	10	7	50 eggs
	Unknown	2 (1.0)	2	-	-	-
Total		59 (60.9)	18	23	18	144
Nestling	Abandonment	13 (13.4)	1	9	3	36 chicks
	Predation	24 (24.7)	10	3	11	64 chicks
	Unknown	1 (1.1)	-	-	-	-
Total		38 (39.1)	11	11	14	100

Figure 2.5.3 shows the variation of nest failure across the breeding season. Nest abandonment increased gradually from August to November and declined in December (Figure 2.5.3. A). Nest predation had the highest peak in September, with a second peak occurring in November (Figure 2.5.3. A and B). Predation earlier in the breeding season increased (Figure 2.5.3) during the peak egg-laying and hatching in late August and September (Figure 2.5.1). During incubation, abandonment was the main cause of nest failure, while during chick raising, predation was the main cause of nest failure (Figure 2.5.3).

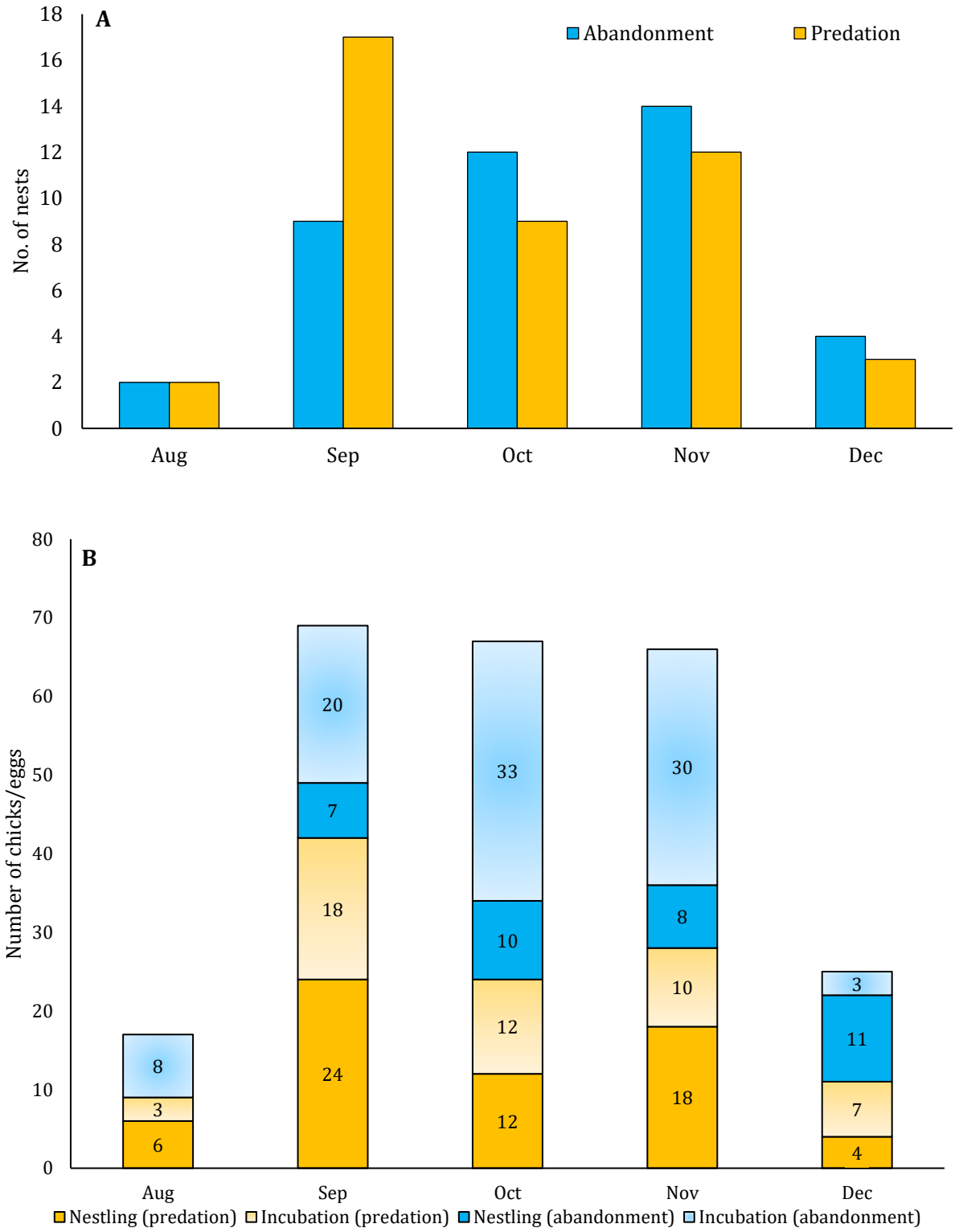

Figure 2.5.3. Causes of nest failure. A) Frequency of nest failure across the breeding season. B) A total of the number of chick and egg failures per month across the breeding season.

2.5.1.4 Variation of breeding length within blackbird pairs

Sixty-seven blackbird pairs at my study site had more than one breeding attempt per season during three consecutive years and 12 pairs had only one breeding attempt from 2017 to 2019. The average length of breeding per pair per season was 54.7 ± 2.1 days (mean ± SE) and ranged 5-125 days (median = 56) (Table 2.5.5). GLMM analysis revealed that the date of the first clutch date did not differ across years in blackbird pairs, whereas the last clutch date and breeding length (BL) varied across years of study (Table 2.5.5 and Table 2.5.6). Although the first clutch size declined from 3.0 to 2.6 across the three years, there was no significant variation in the first clutch size across the years (Table 2.5.6). The last clutch dates significantly occurred later in 2018 (31 October), compared with the last clutch dates from 2017 (20 October) and 2019 (23 October) (Table 2.5.6). In addition, the length of the breeding season in 2018 was significantly longer than years 2017 and 2019 (Table 2.5.6). There was also no difference between first clutch size and last clutch size within pairs (Table 2.5.6). Moreover, GLMM analysis showed that the number of fledged chicks per nest differed significantly between the first and the last clutches and across the years. The last clutch had a greater number of fledged chicks than the first clutch (Table 2.5.5 and Table 2.5.6).

Table 2.5.5. Summary statistics (mean ± SE) of variation in clutch size (CS), fledgling number per nest (FN), first and last clutch dates, and breeding length (BL) within blackbird pairs. Significant variations are indicated with an asterisk (*).

Year	Pairs	First clutch order			Last clutch order			
	N	Day	CS	FN*	Day*	CS	FN*	BL*
2017	23	21.8 ± 2.2	3.0 ± 0.9	1.6 ± 0.3	71.5 ± 4.0	3.0 ± 0.1	2.3 ± 0.3	49.7 ± 5.1
		1 Sep			20 Oct			
2018	24	22.4 ± 3.0	2.9 ± 0.1	1.2 ± 0.3	83.1 ± 4.3	3 .0 ± 0.1	1.7 ± 0.3	60.7 ± 5
		2 Sep			31 Oct			
2019	20	22.7 ± 4.1	2.6 ± 0.1	1.0 ± 0.3	75.1 ± 5.0	3 ± 0.2	1.1 ± 0.3	53.1 ± 5.1
		2 Sep			23 Oct			
Total	67	22.3 ± 1.8	2.9 ± 0.1	1.3 ± 0.1	76.9 ± 2.6	2.9 ± 0.1	1.8 ± 0.2	54.7 ± 2.9
		2 Sep			25 Oct			

The number of fledged chicks also declined from 2017 to 2019 in both first and second clutches. When I included pairs, who had one breeding attempt, the length of breeding season per pair was 45.7 ± 29.3 days (mean ± SD). A study in Poland (Jankowiak et al., 2014) showed that the length of the breeding season in blackbird pairs is 38 ± 11 days (mean ± SD), which is shorter than my current findings.

Table 2.5.6. Results of generalized linear models comparing response variables across the study years. Significant effects are indicated with an asterisk (*).

Response variable	Estimate	ES	SE	z	*p*
First clutch date	Intercept	3.0	0.10	28.4	≤ 0.001*
AIC=592	Year: 2018	0.04	0.1	0.6	0.6
	Year: 2019	0.2	0.1	1.9	0.06
Last clutch date	Intercept	4.2	0.1	82.1	≤ 0.001*
AIC=709	Year: 2018	0.2	0.04	5.3	≤ 0.001*
	Year: 2019	0.1	0.04	1.2	0.2
Length	Intercept	3.7	0.1	41.2	≤ 0.001*
AIC = 724	Year: 2018	0.3	0.1	6.0	≤ 0.001*
	Year: 2019	0.02	0.05	0.1	0.1
Clutch size	Intercept	1.1	0.1	11.0	≤ 0.001*
AIC= 421	Clutch time	0.01	0.1	0.1	0.9
	Year: 2018	-0.01	0.1	-0.1	0.9
	Year: 2019	-0.1	0.1	-0.9	0.4
Fledged size	Intercept	0.4	0.2	2.5	0.01*
AIC= 422	Clutch time	0.3	0.1	2.1	0.03*
	Year: 2018	-0.3	0.2	-1.5	0.1
	Year: 2019	-0.6	0.2	-2.9	≤ 0.001*

2.5.1.5 The consistency of breeding characteristics

In my repeatability analysis, I found that the first clutch date was significantly repeatable (R = 0.45, p = 0.01*) within blackbird pairs. However, the length of the breeding season and the last clutch date were not repeatable (Table 2.5.7).

Table2.5.7. Repeatability of breeding season variables within 67 blackbird pairs. Significant values are indicated with an asterisk (*).

Response variables	R	CI	*p*
First clutch date	0.45	0.2, 0.7	0.01*
Last Clutch date	0.00	0.0, 0.1	0.50
Breeding length	0.39	0.0, 0.7	0.10

2.5.1.6 Urban modification and nest placement

There was no correlation between nest height and number of fledged chicks per nest (Spearman's rank correlation: r = 0.7, p = 0.4, N = 167nests). I found a negative correlation between the nest distance from the road and the number of fledglings per nest (Spearman's rank correlation: r = -0.3, $p \leq 0.001$*, N = 181 nests, Figure 2.5.4).

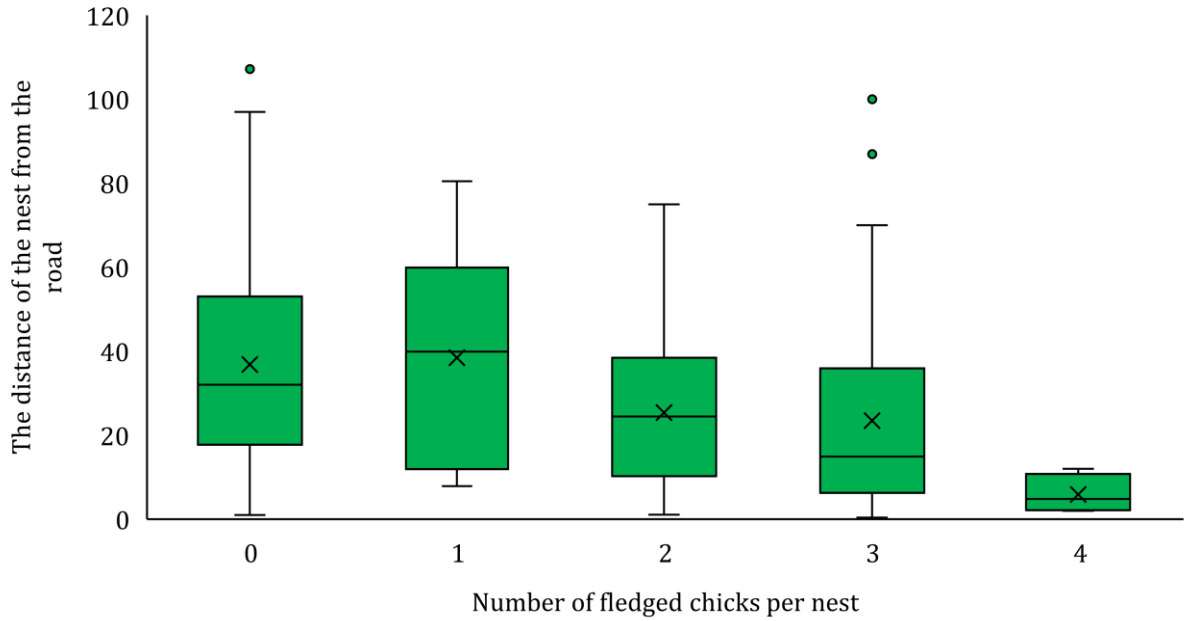

Figure 2.5.4. Variation in nest distance from the road in relation to the number of fledged chicks per nest in blackbirds (Spearman's rank correlation: r = 0.3, $p \leq 0.001$*, Number of nests: 0 fledged chick = 84 nets, 1 fledged chick= 9 nests, 2 = 37 nests, 3 fledged chicks = 48 nets, 4 fledged chicks = 4 nests).

I tested if there was variation between breeding outcomes (abandonment, predated, and successful nests) depending on nest placement using a Kruskal Wallis test. I found no significant variation between different breeding outcomes and nest height (Kruskal Wallis test: $\chi^2 = 0.2$, df = 2, $p = 0.9$, N = 186, table 2.5.8). In addition, I found that there were higher proportions of successful nests closer to the road compared to greater distances from the road (Kruskal Wallis test: $\chi^2 = 12.7$, df = 2, $p = 0.001$**, N = 239 nests, table 2.5.8, Figure 2.5.5). I did not find significant correlations between breeding outcomes and other nest characteristics.

Table 2.5.8. Variation in the nest height and nest distance from the road regarding different breeding outcomes.

Nest characters	Nest	Abandonment	Nest	Predated	Nest	Successful
Nest height (m)	38	1.9 ± 0.1	42	1.9 ± 0.1	106	1.9 ± 0.1
Road (m)	44	23.03 ± 3.0	46	38.2 ± 4.0	111	25.0 ± 1.0

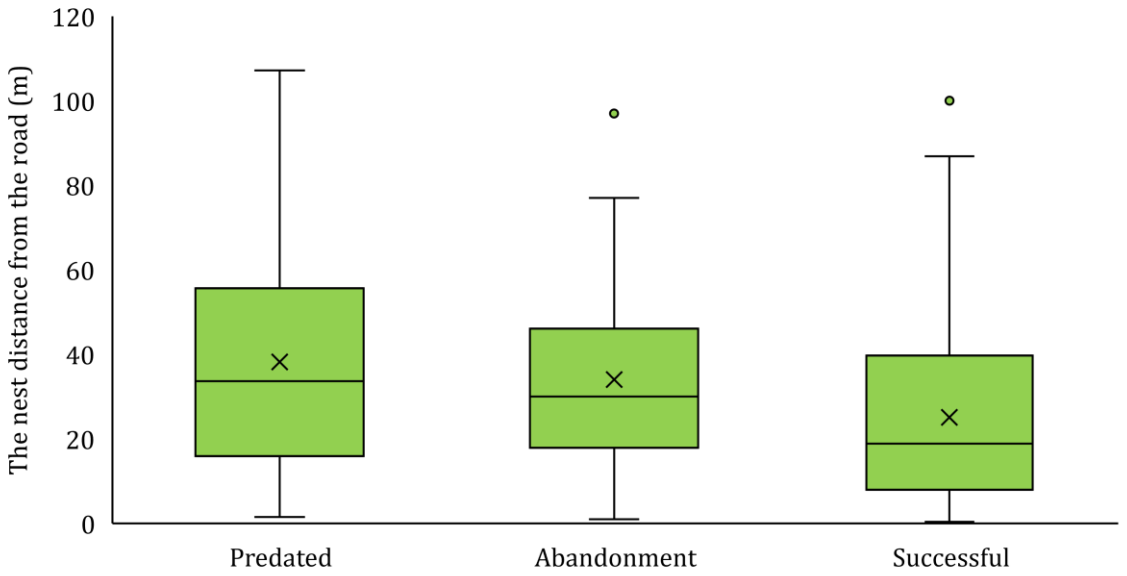

Figure 2.5.5. Variation in nest distance from the road in relation to breeding outcomes among 105 nests (Kruskal Wallis test: $\chi^2 = 7.43$, df = 2, $p = 0.02$, N = 46 predated nest, N = 78 abandoned nests, and N = 111 successful nests).**

2.5.2 Nest characteristics

2.5.2.1 General nest characteristics

Blackbird nests were built in trees, shrubs, and on buildings. General nest characteristics included nest dimensions and nest-site measurements that I present in Table 2.5.9.

Table 2.5.9. Mean ± SD values of the nest characteristics of blackbird nest.

Characteristics	Number of nests	Mean ± SD (cm)	Max	Min
Inner nest diameter (cm)	68	10.6 ± 0.7	12.1	8.8
Thickness (cm)	63	1.9 ± 0.6	4.0	0.5
Internal depth (cm)	67	6.7 ± 1.0	8.8	4.2
External depth (cm)	68	12.5 ± 2.8	19.2	6.4
Trunk to the nest (cm)	106	51.1 ± 62.5	270	0
Nest height from ground (m)	172	2.1 ± 1.1	7	0.6
Distance from road (m)	219	30.7 ± 24.2	107.2	0.4

Blackbird nest diameter (D) in New Zealand were similar to those reported from Ukraine (D = 10.7 cm, n = 25 nests, Kucherenko and Ivanovskaya, 2020). The internal nest depth in the current study was only slightly larger than the report from Ukraine (internal depth = 6 cm, n = 25) (Kucherenko and Ivanovskaya, 2020). In addition, the nest height in the current study was higher than the nest height above ground of blackbirds in Ukraine and Spain (Ukraine = 1.76 m, n = 61 nests; Spain = 1.34, n = 84 nests)(Kucherenko and Ivanovskaya, 2020; Taberner et al., 2012).

Plant species

In terms of nest site selection, the most recorded plant used by blackbirds to build their nests on were *Coprosma, Camellia japonica, Podocarpus totara, Melaleuca alternifolia, Viburnum tinus* and *Myrsine australis.* There was no significant variation between years in the type of plant that was selected for the nest site (Fisher's exact test $p = 0.67$; Table 23, see Appendix 2.5.1 for more information).

2.5.2.2 Factors influencing nest dimensions

Breeding phase

Table 2.5.10 shows variation in blackbird nest dimensions during three breeding phases (built, incubation, and fledged phases). The internal nest diameters ranged from 10 cm in the building stage to 10.6 cm when nestlings left the nest (Figure 2.5.6.A). The thickness of nest edges decreased from 2.1 cm in the built and incubation phases to 1.8 cm after nestlings fledged the nest (Figure 2.5.6.B). In addition, the internal nest depths decreased from 7.2 cm in the building stage to 6.3 cm in the incubation phase and when nestlings left the nest, it increased to 6.7 cm (Figure 2.5.6.C). The external depths of nest cup gradually decreased from 13 cm from the built phase to 12.5 cm when the nestlings left the nests (Figure 2.5.6.D).

Table 2.5.10. Variation in nest dimensions for different breeding phases (mean ± SE). Results from repeated measures correlation show the significant variation in nest dimensions across the breeding attempts. Significant values are indicated with an asterisk (*).

phase	N	Diameter	Thickness	Int-depth	Ext-depth
Built	36	10.1 ± 0.1	2.1 ± 0.1	7.2 ± 0.2	13.1 ± 0.5
Incubation	81	10.0 ± 0.1	2.0 ± 0.1	6.3 ± 0.1	12.9 ± 0.3
Fledged	74	10.6 ± 0.1	1.7 ± 0.1	6.7 ± 0.1	12.5 ± 0.3
Repeated measure correlation					
r		0.3	-0.4	-0.4	-0.4
df		65	65	62	62
p		0.01*	0.001*	0.002*	0.002*

Clutch size

I investigated the linear correlation between nest dimensions and different clutch sizes of 33 blackbird nests from the built phase. I did not find a significant correlation between the internal nest diameter and different clutch sizes (Pearson's correlation: r = 0.2, 0.33, Table 2.5.11 and Figure 2.5.7. A). Nest thickness was thicker in nests with more eggs (Pearson's correlation: r = 0.4, p ≤ 0.008*, Table 2.5.10 and Figure 2.5.7.B). There was no relationship between internal nest depth and different clutch sizes (Pearson's

correlation: r = 0.2, *p* = 0.2, Table 2.5.12 and Figure 2.5.7.C). External nest depth increased in nests with a greater number of eggs (Pearson's r = 0.34 *p* = 0.04*, Table 2.5.12 and Figure 2.5.7. D).

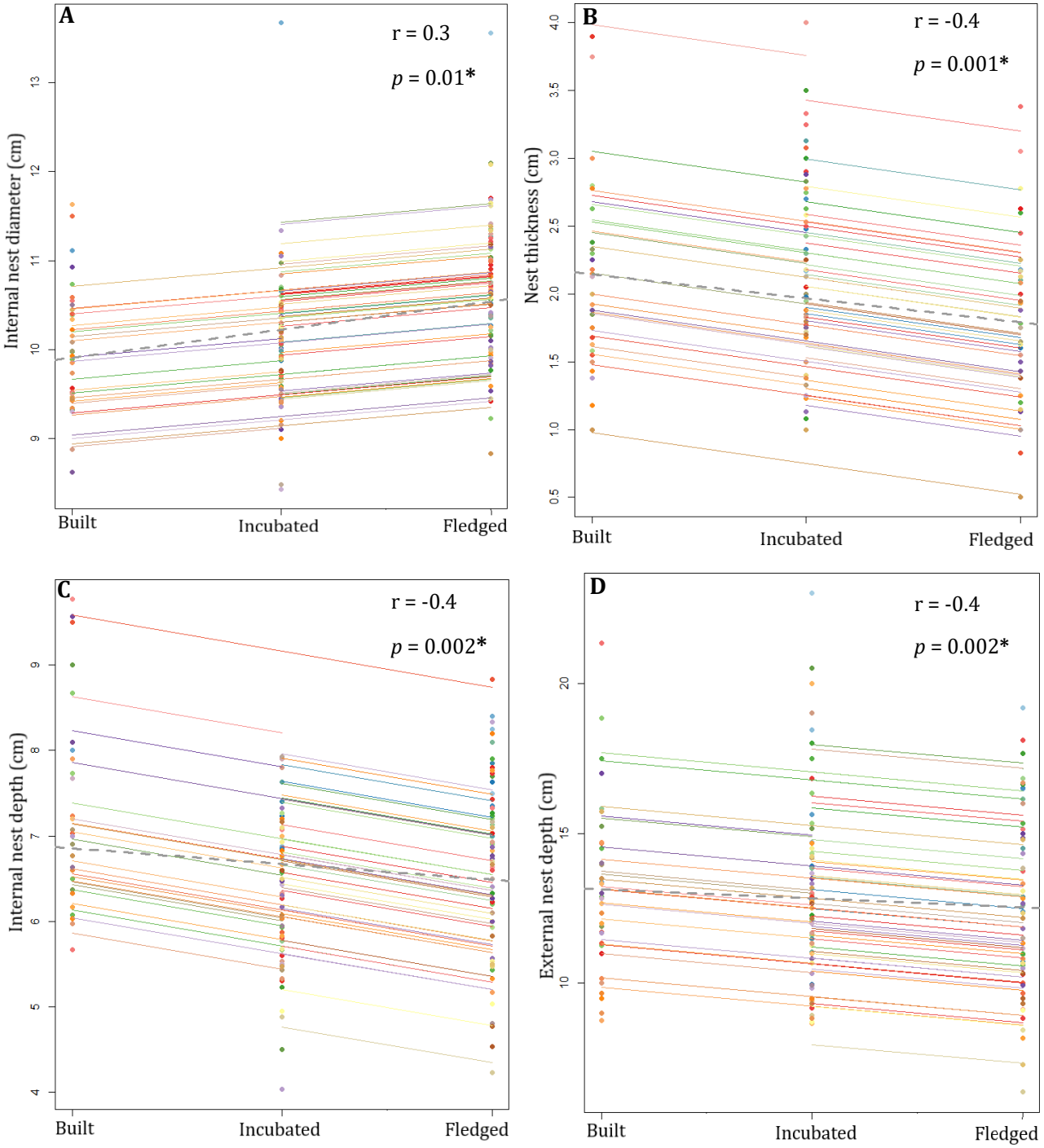

Figure 2.5.6. Variation in nest dimensions across the breeding phases (built = 36 nests, incubated = 81 nests, fledged = 74 nests). Results from a repeated measure correlation also presented. Significant correlations are indicated with an asterisk (*).

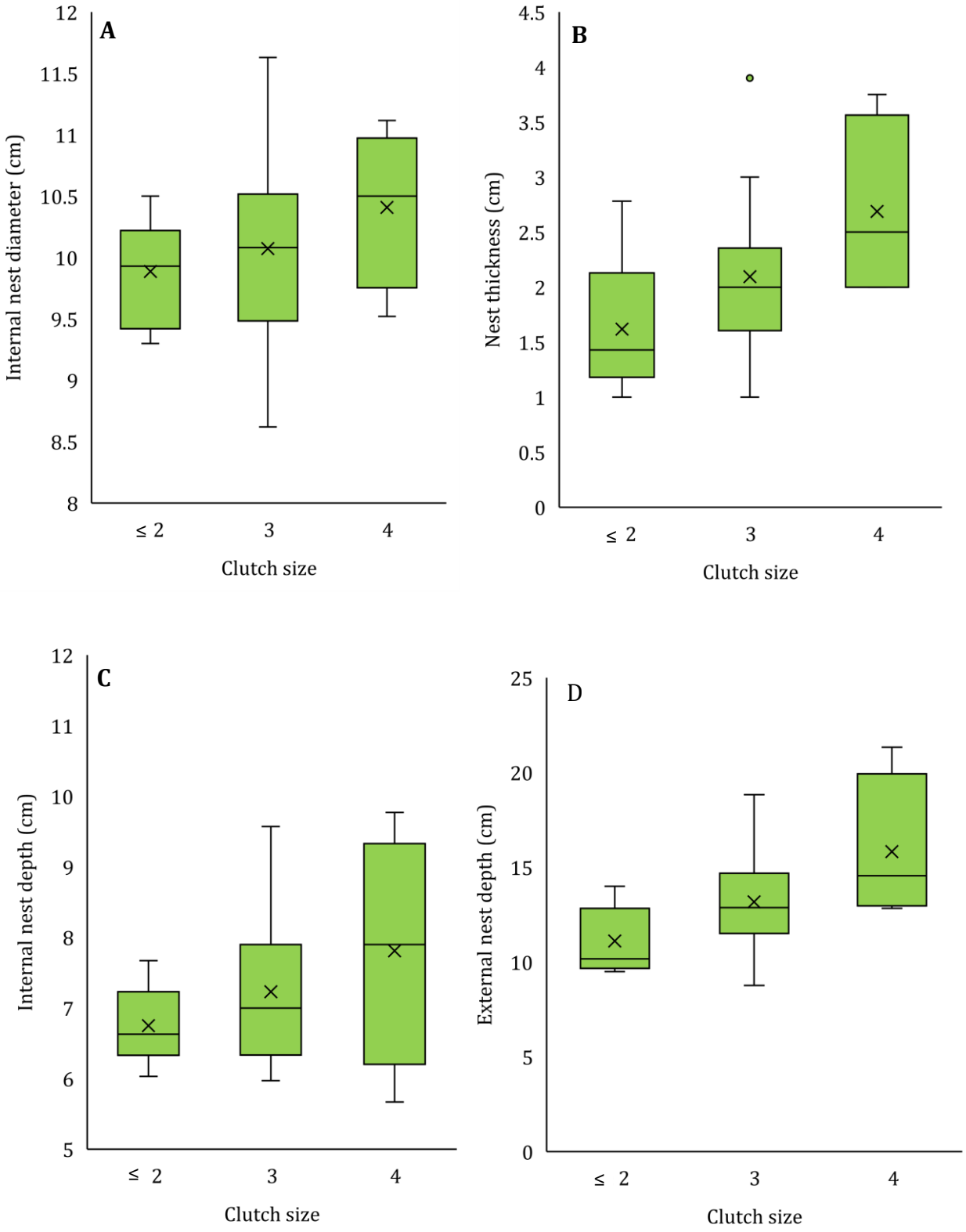

Figure 2.5.7. Variation in the nest dimensions (A = internal nest diameter, B = nest thickness, C = internal nest depth, and D = external nest depth) measured in relation to the different number of clutch sizes (≤ 2 eggs = 4 nests, 3 eggs = 25 nests, 4 eggs = 4 nests). Significant correlations are indicated with an asterisk (*).

Table 2.5.11. Variation in nest dimensions in relation to different clutch sizes (mean ± SE). Significant variations are indicated with an asterisk (*).

Eggs	N	Diameter	Thickness*	Int-depth	Ext-Depth*
≤ 2	4	9.9 ± 0.2	1.4 ± 0.2	6.7 ± 0.3	12 ± 0.1
3	25	10.1 ± 0.1	2.1 ± 0.6	7.2 ± 0.2	13.2 ± 0.5
4	4	10.4 ± 0.3	2.7 ± 0.8	7.8 ± 0.9	15.8 ±1.94

Relationship between nest dimensions and nest-site characteristics

My Spearman's rank correlation results showed a negative correlation between the nest diameter and the nest height (r = -0.2, p = 0.03*). Additionally, nests located higher from the ground were located further from the main trunk (r = -0.3, $p \leq 0.001$*). In addition, nests located near the road were higher from the ground (r = -0.3, p = 0.02*). Although these correlations were significant, they were weak. Furthermore, the correlations between other nest characteristics were not significant (refer to Appendix 2.5.2 for more details).

Consistency of nest characteristics in blackbird females

The thickness of nest edges was low repeatable (R = 0.3, Table 2.5.11). Nest height (R = 0.23) and the distance of the nest from the trunk (R = 0.32) showed low repeatable estimations (Table 2.5.12). The nest distance from the road was also highly repeatable in females (table 2.5.12).

Table 2.5.12. Repeatability of nest characteristics of common blackbirds, repeatability (R), confidence intervals (CI), Bootstrap: 100. Significant results are indicated with an asterisk (*).

Nest parameter	R	SE	CI	*p*	Individuals (observations)
LW	0.14	0.1	[0.0, 0.4]	0.1	25 (81)
Thickness	0.30	0.1	[0.0, 0.5]	≤ 0.001*	24 (77)
Internal depth	0.21	0.1	[0.0, 0.4]	0.06	26 (78)
Eternal depth	0.01	0.1	[0.0, 0.3]	1	25 (80)
Nest height	0.23	0.1	[0.07, 0.3]	≤ 0.001*	41 (172)
Trunk to the nest	0.32	0.1	[0.01, 0.5]	≤ 0.001*	34 (105)
Road	0.70	0.06	[0.5, 0.8]	≤ 0.001*	46 (226)

2.5.3 Parental provisioning

I observed blackbird parental provisioning (nest visits) of 68 pairs (17 pairs in 2017, 27pairs in 2018 and 24 pairs in 2019). Data were also collected when chicks were aged from 3 to 14 days in the nests. Number of nest visits did not vary across years (GLMM: Estimate = -0.07, SE = 0.04, z = -1.6, p = 0.09, AIC= 2066, Figure 2.5.8.A). Visit ratio (female/male, Figure 2.5.8.B, and Table 2.5.13) showed that females had a slightly greater role in feeding chicks (number of nest visits), males increased their nest visits when there were more chicks at the nest (Table 2.513, Figure 2.5.8.B).

Table 2.5.13. Nest visit ratio(female/male) in relation to the different number of chicks at the nest.

Chick	Mean	SE	No. of nests
1	1.6	1.1	4
2	1.2	0.1	22
3	1.2	0.1	39
4	0.6	0.1	2

There is no variation in nest visits between males and females (GLMM model 1: -0.007, SE = 0.1, z = -0.1, p = 0.9, AIC= 2068, Figure 2.5.8.C). In addition, the number of nest visits increased significantly when there were more chicks in the nest (GLMM: Estimate = 0.2, SE = 0.1, z = 2.5, p = 0.02*, Table 2.5.14, Figure 2.5.8.D). In the second model, the number of nest visits increased in nests located higher from the ground (GLMM model 2: Estimate = -0.07, SE = 0.03, z = 2.06, p = 0.04*, Table 2.5.14). None of the daily weather parameters influenced the number of nest visits (Table 2.5.14).

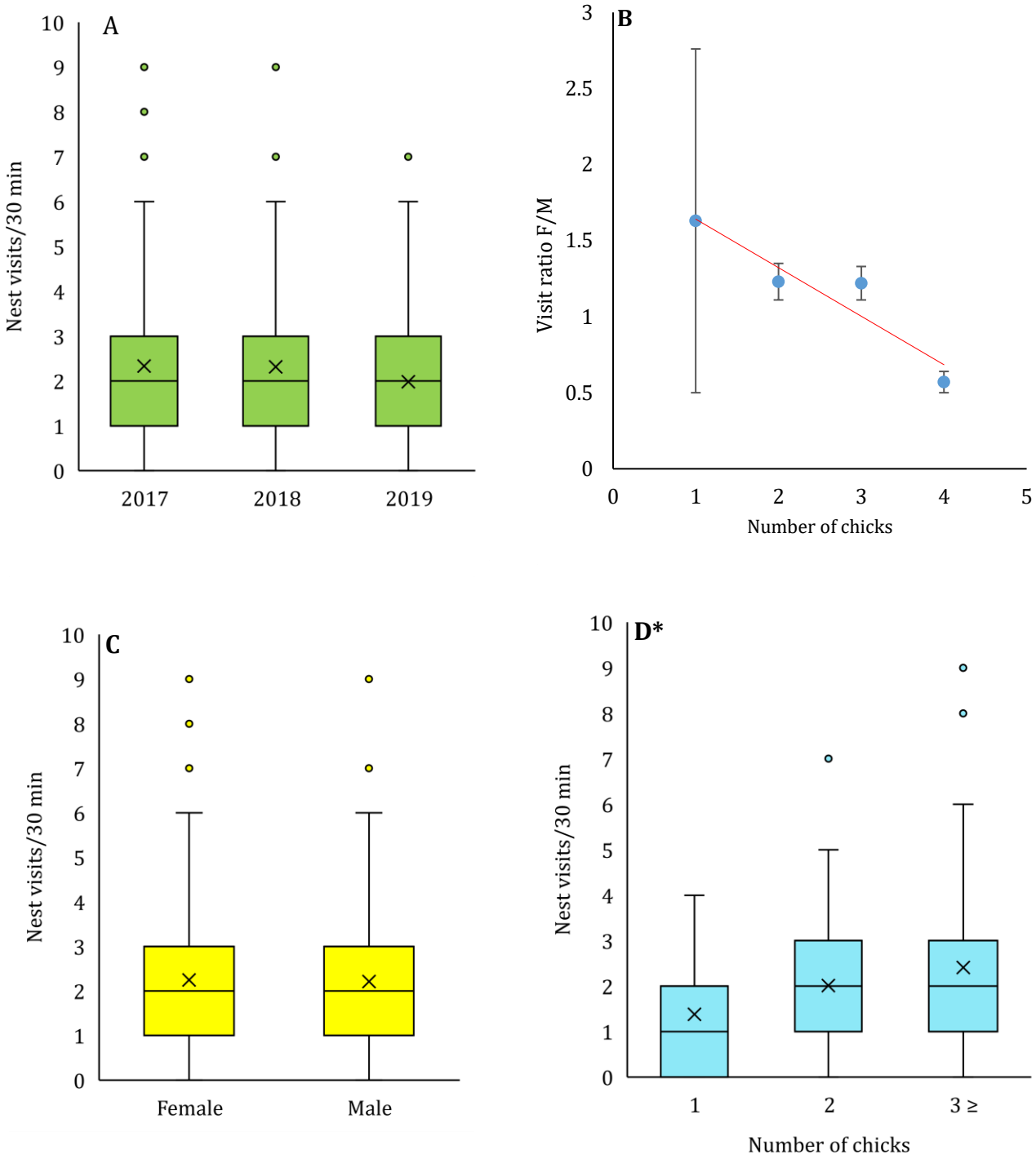

Figure 2.5.8. Variation in nest visits regarding different parameters. A) Across the years (Number of observations: 2017 = 174, 2018 = 270, 2019 = 170). B) Visit ratio (Mean ± SE) in relation to different number of chicks (Number of nests: 1 chick = 4, 2 chicks = 22, 3 chicks = 39, 4 chicks = 2). C) The variation in nest visits of blackbirds between males and females (number of observations: male = 307, female = 307); and D) Across different numbers of chicks in the nest (number of observations: 1 chick = 34, 2 chicks = 194, 3 ≥ chicks = 386).

Table 2.5.14. Results from the GLM models of visit nests in blackbirds. $p \leq 0.05$ required for a significance level, shown by an asterisk (*).

Fixed factors	Estimate	SE	z	*p*
Model 1: Number of chicks, age of chicks	**AIC = 2063**			
Intercept	0.2	0.2	0.9	0.4
Chicks	0.2	0.1	2.5	0.02*
Chick Age	0.02	0.01	1.6	0.12
Model 2: Human, road, nest height	**AIC = 2067**			
Intercept	0.7	0.1	6.5	≤ 0.001*
Human	-0.002	0.0	-0.9	0.39
Road	-0.001	0.0	-0.8	0.47
Height	0.1	0.03	2.1	0.04*
Model 3: Weather	**AIC = 2069**			
Intercept	1.1	0.2	4.5	0.001*
Max temperature (C)	-0.01	0.01	-0.8	0.45
Min temperature (C)	-0.01	0.01	-0.8	0.43
Rainfall (mm)	0.0	0.01	0.6	0.56

2.6 Discussion

2.6.1 Breeding chronology

In this study, I investigated the breeding biology of a blackbird population in New Zealand located in an urban area (Auckland). I studied reproductive biology over time and compared it with other published studies. The blackbird breeding season at my study site started in early August (which corresponds to February in Europe) and ended in late December (5 months long). In North England, Spain and Scotland, the breeding season starts one month later than the corresponding time in New Zealand (February to July, six months, Cresswell, 1997; Ibáñez-Álamo and Soler, 2010a; Snow, 1958b). The start of the breeding season in the current study was similar to other blackbird studies in New Zealand and Australia (Gurr, 1954; Bull, 1946; Kentish et al., 1995a), with a slight difference in the onset of egg-laying.

Different factors influence the start of breeding in birds. Photoperiodism, temperature, rainfall, food viability, habitat characteristic and genetic differences are the most important factors (Evans et al. 2012; Visser et al. 2010 in Ibanez and Soler 2010). When interpreting the variation in New Zealand, there are several explanations. Older studies in New Zealand are recorded from farmland in south Auckland (Bull, 1946) and a suburban area Dunedin, a city in the South Island (Gurr, 1954). In contrast, my study was from an urban population. Urban areas differ from rural, woodland farmland areas in many ways, including food availability, predators, thermal range, habitat type, light and air pollution (James Reynolds et al., 2019). These factors can drive the alteration of traits between urban and non-urban bird populations, including variation in population density, foraging behaviour, breeding commencement, clutch size, and breeding success (Hedblom and Söderström, 2012). Earlier start of breeding in urban populations has been reported in other species of raptors (Kettel et al., 2018). I speculated that the variation in the beginning of the breeding season between the current study and Bull, 1946, may be best explained by variation of breeding between urban and non-urban areas. Further concurrent research could test this hypothesis. The observed differences in breeding seasons between Auckland and Dunedin, are likely due to latitude and photoperiod. Dunedin has a higher latitude and has significantly colder temperatures in August (10 °C max, – 6 °C min) and shorter daylengths (9:33,10:57 hours) compared with Auckland (temperatures:15 °C max, – 8 °C min; daylengths: 10:16, 11:16 hours).

The breeding season in Australia (mainly Melbourne), is strongly influenced by temperature (Australia: minimum temperature is 5.7°C), rainfall and urban environment (well-watered urban gardens)(Kentish et al., 1995a). In European countries like England and France the breeding season is affected by rainfall (April to June), and food availability which reaches a peak during late spring and summer (Biddle et al., 2015; Myers, 1955; Snow, 1958; Venables, 1952). Tibet has the shortest breeding length found in blackbirds because of fluctuation of weather conditions and lower environmental temperature, the breeding season starts later in early May and ends in late July (Lu, 2005). I suggested that photoperiodism, temperature and rainfall generally underlie seasonality in the timing of the breeding season in my study (in late July and early August). As the breeding season in my study start in late July and early August (increasing daytime, temperature, and rainfall). These variations stimulate gonad development and the timing of breeding in blackbirds. Then the breeding season finishes in late December. The end of breeding would be limited by dry and warm weather and the availability of food provided for chicks. Since food availability is another important factor that impacts egg-laying in birds, I also suggest further studies on assessing variation of food availability across the breeding season.

2.6.1.1 Clutch size

The most frequent clutch size was three in my study. In contrast, in Britain, clutch sizes of four and five are most frequent (Myers, 1955a; Snow, 1956, 1958). In my study, I only observed a few nests with four eggs, and I had no record of five eggs per nest. Unlike studies from Algeria (Zeraoula et al., 2016) and England (Snow, 1955), clutch size in New Zealand (my study)did not vary across the season. The clutch size recorded in my study was also lower than those reported from other studies in New Zealand (Gurr, 1954; Bull, 1946), Australia (Kentish et al., 1995a), Scotland (Cresswell, 1997), England (Snow, 1958a), Belgium (Verheyne, 1953 in Snow), UK/Shetlands (Venables, 1952), Slovakia (Havlin, 1963 in Kentish et al., 1995) and Holland (Lack, 1994) (Table 2.5.2). While it was similar to records from Tibet (Lu, 2005), Algeria (Zeraoula et al., 2016), and Tunisia (Selmi, 2007) (Table 2.5.2). Clutch size does have a phylogenetic component but within these constraints it can also depend on available daylight hours, food availability, density and predator pressure (Charmantier et al., 2006; Ewald and Rohwer, 1982; Fletcher et al., 2013; Ricklefs, 1980; Slagsvold, 1982). As latitude increases, summer daylengths are

longer and productivity is generally higher, so more food and feeding time would lead to larger clutch sizes (Balasubramaniam and Rotenberry, 2016; Charmantier et al., 2006). Tibet, New Zeeland (current study and Mangere; Bull, 1946), Algeria, Tunisia and Australia are located between 28° and 40° north and south latitudes. New Zealand (Dunedin), England, Scotland, Holland, Slovakia and UK/Shetlands are located in higher latitudes between 45 ° and 60 ° (Table 2.5.2). Although Niethammer (1970) did not find a correlation between latitude and clutch size in the north and south of New Zealand, the location of data from that study was unknown, so I did not include it in the analysis. In my study, I found blackbirds in lower latitudes have a smaller number of eggs per clutch (Figure 2.5.2).

It is likely that multiple factors influence clutch sizes in blackbirds, such as latitude (explained earlier), predator and population density, multiple clutches, and egg size. Niethammer (1970) and Snow (1955) show that blackbird clutch sizes are smaller in New Zealand than those in England. Similar results are also found for other bird species such as little owl (*Athene noctua*; Fzlla et al., 1966) and great tit (*Parus major*; Kluiiver,1951). Niethammer (1970) also expects that the predator pressure on adult birds is lower in New Zealand than in England. Hence, life expectancy increases, leading to high population density and smaller clutch sizes. Mayer (1965) also states that natural selection will favour lower clutch sizes in areas where life expectancy is higher, for example, in tropical regions. In this study, population density and predator have not been studied. I found evidence of predator presence and its impact on the breeding success of blackbirds. Future research would be valuable to consider the impact of predator and bird density on breeding parameters (clutch size, hatch success, breeding success). Comparative studies of different populations from predator-free sanctuaries, urban and rural areas could help to reveal which factors would influence and control the clutch size in blackbirds. Furthermore, depending on the number of chicks that parents can feed, the clutch size may be limited (Blackburn, 1991). A fewer number of chicks would lead to better parental care compared with a greater number of chicks at the nest (Rohwer, 1988). In addition, large clutches may be limited by food availability to the laying female. Hence by considering food limitation, larger clutch sizes could be compensated by decreased egg size (Blackburn, 1991; Rohwer, 1988; Slagsvold et al., 1984). Therefore, investigating the availability of food, food quality across the breeding season, and parental care can explain the limitation of clutch size in blackbirds.

The incubation period in this study was 13.5 days which was similar to the records from Spain (13.6, 13.5 and 13.2; Ibáñez-Álamo and Soler, 2010), England (13.2 days, Snow 1958) and Algeria (13.7 days; Zeraoula et al., 2016), while blackbirds in Tibet (12 days; Lu, 2005) had a shorter incubation duration. Nestling duration in this study (14.2 days) was also similar to records from New Zealand (14.5 days; Bull, 1946), Slovakia (14.5 days; Pikula & Beklová 1983) and China (14.5 days; Wu and Li, 1984). The longest nestling period belongs to Algeria (15.7 days; Zeraoula et al., 2016), and Tibet (17 days; Lu, 2005), while the shortest nestling duration was recorded from Spain (10.1, 11.8, 11.9 days, Ibáñez-Álamo and Soler, 2010). Overall, food availably is one of the most important factors influencing the duration of the nestling period (Kelleher and O'Halloran, 2006; Wilkin et al., 2009). Limited food sources and quality of food in Tibet (declined incubation; Lu, 2005) and increasing temperature and declining rainfall in Algeria (Zeraoula et al., 2016) constrain the parents' ability to feed their nestlings. Hence nestling period take longer, because parents cannot supply enough food in a standard time duration . However, in this study, the food availability and quality of food have not been studied. More research is needed to understand the impact of food on the incubation and nestling periods in urban populations in New Zealand.

2.6.1.2 Breeding success and breeding failure

Blackbird nest success in New Zealand (54.7%) was similar to urban populations recorded from England (50%; Snow, 1958b), Spain (53%; Ibáñez-Álamo and Soler, 2010a) and Tibet (59%; Lu 2006). Studies around the world show that one of the factors that influence breeding success is the presence of predators. Predators in Europe are reported in higher numbers than in Australia and New Zealand (Snow, 1958). In Australia, nest success is influenced by exotic and native predators, while human presence decreases the number of predators in an area, which then increases blackbird breeding success (Osborne & Osborne 198 and Kentish, 1995). Main predators in Algeria and Tunisia are snakes and lizards (Bensouilah, 2015, Selmi, 2007; Zeraoula et al., 2016). In urban areas of Spain, human activities in cities reduce the daily predation compared with woodland areas (Ibáñez-Álamo and Soler, 2010a). Like other studies, I also found that the predators in urban areas cause nest failure in both the incubation and nestling phases. I found much higher success rates than South Island (33% ; Niethammer)and much more similar to northern hemisphere studies.

Food availability in cities is another selective pressure that affects breeding success. Territory quality, at a larger scale, can represent the habitat quality because the food might not be equally distributed in the area (Chamberlain et al., 1999). For example, blackbird nestling starvation is higher in the urban area than in the woodland and rural regions of Spain (Ibáñez-Álamo and Soler, 2010a). In the alpine environment of Tibet, the weather is harsh and food resources are low; therefore, blackbirds improve their breeding success by investing more reproductive energy into fewer chicks per nest (Lu, 2005). Although human presence might decrease predator activities in cities, it can also distract bird activities. For example, human activities that disturb nesting birds may influence parental roles (particularly during incubation and nestling phases) (Selmi, 2007). Therefore, food availability and human activity can affect the breeding success of urban birds. Although I found that nest abandonment gradually increased across the breeding season, food availability and quality in this area were unknown.

I suggested that earlier in the breeding season, predator presence influenced the breeding success and the number of fledged chicks per nest (Figure 2.5.3, Table 2.5.4). Data from pairs with multiple clutches also showed that the average number of fledged chicks per nest in the first clutches (1.3 ± 0.1) was significantly lower than in the last clutches (1.8 ± 0.2). These data also suggested the evidence of the presence of predators and its impact on the breeding success and failure in blackbirds. Likely predators in my study area were Australian magpie (*Gymnorhina tibicen*), Australasian harrier (*Circus approximans*), common brushtail possum (*Trichosurus vulpecula*), cats (Felis) and rats (*Rattus* spp). In my study, desertion peaked in November and may be the result of reduced food due to warmer drier conditions. The main diet of blackbirds is earthworms, whose availability at the soil surface is strongly influenced by soil moisture and rainfall. Therefore, future studies in food sources , predator pressure can help to improve our understanding on blackbird breeding variation across the breeding season.

2.6.1.3 The consistency of breeding characteristic

Within pairs, the length of the breeding season in blackbirds varied across the years (Table 2.5.6). The commencement of first clutches were moderately consistent in female blackbirds, while the last clutch dates varied among the years. The length of the breeding season in many songbirds is also influenced by photoperiod, temperature, and precipitation (Chamberlain et al., 1999a; Fletcher and Koford, 2004). The first clutch

dates in blackbirds were mostly consistent, likely due to the photoperiodic impacts on daytime and rising temperature, which directly stimulate gonad maturation, release breeding hormones and fecundity (Jankowiak et al., 2014; Meijer et al., 1999; Møller et al., 2010). Overall, the consistent start of the breeding season suggested the potential existence of genetic selection as a sign of the start of the breeding season in blackbirds.

2.6.1.4 Urban modification and nest-site placement

Impacts of roads may vary, many studies show the negative impacts of roads, such as, habitat loss, air pollution (house sparrow, *Passer domesticus;* Herrera-Dueñas et al., 2014), noise (tree Creeper, *Certhia familiaris*; Rheindt, 2003), higher parasite infestation (blackbird; Gregoire et al., 2002), and collisions with vehicles (Reijnen and Foppen, 2006). In contrast, studies have found positive aspects of proximity to roads, such as, reduction the predation pressure (European turtle-dove, *Streptopelia turtur*; Ceresa et al., 2012), warmer local environments (vesper sparrow, *Pooecetes gramineu*; Whitford,1985), diurnal activities (lesser kestrel, *Falco naumanni*; Kmetova et al.2010), and higher food supplies (Eurasian magpie, *Pica pica*; Yamac and Kirazli, 2012). In my study I found the most successful nests were closer to the road, while predated nests were further from the road. however, this was not a strong correlation. I also found clutch sizes were higher (more four eggs nests) closer to the road. These results suggest that road areas may provide a safer environment for eggs and nestlings in terms of lower predation pressure. Future studies could explore this hypothesis by monitoring predator numbers or activity.

2.6.2 Nest characteristics

Consistent with my expectation, nest dimensions were influenced by the clutch size and changed across breeding phases. In many animal taxa, insects, fish, reptiles, birds, and mammals, parents build their nest by considering the clutch size and/or offspring for a specific time (Hansell, 2000, 2007; Taylor et al., 1998). Although females might adjust the clutch size during incubation and even timing of the nestling period (Moller, 1987), nests are generally built depending on the clutch size before the first egg being laid (Møller et al., 2014a). Several studies also show that larger nests often have larger clutch sizes, for example in northern flickers (*Colaptes auratus*; Wiebe and Swift, 2001), Eurasian magpies (*Pica pica;* Soler et al., 2001), pied flycatchers (*Ficedula hypoleuca*; Karlsson and Nilsson, 1977), tree swallows *(Tachycineta bicolor*; Rendell and Robertson, 1993) and collared

flycatchers (*F. albicollis*; Gustafsson and Nilsson, 1985). I found that blackbirds are consistent with this trend and my results show that female blackbirds made thicker and stronger nests for anticipated larger clutch sizes. Other researchers have concluded that there is no relationship between nest dimensions and clutch size. For example, a study on blackbirds in Szczecin (Poland) found no significant relationship. However, Wysocki (2015) measured nests after nestlings fledged. In my study, I measured the nest dimensions before females laid eggs, thereby ignoring changes to nest dimensions that may happen due to the stresses of chicks in the nest.

I found that nest diameter increased, and the internal nest depth, external nest depth, and nest thickness reduced over the breeding phases. These significant changes in nest dimensions align with nest use - the nest becomes stretched with use (flexibility). Many studies show that nest dimensions and flexibility can also be influenced by female experience (Desrochers and Magrath, 1993; Wysocki, 2004), predation pressure (Álvarez and Barba, 2008; Desrochers and Magrath, 1993b; Wysocki, 2005), nest placement (Heenan and Seymour, 2012), latitude, temperature (Mainwaring et al., 2014b), and structural properties of nests (Biddle et al., 2015). Further research would be helpful to determine the influence of different factors on nest dimensions in blackbirds.

I had expected that blackbirds select specific plant species in which to build their nests, but I found that there was a large variation. I also found only weak negative correlations between nest height and nest diameter, nest height and the nest distance from the trunk. Similarly, I found a weak correlation between the nest height and the distance of the nest from the road. A study of blackbird nest placement in Turkey shows a significant relationship between nest height and the external nest diameter (Kucherenko and Ivanovskaya, 2020). This was not something I found in my study. Birds should place nests to reduce the visibility of their nests from avian and mammalian predators (Kucherenko and Ivanovskaya, 2020). Terrestrial predators like rats and possums climb the trunk of trees to reach nests, so higher nests and nests more distant from the trunk should impede these predators reaching the nest. This increase in distance should also facilitate the concealment of the nest due to increased vegetation cover (Taberner et al., 2012). Higher nest place may also have energetic costs; birds tend to decrease their energy costs by constructing nests closer to the ground (Mainwaring and Hartley, 2013). However, my results were not strong enough to support these hypotheses. Anthropogenic activities

and predation pressures may lead to high variation in characteristics of the nests in blackbirds that I found in my study.

2.6.2.1 Consistency of nest characteristics

Overall, I found a substantial degree of repeatability in some nest characteristics over time. I suggested that repeatability of nest characteristics may represent the quality of females and the potential for a genetic component. I found that the nest thickness, the nest distance from the trunk, and the distance of the nest from the road were significantly, although to a moderate degree, repeatable. Similar to my finding, studies show the repeatability of nest dimensions in southern masked weavers (Walsh et al., 2010), and nest size and nest-building behaviour in penduline tits (Schleicher et al., 2021b; Walsh et al., 2011). Although I expected that the nest height would be highly repeatable, the repeatability of the nest height was relatively low (R = 0.2). Australian magpie, Australasian harrier, common brushtail possum, cats, and rats (aerial and terrestrial predators) could reach nests at any heights. I assumed that predation pressure and human disturbance in the area might influence the female decision for nest height selection. Therefore, female blackbirds might change the nest heights based on their experience in finding a safe nesting place, demonstrating adaptive behavioural plasticity in nest height selection (Marzluff 1988). In addition, it could be the limited vegetation that was available on their territories, and there were not very high trees in some parts of the study site.

Both nest thickness and nest distance from the trunk were moderately repeatable. I assumed that this consistency of nest characteristics would provide benefits for females and also was related to the number of eggs per clutch. Females might find the benefits of how close to the trunk and thicker edges make a solid and safe place for the specific number of eggs and nestlings. My results also showed high repeatability of the distance of the nest from the road. It is possible that the female would be expected to select their nests closer to the road in her territory. Because it could reduce predation impact on both nestlings and parents. My results provide reliable information to compare with other behavioural studies. However, more information is required to investigate genetic and heritability links among nest characteristics and fitness consequences of nest constructing in birds.

2.6.3 Parental care

My results from parental provisioning demonstrated that the number of nest visits increased only marginally with the number of nestlings in both males and females. Similar to my results have been reported for slaty-backed nightingale-thrush, *Catharus fuscater*, northern wheatear, *Oenanthe Oenanthe* (Dyrcz et al., 2015; Öberg et al., 2015). In these studies, quality of food, rainfall similar feeding rate are associated with feeding nestlings. However, I did not have information on food quality, and I did not find an influence of rainfall. Approximately 80% of total nests (170 out of 214 nests) had three eggs per clutch in my blackbird population. In addition, 75.8% of entire nests (116 out of 153 nests) had three chicks per nest. I collected nest visit data of four nests with one chick and two nests with four chicks per nest.

Contrary to my prediction, even though chicks were growing quickly from day 3 to day 14, results did not show a significant variation in nest visits with increasing nestling age. Similar to my results, a study by Chamberlain et al. (1999b) found that the number of nest visits in blackbirds does not increase as nestlings grow. Similar results observed in Neotropical passerines: bay-capped wren-spinetail (*Spartonoica maluroides*; Dias et al., 2009), white-throated woodcreeper (*Xiphocolaptes albicollis*; Cockle and Bodrati, 2013) and slaty-backed nightingale-thrush (*Catharus fuscater*; Dyrcz et al., 2015). In contrast, results from other temperate zone studies reported where visitation rates in some species of the thrush family (song thrush and blackbirds) gradually increase with nestling age (Gill 1990, Hill et al., 1999). In addition, variation of nest visits regarding the nestling age is reported from an urban population of blackbirds in Dijon, France (Préault et al., 2005). Although the demand for food to provide the energy necessary for growth, I did not find variation in nest visits across different nestling ages. Therefore, I assume that the parents might carry more food per visit as chicks grow. The growth pattern is also different. Chicks consume lots of food if growing fast but if older chicks grow slower than perhaps do not require more energy than when younger but growing faster. Hence, I suggested taking measurements of growing chicks would help with this.

I found that both parents made similar numbers of visits to nests. Females visited the nest more than males when there were less than four chicks in the nest, but my results show that blackbird males and females express similar levels of parental. In contrast, females have greater parental care investment than males in small tree finches (*Camarhynchus*

parvulus, Heyer et al., 2021). In the red-winged blackbird, *Agelaius phoeniceus*, the lower provisioning by the male is related to the male spending more time attracting additional mates (Yasukawa et al., 1990). The equity in the partitioning of parental care (i.e., chick feeding rates) can be influenced by several factors such as the age of parents, male and female reproductive experience, nestling sex ratio, rainfall and diet, and predator and human disturbance. Generally, more experienced parents visit at higher rates than less experienced birds (Limmer and Becker, 2009). In addition, feeding rates might be influenced by temperature and rainfall, which affect food availability (Mueller et al., 2019). Although I was unable to examine the effect of parental age on the rate of nest visits, I did look at the effects of year and weather parameters. I found no influence of either factor on the frequency of visits. Furthermore, contrary to my prediction, blackbird nest visits were not influenced by human modification factors (number of humans and distance from the road). Other studies have found human disturbance in crowded urban areas caused increased mortality of breeding birds due to vehicle strikes affecting urban birds' breeding activities (Groom, 1993a; Klein, 1993; Møller, 1988).

In conclusion, my research provides new insights into the breeding ecology of blackbirds in urban habitats in New Zealand. My research also presented comparative information of blackbird breeding around the world. There was strong evidence of the correlation between clutch size and latitude. My result details on breeding success and failure in the blackbird population and presented evidence of the influence of predators in urban areas. I conclude that blackbirds are an urban species adapted successfully to urban areas, indeed they are more likely to have a successful nesting attempt when nests are placed closer to the road. In addition, I found that the nest diameter increased across the breeding phases (from built to fledged chicks). In contrast, the nest thickness, internal nest depth, and external nest depth decreased. The results obtained from nest measurements showed that variation in nest dimensions aligns with nest use - nests become stretched with use but retain their overall shape – indicating flexibility. I also confirmed that females build thicker and stronger nests based on anticipated clutch size. Moderate to high repeatability of some nest characteristics presented evidence of genetic component and the influence of the number of eggs in the nest dimension and nest-site selection.

I also suggest future comparative research on life-history traits of blackbirds in different areas (urban, rural, and predator-free parks, mainland, and island). Additional research should investigate the life history of blackbirds in different habitats in New Zealand (urban, suburban). Further studies should focus on the availability and quality of food that males and females supply for their nestlings. Although blackbirds appear to be well adapted for urban habitats and may even benefit from urbanisation, other urban avifauna may be more vulnerable. Hence future research can use blackbirds as a thriving urban bird model to assess the balance between the costs and benefits of urbanisation and the role of specific life-history traits. Results from these studies help in the management of wildlife and conservation in urban areas.

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2.8 Appendices

Appendix 2.8.1. Plant species used as nest sites by common blackbirds each breeding season.

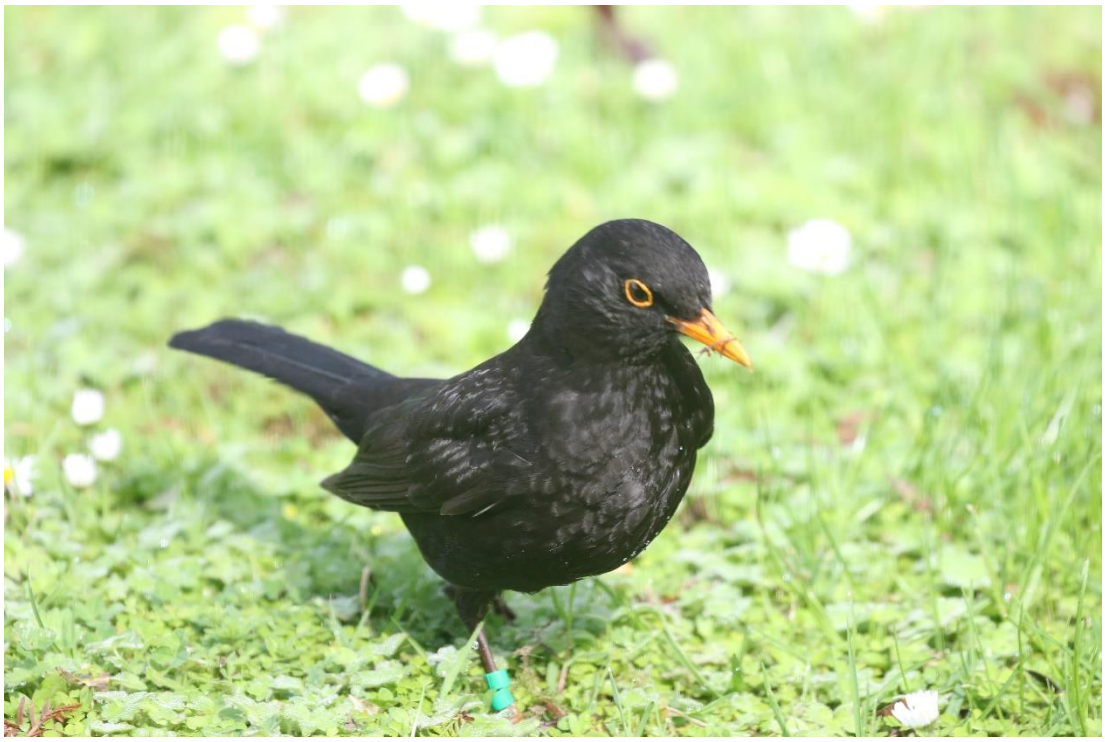
Plant species	**2017**		**2018**		**2019**		**Total**	
	N	%	N	%	N	%	Nest	%
Coprosma	7	12.0	15	19	10	14.5	32	15.5
Camellia japonica	11	19	8	10.1	14	20.3	33	16
Podocarpus totara	10	17.2	12	15.2	10	14.5	32	15.5
Melaleuca alternifolia	6	10.3	4	5.1	5	7.2	15	7.3
Viburnum tinus	3	5.2	5	6.4	3	4.3	11	5.3
Myrsine australis	1	1.7	10	12.6	2	2.9	13	6.3
Others	20		25		25		70	34
Total	58		79		69		206	100

Appendix 2.8.2. Correlation coefficients between nest characteristics. Significant correlations are indicated with an asterisk (*), N = number of nests.

	Nest height	**Trunk to the nest**	**Road**
Nest diameter	r = -0.2	r = -0.3	r = -0.04
	p = 0.03*, N = 80	$p \leq 0.001$**, N = 67	p = 0.7, N = 81
Nest thickness	r = 0.1	r = 0.1	r = -0.1
	p = 0.3, N = 79	p = 0.2, N = 67	p = 0.3, N = 80
Internal nest depth	r = -0.1	r = -0.02	r = 0.01
	p = 0.5, N = 75	p = 0.8, N = 63	p = 0.8, N = 76
External nest depth	r = -0.001	r = -0.2	r = 0.2
	p = 0.9, N = 79	p = 0.06, N = 67	p = 0.10, N = 80
Nest height		r = 0.3	r = -0.3
		$p \leq 0.001$*, N = 67	p = 0.02*, N = 80
Trunk to the nest			r = 0.06
			p = 0.6, N = 67

Chapter 3:

Assessment of behavioural traits in a free-living blackbird population



A male blackbird foraging.

3.1 Abstract

Behavioural ecologists have revealed that behavioural variation in animals can be predictable and quantifiable. The degree of variation is dependent on the context and function of behavioural traits and how individuals interact with their specific environments (Roche et al., 2016b). I investigated intra-individual variation in behavioural traits in an introduced bird population of the common blackbird, *Turdus merula*. Behavioural traits were measured in the context of foraging. The study was carried out during three successive years from 2017 to 2019 in New Zealand. Behavioural traits included activity, vigilance, aggressiveness, and shyness. I estimated behavioural variation, behavioural repeatability and behavioural syndromes in common blackbirds and assessed the correlation of behavioural traits on individual breeding success. Finally, I also estimated the correlations between behavioural traits and daily weather parameters.

Overall, GLMM analysis showed that individual activity and aggressiveness were significantly higher in the morning. Activity (hop rate) and aggressiveness (interaction with conspecifics) also increased during the breeding season. In contrast, peck rate (vigilance) declined over the breeding season. Regarding shyness, I found that juveniles spent less time under cover of vegetation (were bolder) compared with males and females. Minimum temperature strongly influenced variation of behavioural traits. In addition, selected behavioural traits were not repeatable and individuals presented high plasticity in their behavioural traits during their foraging. Results for behavioural syndrome analysis revealed that more active individuals were also shyer. Finally, there was a positive relationship between shyness of an individual and the number of fledglings per season.

Together these results suggest individuals with more plasticity in their responses may be better suited to inhabiting diverse habitats. For my study, highly behavioural variations appeared to be an important feature of the successful invasion of blackbirds into urban environments.

3.2 Introduction

Behavioural variation in animal species can dramatically, or often predictably, determine how individuals interact with their environment and can influence the outcomes of biotic interactions, such as, competition, mate choice, parasitism and predation (Roche et al., 2016b). Animal behavioural researchers suggest that variation of behavioural traits has two levels. Phenotypic variation at the level of intra-individual variation is explained as "Plasticity" (Ogden, 2012b). Plasticity refers to behavioural flexibility of the individual in response to environmental stress during short time scales (Groothuis and Carere, 2005b; Peluc et al., 2008; Zemanova et al., 2010). In contrast, consistent inter-individual variation of behavioural traits over an environment gradient (specific content) and time is defined as "Personality". This term commonly explains more than 30% of the phenotypic variance within populations (Biro et al., 2010; Briffa and Greenaway, 2011b; Stamps et al., 2012). Therefore, personality influences how efficiently natural selection can generate an adaptive response across generations (Carere and Locurto, 2011; Frost et al., 2007b).

Many studies of animal behaviour attempt to explain the consequences of behavioural variation. Hence, multiple theoretical models have been suggested to explain the evolution and maintenance of behavioural traits either in plasticity or in personality concepts (Blondel et al., 2006; Dammhahn, 2012; Peluc et al., 2008; Reichert and Hedrick, 1993). For instance, in response to variation in spring temperature, female great tits, *Parus major*, are able to adjust their timing of breeding. This plasticity in breeding behaviour results in higher reproductive success (Nussey et al., 2005). In another example, personality research on a long-lived seabird shows that both boldness and foraging traits are correlated with fitness consequences, depending on sex and food availability. Bolder females and shyer males have higher fitness, but the power of this relationship depends on food availability (Patrick and Weimerskirch, 2014). Together, these studies reveal the potential significance of personality and plasticity in animals and the fitness consequences of behavioural traits for individuals.

Variation in breeding success and survival rate among individuals are influenced by energy acquisition related to foraging (Annett and Pierotti, 1999; Patrick et al., 2015). Parameters such as trip duration, offspring feeding rates, and foraging effort can also determine intra-individual or intra-pair differences in breeding success and offspring

quality. For example, females in the European shag, *Phalacrocorax aristotelis*, with high repeatability in foraging site fidelity are in better body condition and they have an earlier egg hatching date (Morgan et al., 2019). Thus, foraging is a key element in many individuals' daily routines and can be an important determinant of fitness and reproductive success in individuals.

Few studies have addressed the link between variations of behavioural traits in the context of foraging. Behavioural traits such as boldness–shyness, aggression, vigilance, risk-taking, activity and feeding behaviours are all employed by individuals during their foraging activities (Toscano et al., 2016). Vigilance behaviour during foraging activities helps to protect individuals and their offspring from threats (predators) but reduces the time available for directly obtaining food and therefore decreases food intake (Bergvall et al., 2011; Brown, 1999; Whittingham et al., 2004). Hence, there is a trade-off between time spent on foraging, time spent on assessing hazards (vigilant behaviour), and food intake (Blanchard and Fritz, 2007).

Activities during foraging are defined as the amount of temporal and spatial movement in a familiar environment of an individual (Bell et al., 2009b; Careau et al., 2008b). This term is in contrast with another behavioural term "exploration", which is related to the movement of the individual in a novel environment (Arvidsson et al., 2017). There have been several studies regarding the foraging activities in mammals (Brehm et al., 2019; Lantová et al., 2011), birds (Thys et al., 2017), fish (Hirsch et al., 2017), amphibians (Kelleher et al., 2018), and invertebrates (Kralj-Fišer and Schuett, 2014; Mather and Carere, 2019). Recent studies have successfully linked activity levels within the context of foraging to different personality traits. A study on mosquitofish, *Gambusia affinis*, explained that variation of activity varied consistently with predation pressure, dispersing individuals are less social than non-dispersing ones when there is no predator in the environment (Cote et al., 2013).

Individuals behave differently when foraging among conspecifics and non-conspecifics (van Baaren and Candolin, 2018). An important part of the life history of animals is territorial aggression toward conspecifics (van Oers and Naguib, 2013b). Territorial aggression has been studied throughout the animal kingdom and is used to defend limited resources, such as food-limited resources, mates and breeding territories (Foltz et al., 2015). Interactions between individuals of a population depend on local conditions and

the quality of their territory. So they may show consistent behavioural responses (personality), or they may respond more flexibly to environmental changes (plasticity) (Fülöp et al., 2019; Greenwood and Harvey, 1978; Patrick and Weimerskirch, 2014). For example, bolder cane toads, *Rhinella marina*, forage in a novel environment in the presence and absence of conspecifics, while shy individuals are more likely to forage in a novel environment in the presence of a conspecific (González-Bernal et al., 2014). Another study on song sparrows, *Melospiza melodia*, shows that the urbanisation-related difference in territorial aggression by individuals is repeatable within a breeding season (Davies and Sewall, 2016).

Individuals vary in the way they deal with challenges and hazards and appear to differ along a behavioural continuum from shy to bold (Carere and van Oers, 2004). In a forging context, which requires intensive handling time and economising tactics, different behavioural phenotypes may imply different foraging tactics. In addition, the availability of food varies in different habitats (van der Merwe and Brown, 2008). Boldness variation between different habitats leads to the variation in the risk of hazards. Shy individuals may forage in low-risk habitats, which may have lower food availability because of intraspecific competition or lower quality habitat. A study of the boldness trait of the common mud crab, *Panopeus herbstii*, reveals a link between personality, habitat quality and survival of individuals (Belgrad and Griffen, 2018). Such behavioural variability in personalities has been proposed as a mechanism that can generate diverse population dynamics across different habitat qualities (Toscano et al., 2016).

Suites of behavioural traits that are correlated across situations and contexts are known as "behavioural syndromes" (Pruitt et al., 2008; Urszan et al., 2015). For example, very bold individuals may also be relatively aggressive (Bell, 2005b). Observers of animal behaviour have recognised important consequences of behavioural syndromes. They have found that correlated behavioural traits may not evolve independently, so that selection favouring one type of behaviour, e.g. boldness, could lead to changes in a completely different, but associated, behaviour e.g. aggression (Dingemanse et al., 2010). Studies on three-spined stickleback, *Gasterosteus aculeatus,* show that in populations where predators are present (versus absent), there are positive strong correlations between aggressiveness and boldness. This is because predators enforce selection, which favours correlations between behavioural traits (Bell, 2005b; Bell and Sih, 2007b).

Several lines of research, including studies of selection lines, propose that these differences are part of a coherent and heritable behavioural association and are preserved by natural selection (Pruitt et al., 2008; Sih et al., 2004c).

Behavioural ecologists have hypothesised that variability in behavioural traits have important evolutionary and ecological consequences depending on shifting environmental conditions, such as, food availability (Dingemanse et al., 2004; Smith and Blumstein, 2008), the pressure of predation presence (Grant E. Brown et al., 2013; Réale and Festa-Bianchet, 2003), and social conditions (Both et al., 2005). For instance, more aggressive individuals may be at an advantage when challenging conspecifics for mates and therefore, have higher reproductive success. However, such a personality trait may be expensive if this behavioural pattern is maintained in the antipredator context (in presence of a predator, individuals might show different reactions such as attack , alarm , hid or run away), thus lowering survival (Sih et al., 2004c; Stamps, 2007). So, depending on the context in which they are displayed, the fitness of personality dimensions differs based on relative costs and benefits.

Blackbirds are now among the most successful urban bird species that are globally widespread and one of the best-studied urban colonisers (Evans et al., 2010c). Variations of behavioural traits in blackbirds have been mostly studied in urban and rural populations. These traits include breeding, migration, song, disease risk, and stress physiology (Evans et al., 2009; Faivre et al., 2001c; Gryczyńska and Welc-Falęciak, 2016; Kentish et al., 1995b; Meillère et al., 2016; Mendes et al., 2011; Møller et al., 2014b). In addition, studies on blackbird foraging have been mainly focused on features of foraging behaviour, seasonal variations of foraging strategies, predation risks and forging effort, foraging and territory utilisation, age and foraging success, and the influence of human-derived foods on foraging (Desrochers, 1992; Greenwood and Harvey, 1978; Post and Götmark, 2006a; Shukshina, 2019; Støstad et al., 2017; Török and Ludvig, 1988). Although significant research on different aspects of blackbirds has been done, behavioural plasticity and personality are still a new field of research for this species.

My study asks if variations of behavioural traits in individuals occurs during daily foraging in the common blackbird (hereafter blackbird). Behavioural traits were investigated using an observational approach during foraging activities. I measured four types of behavioural traits, including activity, vigilance, aggression, and shyness-

boldness. The observations of behavioural traits of individual blackbirds took place over the short-term (seasons) and long-term (three years). This allowed for the investigation of the expected behavioural traits of blackbirds as well as the behavioural variations within and amongst individuals. To date, no published research exists that has studied the concept of personality and plasticity in a free-living population of blackbirds. Hence, my research results provide new insights into behavioural variations in the context of foraging under natural conditions.

The primary goal of my study was to evaluate factors influencing behavioural traits within blackbirds. Factors included time of day, sex, age, year, and season. I also looked at the impact of other components within the environment like proximity to urban modifications (number of humans) and the presence of intraspecific birds on blackbird territories. Movement by individuals can be influenced by external factors such as temperature or day length and individual-specific factors such as hormone levels, body condition, age and sex (Schlicht and Kempenaers, 2020). It was expected that the percentage of movement (long distance activity, during a long observation timeline) when they were foraging in their territories declined or is constrained in the breeding season, while the hope rate (short distance activities in a minutes) would increase during the breeding season. Adult blackbird movement would be limited around the centre of their territories during the breeding season to guard mate and territory and protect the nest and chicks from predators. Hence blackbird movement behaviour would change to a quick foraging strategy. Blackbirds would try to provide food in the shortest time and concentrate on breeding activities and protecting territory. Depending on yearly rainfall and temperature, I predicted that blackbird activity would increase in drier and warmer years. This increase would result because weather parameters influence food availability (earthworms) for blackbirds and the greater search time is required when the weather is unfavourable (drier soil).

There has been no systematic attempt to answer how some individuals are more vigilant than others. In birds who are foraging, there is a trade-off between time spent vigilant and feeding rates. In addition, factors such as body mass, group size, experience and foraging technique may influence vigilance (Beauchamp, 2010). I expected vigilance to be higher in areas with more human disturbance and when more intraspecific neighbours were present. I also expected that juvenile blackbirds would show less vigilance because

of naivety to urban environmental stimuli. For territorial aggression, I predicted that blackbird aggressiveness would increase during the breeding season specifically prior to egg laying when males defend mates and female search for the nest locations. Moreover, blackbirds that with intraspecific neighbours should have higher rates of aggressiveness. Finally, I expected shyness to be influenced by sex and the number of human disturbances. Male blackbirds were expected to be bolder and forage in open areas. Both male and female blackbirds in crowded human areas should spent less time in open areas.

Second, I tested if selected behavioural traits of this urban population were individually consistent and repeatable over the long-term (three years) and among males, females and juveniles. Repeatability is an important aspect to understand the factors responsible for behavioural differences. On the one hand, I predicted that behavioural traits such as activity and vigilance would not be repeatable because the urban environment would present many daily challenges during daily foraging. Hence blackbirds would present plastic behavioural traits. On the other hand, I predicted that shyness and aggressiveness would be repeatable. Specifically, shyness in blackbirds would be associated with territory quality (safety, food availability, proportion of vegetation, human disturbance) and reflect a preference to forage in the open or within vegetation cover. I also predicted that male and female blackbirds should show consistent but different aggressive behaviour during breeding and non-breeding seasons.

Third, I investigated if there was a relationship between behavioural traits to confirm the evidence of behavioural syndromes. I expected more active blackbirds would be more vigilant. In addition, I expected a negative correlation between shyness and activity. Bolder blackbirds would spend more time foraging in open areas, while shyer ones would overall be less active. In addition, I predicted that more active birds had a higher level of aggression because more active birds would come in to contact with more conspecifics when they were foraging. Finally, I measured the reproductive success of individual blackbirds to determine the degree of correlation between behavioural traits and reproductive success. On the one hand, I expected that active birds had a higher breeding success because active birds have a higher chance of obtaining food resources and more options for their nest-site selection. On the other hand, I also predicted that shyer and more vigilant blackbirds would have a better chance of finding a safe location for their

nests and raising chicks because of their preference for more vegetated areas; hence shyer individuals might have higher reproductive success in urban areas.

3.3 Methodology

3.3.1 Species and study area

The common blackbird is a medium-sized thrush. They are sexually dimorphic in plumage, socially monogamous and partially settle on their territory year-round (Hatchwell et al., 1996). Male blackbirds have entirely black plumage with an orange-yellow bill, while females have dark brown plumage with brown-black wings, tail, and bill (Myers, 1955; Snow, 1956, 1958a). They mainly feed on invertebrates (earthworms, insects). They usually forage on the ground in pastures and lawns (Shukshina, 2019). Their foraging behaviour depends on rainfall, which influences the soil moisture and food availability in the soil (Greenwood and Harvey, 1978).

The European blackbird population is reported to have suffered from a sustained period of decline from 1970 to 1990s, followed by a recovery period between 1995 and 2008 (British Trust for Ornithology, https://www.bto.org/). Consequently, the species is evaluated as secure and has been listed in the green category since 2002. The population size is estimated between 79 to 160 million individuals, and 7.3 pairs per hectare in Europe alone (Bird Life International, 2012, Snow, 1988). Blackbirds in Europe are found in many habitats, including parklands, orchards, farmland, and urban areas.

Blackbirds were introduced to New Zealand between 1867 and 1879. Blackbirds are often considered as pests because they damage many fruit products in orchards and spread unwanted plant seeds like blackberry and elderberry (Williams, 2006). Nonetheless, blackbirds are also valuable dispersers of native plant seeds and consume pest species such as slugs, snails and other invertebrates.

Approximately seven pairs per hectare inhabit my study area. The study area is approximately 15 ha. Auckland is in a sub-tropical climate zone. The study area is composed mainly of open lands (lawns), bushes, green walls, and buildings. The low vegetation surroundings provide a range of potential nesting and brood-rearing locations. The open pastures provide extensive foraging areas and likely year-round food resources. The low topology and open vegetation of this area provides a suitable habitat for blackbirds.

3.3.2 Data collection

I collected behavioural data related to the blackbird's foraging activity in its territory over the daytime period (0800-1700 hours). Observations were mainly made in the non-breeding seasons from January to July and a few additional observations during the breeding seasons from August to November between 2017 and 2019. Blackbirds were mainly busy with breeding activities during breeding seasons, so their foraging was affected by mate attraction, nest building, incubation, etc. Hence, I primarily collected data from blackbirds prior the egg-laying stage.

As a part of another project in this area, many blackbirds were banded during 2017 at this campus. In this study, banded blackbirds were observed for as long as possible, from 4 to 28 minutes. At each location, once a blackbird had been sighted, the observer identified the bird by its colour band and waited for 5 minutes before recording observations to reduce the effect of the initial human disturbance (any encounter of a focal blackbird with human that stop and disturb the blackbird's normal daily activities). The observation was from at least 10 meters away to minimise the impact of observer presence on the blackbird's behaviour. All observations were taken with binoculars to identify the focal blackbirds and their neighbouring blackbirds. Furthermore, all information about blackbird activity was recorded in an ethogram. I measured behavioural traits using the data extracted from the ethogram. Two types of behavioural data were recorded. First, the proportion of time that the focal bird used the behavioural trait (state behaviour). Second, the occurrence rate of the behavioural trait (event). State behavioural traits included activity (movement), shyness-boldness and vigilance. Event behavioural traits included activity (hop rate), vigilance (peck rate) and aggression rate (Table 3.3.1). Behavioural observation normally took 28 to 30 minutes unless focal blackbird flew away or were not found by observer more than five minutes. Hop rate and peck rate were recorded separately from foraging behavioural observations to minimise the impact of individual habituation to the observer.

I also collected daily weather data from the nearest weather station, Auckland, North Shore Albany Ews station (obtained from Cliflow; https://cliflo.niwa.co.nz/). Daily weather data included maximum temperature (°C), minimum temperature (°C) and precipitation (mm). Moreover, reproductive measurements of blackbirds were recorded

by using a standard methodology (Murray Jr, 2000). Clutch size and number of fledglings were recorded during each breeding season from 2017 to 2019.

All aspects of this study were approved by the New Zealand Department of Conservation and Massey University Animal Ethics Committee (AEC/17 (Amended 01/14)).

Table 3.3.1. Behavioural traits of free-living blackbirds recorded during blackbirds' foraging. General definition and measurement criteria are presented in the following column.

Behavioural traits	General definition	Measurement parameters
Activity Movement (%)	Individual activity in a familiar environment (Spiegel et al., 2017).	• Percentage of time focal bird walked on the ground or moved in the tree during the observation period.
Hop rate		• The number of hops per minute.
Shyness	Response to a risky situation in the context of human avoidance (Azevedo and Young, 2006a).	Time spends in different coverage (not covered or open land (boldness) to highly covered (shyness). Hereafter, I only present the percentage of time that focal bird spent inside the vegetation.
Aggressiveness Aggression rate	Antagonistic responses to conspecifics (Benus et al., 1989).	• The number of aggressive conspecific interactions per 20 minutes
Vigilance: Vigilance (%) Peck rate	An alertness behaviour during foraging (Roche and Brown, 2013).	Percentage of time that the focal bird observed around himself/ herself to assess possible hazards in the open area. • The number of pecks per minute.

3.4 Statistical analysis

3.4.1 Behavioural variations

All analyses were conducted in R 4.0.4 (R Core Team 2021). Based on observations, I first presented the overall variation of behavioural traits as mean ± standard deviation (SD). I applied a generalised linear mixed model (GLMM) using package *lme4* (Bolker et al., 2009; Knudson) to test the impact of different factors (sex, age, season, year, time, the number of conspecific neighbours and human disturbances) on behavioural traits. I combined males, females, and juveniles as one category (age-sex). Bird identification (ID) was included in the models as a random factor. A GLMM with gaussian distribution was fitted for: movements (time%), vigilance(time%), aggression rate and shyness(time%). I also fitted a GLMM with poisson distribution for: hop (number of hops per minute), peck (number of pecks per minute) (Bates, Maechler, Bolker, & Walker, 2015). I also used the *lmerTest* package for quantifying p-values of fixed effects via Satterthwaite approximation of degrees of freedom (Kuznetsova et al., 2017). Accordingly, for each behavioural trait, I ran several models with different combinations of fixed factors. To select the final model, I performed the backward step removal of fixed factors, starting with the highest p-value. I used the following process to determine the best model. I first fit all the factors and ran the full GLMM model and calculated the AIC. I then removed the factor with the highest non-significant p-value and reran the reduced model. I compared the new AIC value with the previous model, if the AIC was lower, I continued the process and removed another factor. If the AIC of the reduced model was higher, then I stopped the model selection. The model with the lowest AIC value was selected as the final model for each behavioural trait.

3.4.2 The link between behavioural traits and daily weather parameters

I also applied a GLMM analysis to investigate the impact of daily weather parameters on behavioural traits. In all models, I used mean-centred behavioural traits as the response variables and daily weather parameters (maximum temperature, minimum temperature, and average rainfall) as fixed factors. Bird identification (ID) was included in the models as a random factor. I also selected the best model with the lowest AIC value as mentioned above.

3.4.3 Repeatability

To assess if blackbirds showed personality, I estimated the repeatability of the different selected behavioural traits. To calculate repeatability estimates (i.e., intra-class correlation, ICC; *sensu* Stoffel et al., 2017), I applied a repeatability analysis. The *rptR* package was applied for estimating repeatability and standard errors based on parametric bootstrapping (Stoffel et al., 2017). All assumed behavioural traits such as activity (movements and hop), aggressiveness, vigilance (vigilance%, peck rate), and shyness were included as the response variables and bird identification as a random variable. I tested the repeatability of traits across study years, seasons, and the age-sex group.

3.4.4 Correlation between behavioural traits

To determine the strength of correlation between behavioural traits (behavioural syndrome) recorded from observational data, I applied Pearson correlation coefficient using "*ggpubr*" package and significant results were presented by a linear regression graph. First behavioural traits were mean centred to allow us to estimate the strength and direction of selection on the trait (mean-centred behavioural traits). Then I tested for behavioural syndromes, for those traits were repeated significantly. I included the behavioural types (mean) of each individual. In this analysis, I excluded individuals with only one record of behavioural traits.

3.4.5 The link between behavioural traits and reproductive success

I assessed the impact of behavioural traits on reproductive success using package lme4 by running a GLMM analysis. First, I excluded behavioural data related to juveniles. In all models, I fitted reproductive parameters (number of eggs and fledged chicks per season) as the response variables in the models. In addition, I used mean-centred behavioural types of selected traits including movement (%), vigilance (%), shyness (%), and aggressiveness as fixed factors. Individual identification was included in the model as a random variable. I ran several models of combinations of selected behavioural traits. The best model was presented here as a final model. Finally, I presented the linear relationship result using package "*ggplot2*".

3.5 Results

3.5.1 Behavioural variations

Sixty-three colour-banded blackbirds were observed foraging for periods that ranged from 4 to 28 minutes. Observation periods of less than 4 minutes were excluded, resulting in 425 observations. Behavioural traits of 17 females ,11 juveniles and 29 males were recorded from 2017 to 2019. For general information regarding behavioural trait measurements and sample sizes, see Table 3.5.1.

Table 3.5.1. Observational data and focal behavioural traits (mean ± SD) of blackbirds from 2017 to 2019. The total number of observations (N) that recorded blackbird behavioural traits during foraging (sample size).

Trait	Sample size (N)	Mean ± SD
Record time (minutes)	425	15.3 ± 5.6
Movement (time %)	425	40.2 ± 26.8
Activity (hop rate)	449	15.6 ± 9.8
Shyness (time %)	425	30.0 ± 31.2
Vigilance (time %)	425	35.1 ± 27.3
Vigilance (peck rate)	466	12.6 ± 11.2
Aggressiveness (rate)	425	1.3 ± 2.40

3.5.1.1 Activity (percentage of movement)

In the movement model, I found that movement during foraging significantly differed across years (Table 3.5.2). The lowest percentage of foraging movement (mean ± SE: 30.7 ± 3.4) was recorded in 2018, while the highest percentage (mean ± SE: 50.4 ± 2.68) was reported in 2019 (Figure 3.5.1.A). Juvenile movement (mean ± SE: 36.5 ± 3.0, N = 67 observations) was not significantly different to movement by males (mean ± SE: 40.8 ± 1.8, N = 251) and females (mean ± SE: 41.3 ± 2.5, N = 107), (Kruskal Wallis test: $\chi^2 = 1.1$, df = 2, $p = 0.6$). However, blackbird movement in the morning was significantly greater than their movement in the afternoon (Figure 3.5.1.B). Blackbird foraging movement was highly variable within both breeding and non-breeding seasons and was not significantly

different between seasons (breeding season: mean ± SE: 33.1 ± 3.5, N = 58; non-breeding season: mean ± SE: 41.3 ± 1.3, N = 367) (Table 3.5.2).

Table 3.5.2. Results from the final model for the movement (%) in blackbirds (AIC= 3930.1). A significance level of $p \leq 0.05$ is shown by an asterisk (*).

Fixed variable	Estimate	SE	*z*	*p*
Intercept	29.78	4.69	6.35	≤ 0.001*
Intraspecific neighbour	0.65	0.79	0.82	0.41
Sex: Juvenile	-3.47	4.58	-0.76	0.45
Sex: Male	-0.57	3.47	-0.16	0.87
Season	6.28	4.03	1.56	0.12
Year: 2018	-7.53	3.71	-2.03	0.04*
Year: 2019	9.86	3.60	2.74	0.006*
Time category	7.06	2.80	2.52	0.01*

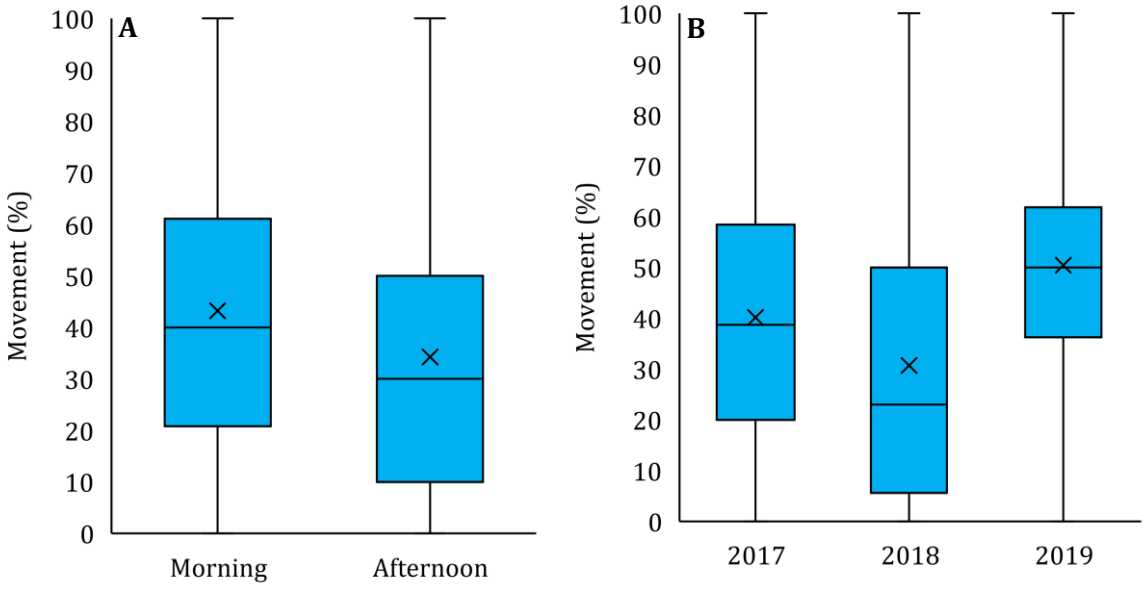


Figure 3.5.1. Box and whisker plots of movement (%) in blackbirds. A) Across study years (Observations 2017: N = 276, 2018: N = 76, 2019: N = 73). B) During the morning (N = 283) and afternoon (N = 142).

3.5.1.2 Hop rate

The hop rate (number of hops/minute) was strongly influenced by the year and season (Table 3.5.3). Among different years, the lowest yearly record of hop rate occurred in 2019 (mean ± SE: 10.2 ± 0.9), while the highest occurred in 2018 (mean ± SE: 18.0 ± 1.0; Figure 3.5.2.A). The hop rate also increased significantly in the breeding season (Table 3.5.3; Figure 3.5.2.B).

Table 3.5.3. Results from the final model for the hop rate in blackbirds (AIC= 4684.1). A significance level of $p \leq 0.05$ is shown by an asterisk (*).

Fixed variable	Estimate	SE	*z*	*p*
Intercept	2.78	0.06	48.12	≤ 0.001*
Season	-0.10	0.03	-3.69	≤ 0.001*
Year: 2018	0.09	0.03	2.69	≤ 0.007*
Year: 2019	-0.41	0.05	-8.51	≤ 0.001*

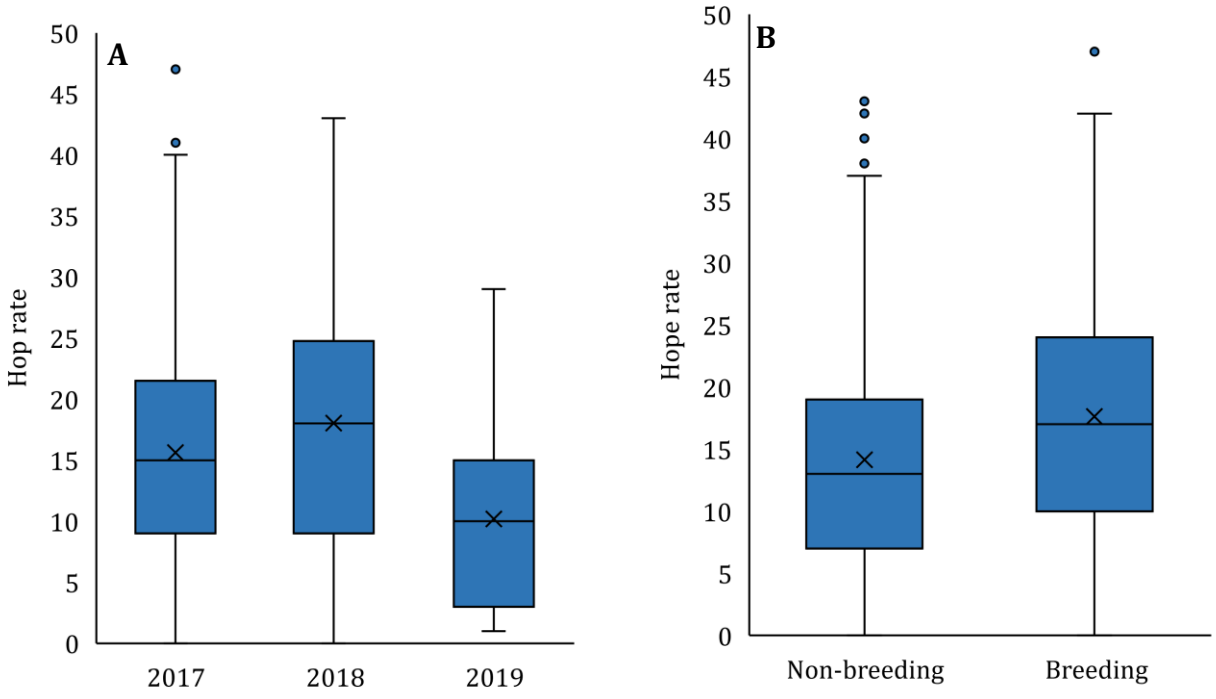


Figure 3.5.2. Box and whisker plots showing variation of hop rate in blackbirds. A) Across study years (2017: N = 293, 2018: N = 120, and 2019: N = 56). B) Across seasons (breeding season: N = 274, non-breeding season: N = 195).

3.5.1.3 Vigilance (%)

In the vigilance model, the year and number of neighbours influenced the model (Table 3.5.4). The lowest variation in vigilance occurred in 2019 (mean ± SE: 18.3 ± 1.9, N = 73 observations), while 2017 (mean ± SE: 20.6 ± 1.1, N = 276 observations) and 2018 (mean ± SE: 28.8 ± 2.8, N = 76 observations) were similar. Variation of vigilance behaviour varied significantly between 2018 and 2017 (Table 3.5.4).

Table 3.5.4. Results from the final model for the vigilance behaviour (%), (AIC = 3942.7). A significance level of $p \leq 0.05$ is shown by an asterisk (*).

Fixed variable	Estimate	SE	*z*	*p*
Intercept	17.25	1.85	9.31	≤ 0.001*
Intraspecific neighbour	1.49	0.62	2.38	0.01*
Year: 2018	8.68	2.60	3.33	≤ 0.001*
Year: 2019	-2.10	2.49	-0.84	0.39

3.5.1.4 Vigilance (Peck rate)

There was also significant variation in peck rate (number of pecks per minute) across the study years (Table 3.5.5; Figure 3.5.3.A). The peck rate was also significantly higher during the non-breeding season (Table 3.5.5; Figure 3.5.3.B).

Table 3.5.5. Results from the final model for the vigilance trait (peck rate, AIC= 5679.1). A significance level of $p \leq 0.05$ is shown by an asterisk (*).

Fixed variable	Estimate	SE	*z*	*p*
Intercept	1.96	0.14	13.54	≤ 0.001*
Sex: Female	0.20	0.15	1.38	0.2
Sex: Male	-0.06	0.16	-0.41	0.7
Season	0.34	0.03	10.05	≤ 0.001*
Year: 2018	0.15	0.04	3.44	≤ 0.001*
Year: 2019	0.11	0.04	2.51	0.01*

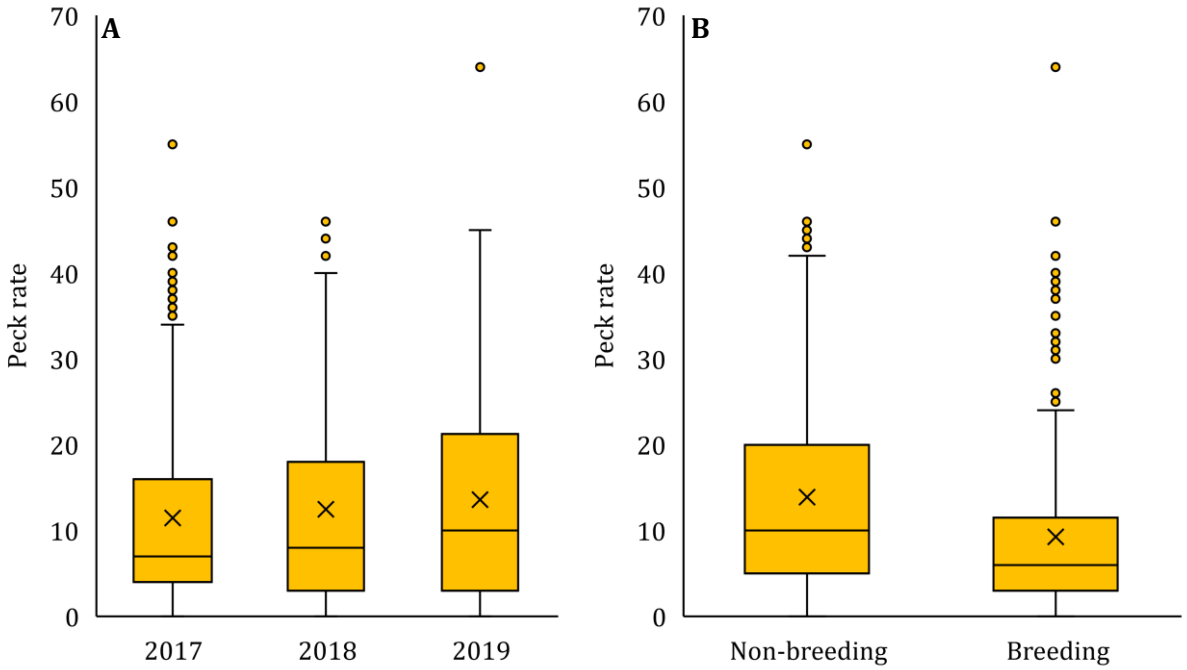


Figure 3.5.3. Results showing variation of peck rate. A) Across study years (2017: N = 329, 2018: N = 105, and 2019: N = 28); B) Across seasons (breeding season: N = 209, and non-breeding season: N = 283).

3.5.1.5 Aggressiveness (aggression rate)

In this model, year influenced the aggression rate (number of aggressive interactions between focal blackbirds and other blackbirds during the observation time, Table 3.5.6). Aggression rate was significantly higher during the breeding seasons (breeding season: mean ± SE = 2.4 ± 0.4, N = 58; non-breeding season; mean ± SE = 1.1 ± 0.1, N = 367). Moreover, aggressiveness was significantly higher in the morning (mean ± SE = 1.4 ± 0.1, N = 283) than the afternoon (mean ± SE = 1.1 ± 0.15, N = 142, Table 3.5.6). There was also a positive relationship between aggression rate and the number of blackbird neighbours present during observations (Table 3.5.6, Figure 3.5.4).

Table 3.5.6. Results from the best model for aggressiveness in blackbirds (AIC = 1895.20). A significance level of $p \leq 0.05$ is shown by an asterisk (*).

Fixed variable	Estimate	SE	*z*	*p*
Intercept	0.80	0.41	1.97	0.05*
Human disturbance	0.13	0.07	1.85	0.06
conspecific neighbour	0.63	0.07	8.51	≤ 0.001*
Sex: Juvenile	0.61	0.39	1.55	0.13
Sex: Male	-0.33	0.30	-1.11	0.28
Season	-1.29	0.33	-3.88	≤0.001*
Year: 2018	0.61	0.31	1.98	0.05*
Year: 2019	0.94	0.30	3.16	≤ 0.001*
Time category	0.54	0.23	2.33	0.02*

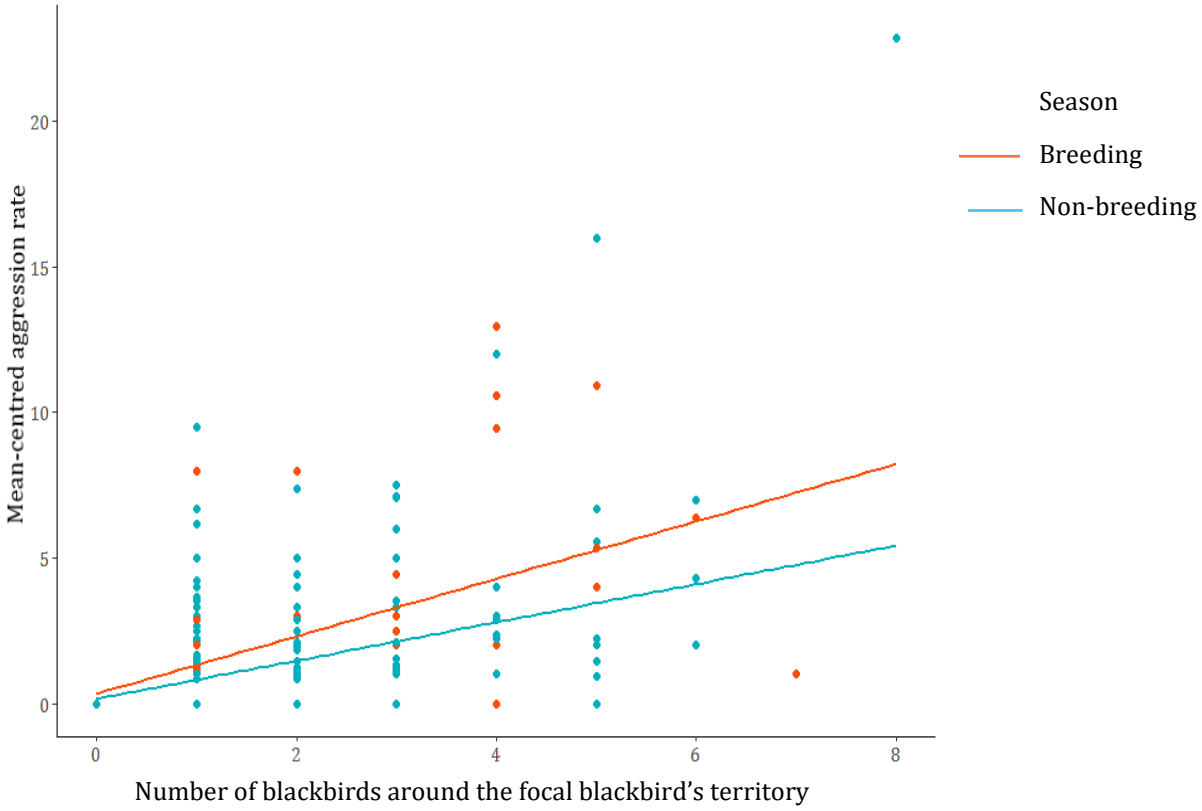


Figure 3.5.4. Correlation between the number of blackbirds (neighbours) observed near the focal bird's territory and aggressive behaviour.

3.5.1.6 Shyness

In the shyness model, year and age-sex variables affected the model (Table 3.5.7). Juvenile blackbirds spent less time within the vegetation compared to males and females (Figure 3.5.5.A). There was also a significant variation in shyness across years (Table 3.5.7; Figure 3.5.5.B). However, there was no significant variation in proportion to the time that blackbirds spent within vegetation between breeding (mean ± SE: 30.1 ± 3.9, N = 58) and non-breeding (mean ± SE: 29.9 ± 1.6, N = 367) seasons.

Table 3.5.7. Results from the final model for shyness (%), (AIC=4021.59). A significance level of $p \leq 0.05$ is shown by an asterisk (*).

Fixed variable	Estimate	SE	*z*	*p*
Intercept	35.72	5.40	6.61	≤ 0.001*
Intraspecific neighbour	-0.50	0.89	-0.56	0.6
Sex: Juvenile	-14.35	5.68	-2.53	0.01*
Sex: Male	-1.13	4.43	-0.26	0.8
Season: Breeding	7.46	4.49	1.66	0.1
Year: 2018	-26.43	4.17	-6.33	≤ 0.001*
Year: 2019	-21.48	4.06	-5.29	≤ 0.001*

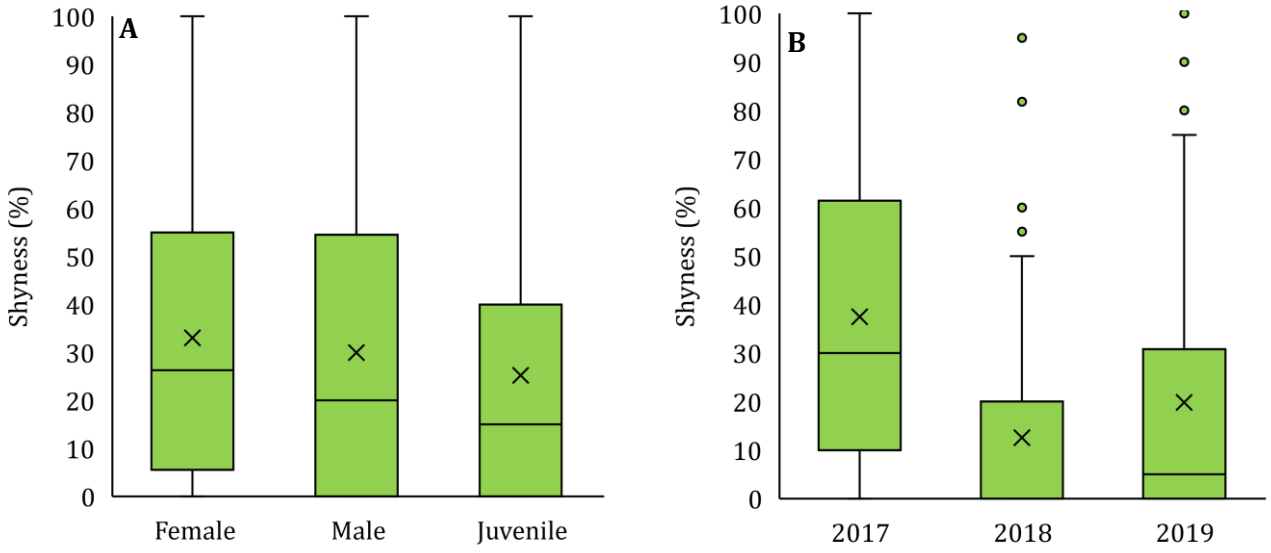


Figure 3.5.5. Results showing the variation of shyness (%) in blackbirds. A) Among males, females, and juveniles; B) Across years (2017: N = 276, 2018: N = 76, and 2019: N = 73).

3.5.2 Link between behavioural traits and daily weather

Results from the best model showed that blackbird movement was positively affected by daily maximum temperature during the non-breeding season (GLMM: Estimate = 1.08, SE = 0.43, z = 3.5, p = 0.001*, N = 347, Figure 3.5.6.A) and negatively affected by daily maximum temperature in the breeding season (GLMM: Estimate = -2.25, SE = 0.91, z = -2.46, p = 0.01*, N= 58, Figure 3.5.6.A). Hop rate declined with raising minimum temperatures (GLMM: Estimate = -0.26, SE = 0.10, z = -2.63, p = 0.01*, N = 449 records, Figure 3.5.6.B). Result showed that hop rate was negatively influenced by minimum temperature during breeding season (Figure 3.5.6.B). Vigilance increased with increasing minimum temperature in non- breeding season (GLMM: Estimate = 0.16, SE = 0.06, z = 2.35, p = 0.01*, N = 422, Figure 3.5.6.C). While minimum temperature did not influence the vigilance during the breeding season (GLMM: Estimate = -0.25, SE = 0.18, z = -1.35, p = 0.17). In addition, aggressiveness decreased with increasing maximum temperature (GLMM: Estimate = -0.11, SE = 0.03, z = -3.5, p = 0.001*, Figure 3.5.6.D). During non-breeding season aggressiveness declined by increasing temperature, while it did not change across the breeding season (Figure 3.5.6.D). None of the weather parameters were associated with shyness and peck rate.

3.5.3 Repeatability

Repeatability analysis was done for the measured behavioural traits. Aggressiveness, vigilance, activity, shyness, peck rate and hop rate had low repeatability scores (less than one; Table 3.5.8). Since R-values (repeatability) for some traits were low, I selected those behavioural traits that had a repeatability score of more than one for further analysis. I tested whether the selected traits were consistent across each of the three years (long-term). Results showed selected behavioural traits had low repeatability scores in 2017, while they were not repeatable in 2018 and 2019 (Table 3.5.9). In addition, repeatability estimations across the sex-age group showed that vigilance in juveniles was moderately repeatable (R = 0.45, $p \leq 0.001$*, N = 31 individuals). Repeatability of vigilance for both males and female were low (Male: R = 0.1, $p \leq 0.001$*, N = 26 individuals; Female: R = 0.01, p = 0.1, N =15 individuals). In addition, shyness had a low repeatability score in males; and it was not repeatable within females and juveniles (Male: R = 0.17, p = 0.08; Female: R = 0.1, p = 0.1; Juveniles: R = 0.07, p = 0.2).

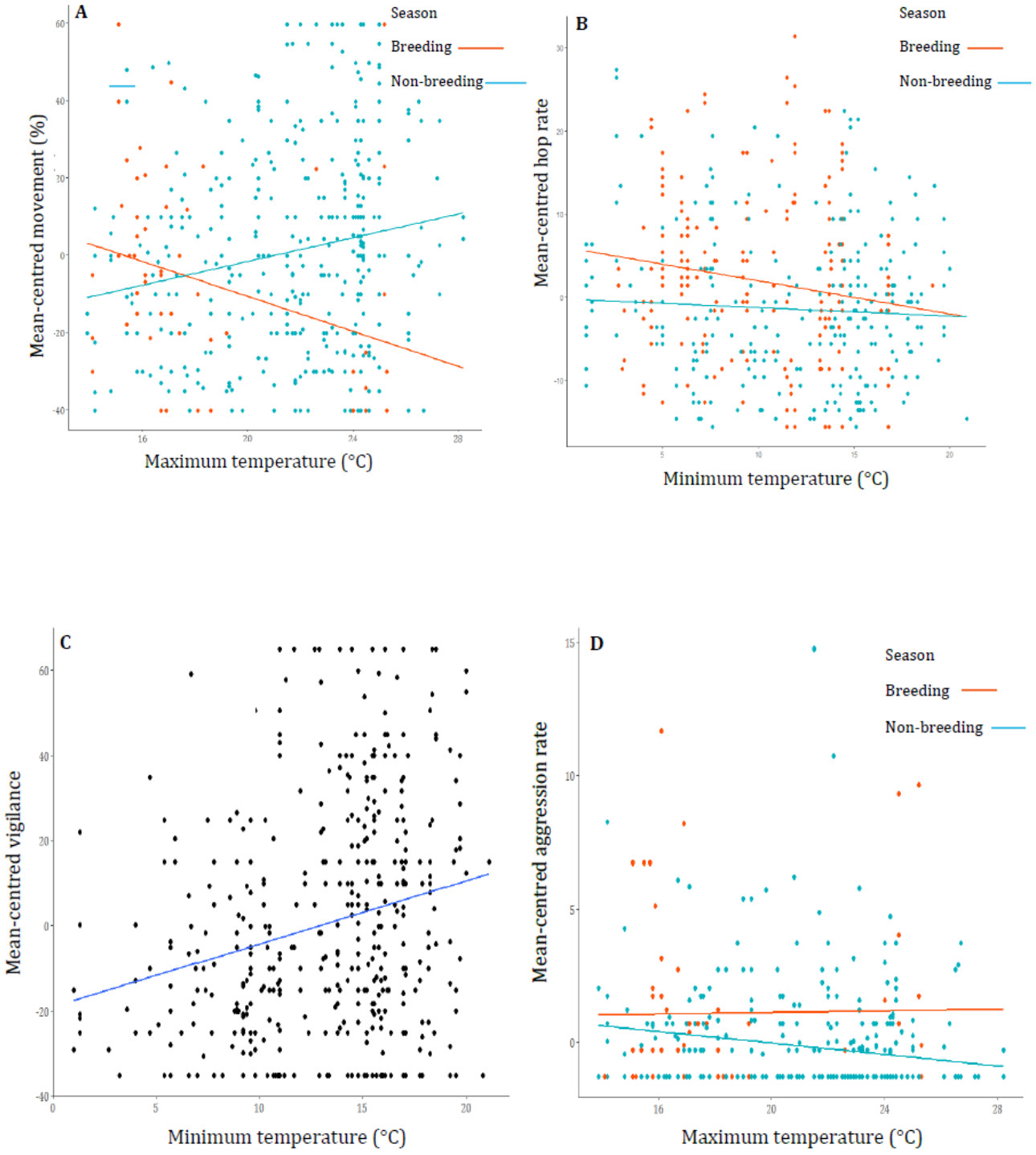


Figure 3.5.6. Relationship between behavioural traits and daily temperature. A) Relationship between percentage of movement and maximum temperature across breeding (N = 58) and non-breeding seasons (N = 347). B) Correlation between hope rate and minimum temperature cross breeding (N = 195)and non-breeding seasons (N = 274) in blackbirds. C) Relationship between mean-centred vigilance and daily minimum temperatures (N = 422). D) Relationship between mean-centred aggressiveness and daily maximum temperatures (non-breeding season N = 364; breeding season: N = 58).

Moreover, aggressiveness had low repeatability in males and was not repeatable in females and juveniles (Male: R = 0.1, p = 0.002; Female: R = 0.1, p = 0.10; Juveniles: R = 0.0, p = 1).

Table 3.5.8. Repeatability estimations for the measured behavioural traits over three-years of study. A significance level of $p \leq 0.05$ is shown by an asterisk (*).

Gaussian variables	R	SE	CI	*p*	*N*
Movement (%)	0.04	0.03	[0.00, 0.31]	0.04*	45
Vigilance (%)	0.13	0.04	[0.10, 0.23]	≤ 0.001*	45
Aggression	0.10	0.03	[0.06, 0.16]	≤ 0.001*	45
Shyness (%)	0.10	0.03	[0.05, 0.15]	≤ 0.001*	45
Activity (Hop rate)	0.04	0.02	[0.00, 0.06]	0.04*	64
Vigilance (Peck rate)	0.06	0.03	[0.00, 0.08]	0.02*	64

Table 3.5.9. Repeatability estimations for the selected behavioural traits for different years (N = number of individuals).

2017	**R**	**SE**	**CI**	***P***	**N**
Vigilance (%)	0.07	0.04	[0.05, 0.18]	0.02	30
Aggression (%)	0.10	0.06	[0.02, 0.16]	0.003*	30
Shyness(%)	0.14	0.07	[0.02, 0.27]	≤ 0.001*	30
2018	**R**	**SE**	**CI**	**p**	**N**
Vigilance (%)	0.09	0.11	[0.001, 0.31]	0.33	18
Aggression (%)	0.06	0.09	[0.00, 0.24]	0.16	18
Shyness(%)	0.21	0.08	[0.13, 0.30]	0.11	18
2019	**R**	**SE**	**CI**	**p**	**N**
Vigilance (%)	0.05	0.05	[0.00, 0.14]	0.9	18
Aggression (%)	0.35	0.16	[0.24, 0.51]	0.3	18
Shyness(%)	0.00	0.1	[0.00, 0.25]	0.4	18

3.5.4 Behavioural syndrome

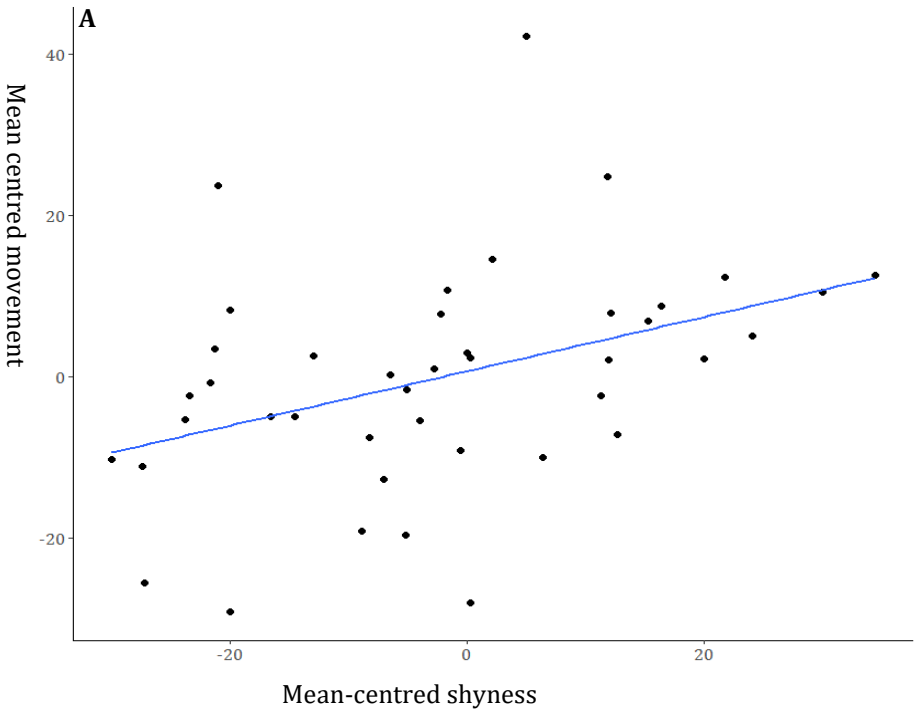
I tested my data for behavioural type correlations, and I found a positive correlation between activity and shyness traits (Pearson correlation: r = 0.40, p = 0.008*; Figure 3.5.7.A). Shyer blackbirds displayed more movement during their foraging.

Table 3.5.10. Pearson correlation coefficient and *p* value between selected behavioural types (N = 45 individuals). A significance level of $p \leq 0.05$ is shown by an asterisk (*).

	Vigilance	Aggressiveness	Shyness
Activity	0.1	0.12	0.40
P value	0.5	-0.23	0.008*
Vigilance		-0.2	-0.15
P value		0.3	0.31
Aggressiveness			-0.2
P value			0.25

3.5.5 The link between behavioural traits and reproductive success

The number of fledged chicks per year was associate by shyness (GLMM: Estimate = 0.01, SE = 0.01, z = 3.07, $p \leq 0.001$*). There was a positive relationship between shyness behavioural type and number of fledged chicks per season per individual (Pearson correlation: R = 0.51, $p \leq 0.001$*, Figure 3.5.7.B). In the best GLMM model for reproductive investment (the number of eggs), shyness was the only fixed factor and none of the other behavioural traits were associated with the number of eggs laid per season in blackbirds (GLMM: Estimate: SE = 0.01, z = 1.59, p = 0.13).



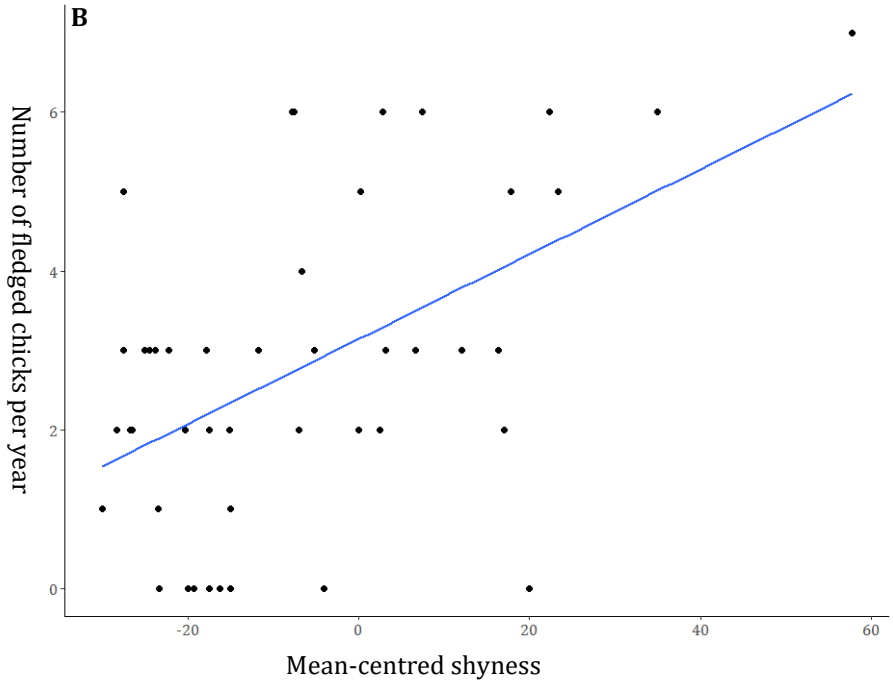


Figure 3.5.7. Correlation between behavioural traits and breeding paramters. A) Correlation between mean-centred shyness and mean-centred movement behavioural types (dots present individual behavioural type, N = 42 blackbirds). B) Correlation between total numbers of fledged chicks per season per individual and mean-centred shyness behavioural type, N = 45 blackbirds across 3 years of study.

3.6 Discussion

3.6.1 Behavioural variations

In this chapter I presented novel research on the behavioural traits of blackbirds. I investigated the intra-individual variations of traits in a free-living blackbird population. Although previous studies have examined blackbird foraging activities (Cresswell et al., 2001; Desrochers, 1992; Wysocki et al., 2015b; Greenwood and Harvey, 1978; Post and Götmark, 2006a), no studies to date have assessed foraging in blackbirds from the context of personality and plasticity of behavioural traits. I investigated variations in behavioural traits of blackbirds during their daily foraging activities and determined the level of plasticity and personality of these traits. Then I explored the link between behavioural traits and breeding success in blackbirds. I found that depending on the trait, behavioural variation significantly varied among years, seasons, and time category. Weather parameters significantly affected activity, vigilance, and aggression. In addition, I found that shyer blackbirds displayed more movement within their territories and had a higher reproductive success.

Since foraging success is unpredictable, individuals may face strong selection to begin their activity early in the day. I found that the movement levels of blackbirds were higher during the morning. I speculated that during the morning, conditions are best for foraging when more invertebrates are available (earthworm), and the ground is damp. Similar results reported for hooded Cranes, *Grus monacha*. It explains that individuals ensure that they have enough time during the day to search for food sources to survive the coming night, (Li et al., 2015). Foraging behaviour to be traded off against breeding activities such as singing behaviour in males, nest building, egg-laying and incubation in females, and parental care (Schlicht and Kempenaers, 2020). I did not find significant variation in the percentage of movement across the breeding and non- breeding season, while I found hop rate increased during breeding season. It could be interpreted that during the breeding season overall time for foraging would change because of longer day length and breeding activities, so any trade off with other breeding activities is compensated for by these longer daylengths. In addition , increasing hope rate during the breeding season can suggest an optimising strategy foraging in blackbird.

As I found that behavioural traits were highly varied among study years. Annual difference in weather is a possible explanation. Weather conditions strongly influence the decisions of individuals to express different levels of a trait like activity (Pravosudov and Grubb, 1995; Schlicht and Kempenaers, 2020). Weather parameters also influence food availability and metabolic costs (keeping warm) (Grubb, 1978; Lambertucci and Ruggiero, 2013; McKinnon et al., 2012; Tulp and Schekkerman, 2008). Therefore, exploration of the relationship between behaviour and weather would help to further explain behavioural variation in common blackbirds.

From 2017 to 2019, the highest yearly rainfall was recorded in 2018 (mean ± SD: 4.2 ± 9.1 mm), 2017 (mean ± SD: 3.8 ± 11.5 mm), and 2019 (mean ± SD: 2.5 ± 5.6 mm). The highest records of blackbird yearly activities (the percentage of movement) were reported in 2019 (mean ± SE: 50.4 ± 2.7), 2017(mean ± SE: 40.1 ± 1.6), and 2018 (mean ± SE: 30.7 ± 3.4). I speculated that there may be a relationship between higher yearly rainfall and lower activity in blackbirds, perhaps due to greater or more accessible food resources. I suggested that during drier years (i.e., 2019) blackbird required to move more to obtain food, but in years with high rainfall (i.e., 2018), the damp ground provides good access to food (earthworm); therefore, they did not spend time moving over longer distances. However, yearly variation of hop rate across different years, another indicator of activity, did not follow the same pattern. My research also found a positive correlation between daily maximum temperature and the percentage of movement in blackbirds. Confirming my results, studies on songbirds explain that songbirds are generally day-active and vision-dependent, so there is a positive correlation between daylight and activity (Steinmeyer et al., 2010). Longer days (longer daylight) are generally warmer (spring and summer), so blackbirds spent more time moving during warmer and longer days.

Vigilance is considered the result of a compromise between time spent consuming/catching enough food (foraging) and avoiding predators (Li et al., 2015). Different parameters may influence vigilance and foraging behaviour in an individual, such as, the degree of hunger, group size and weather conditions (Beauchamp, 2010; Reboreda and Fernandez, 1997; Westcott and Cockburn, 1988). Assessing these factors can explain the variation of foraging and vigilance behaviour in many species (Li et al., 2015). In lower temperatures, individuals must maintain and increase their metabolic

rate; a higher metabolic rate requires more energy, which leads to more intensive foraging and less time being vigilant (Pravosudov and Grubb, 1995). I found that in higher temperatures, the percentage of time that birds were vigilant increased. I suggested that this could be to seasonal increase in predator numbers, but it could also be related to breeding activities such as nestling stages where parental vigilance is beneficial for chick survival.

I did not find sex differences in vigilance or peck rate, but there were significant seasonal differences in peck rate. Seasonal differences in peck rate were possibly affected by food sources (in different seasons) and breeding activities. A study on the greater Rhea, *Rhea Americana*, shows that birds are more vigilant towards possible predators and hazards that threaten their breeding, and consequently, peck rates decrease (Reboreda and Fernandez, 1997). During the breeding season, blackbirds also decrease their peck rate during foraging and are potentially influenced by the breeding stage and territorial defence. In many species, energy stores are deleted following breeding and peck rate and time spent foraging increase to compensate (Beauchamp, 2010; Blanchard and Fritz, 2007; Brown, 1999). I found that blackbirds also spent more time searching for food in non-breeding seasons and less time in vigilance behaviour, but the ultimate cause could not be determined.

In this study, I demonstrated that blackbird aggressiveness was influenced by year, season, time of day, and the number of conspecific neighbours. There was a possibility that in drier/warmer years individuals must spend more time finding food sources and the availability of food was limited in years with less rain (from highest to lowest: 2018 = 4.19 mm, 2017 = 3.76 mm, 2019 = 2.51) and warmer days (from highest to lowest: 2019 = 20.15 °C, 2017 = 19.57 °C, 2018 = 19.58 °C). Therefore, there may be higher levels of competition between individuals, which results in variation in aggressive behaviour across years (aggression rate from highest to lowest: 2017 = 1.23, 2018 = 1.28, and 2019 = 1.74). Results also showed a significant variation of aggressiveness between the years 2017 and 2019. In 2019, the average yearly rainfall was lower than years 2017 and 2018. In addition, the average maximum temperature was also higher than the other years. In my study, the highest aggression rates in blackbird were recorded in 2019 (aggression rate per 20 minutes: 22. 86, 16, and 12.94).

Additionally, many studies explain that an increase in the steroid hormone testosterone leads to a higher rate of territorial aggression of individuals during the breeding season. Competition and protecting for territories and mating is expected to be high during breeding seasons (Araya-Ajoy and Dingemanse, 2017; CôTé, 2000). This study also confirmed a rise in aggression rate during the breeding season. Moreover, aggressions rates were higher in the morning for blackbirds, individuals moved more around their territories during the morning, so the chance that they encounter more intraspecific individuals also increases, hence they showed more territorial aggression toward conspecifics.

While there were no significant differences between males and females in shyness, my GLMM model for shyness detected a significant variation between juveniles and females. Different demographic factors likely combine for individuals that make decisions about where to forage i.e., open versus vegetated areas. These factors include predation pressure, age, sex, body size, and internal state, including hunger (Guinet et al., 1998; Jennions and Telford, 2002). In blackbirds I found that juveniles appear to take more risks by spending more time in the open, this may be due to predator naivety in contrast to adult blackbirds that prefer to forage in more vegetated areas , or adult blackbirds push juvenile toward the open lands .

3.6.2 Repeatability

I found the behavioural traits I compared in blackbirds to overall lack repeatability. Similarly, research on dunnocks, *Prunella modularis*, has reported low repeatability for activity and vigilance (peck rate) (Holtmann, 2016); in contrast, studies on chestnut thrush (*Turdus rubrocanus),* sparrows (*Passer domesticus)* and great tits(*Parus major)* show consistency of aggressiveness and boldness (Bókony et al., 2012; Funghi et al., 2015; Holtmann et al., 2017a). My results demonstrated that the behavioural traits I measured were relatively plastic or flexible (less repeatable) within blackbirds. Plasticity of behavioural traits in free-living blackbirds may be related to a greater environmental variance in natural environments compared to laboratory situations (Bell et al., 2009; Mousseau et al., 2000). Habituation and adaptation in urban environment might increase their behavioural plasticity in response to environmental challenges. Although some studies have estimated high repeatability of behavioural traits in a controlled laboratory situations (for example, Riyahi (2017) reports for great tit), I quantified traits in the

foraging context of natural environment. Thus, the circumstances resulting in the emergence of behavioural repeatability were not controlled.

In a wild situation, different factors such as the degree of hunger, weather, body condition and intraspecific interactions may affect the decision of an individual to express specific degree of a trait (more or less plastic). Even though estimating personality traits under natural situations may be difficult, there are some issues with laboratory studies. First, behavioural traits that are expressed under laboratory situations may not reflect the expression of a trait under natural situations (Bell et al., 2009). Second, catching, handling and introducing wild birds into an experimental set up will elevate stress levels in individuals, which may alter the expression of some of all behaviours (Fisher et al., 2015). Hence, measuring behavioural traits in a natural environment will provide more relevant information on variations of behavioural traits.

I only found a moderate repeatability of vigilance within juvenile blackbirds, I concluded from these results that juveniles were less aware of predator or human disturbance in open areas and consistently present a less vigilance behaviour. This repeatability declines with age as (presumably) experience with predators is gained by an individual. Vigilance in adults was more plastic and was expressed with flexibly in response to daily disturbances in human environment (human disturbance, lawn mowing, sound noise). Within the context of a diverse environment, plasticity in traits may provide a successful adaptation to urban environments in urban birds.

3.6.3 Behavioural syndrome

I only found a strong correlation between shyness and activity behavioural types. Shyer individuals were moved more within their territories compared with bolder individuals. In many studies on animal behaviour, behavioural syndrome analysis has shown that "Proactive" individuals vary in a suit of correlated behaviours where individuals are bold, active, fast explorer and aggressive, while "Reactive" individuals are shy, less active, slow explorer and less aggressive (Bell, 2005b; Bell and Sih, 2007b; Dingemanse et al., 2010). Positive correlation between shyness and activity are not consistent with these other studies and the drivers of this correlation should be explored in the future. For example, do shyer birds occupy lower quality territories and hence need to spend more time foraging?

3.6.4 The link between behavioural traits and reproductive success

Despite a growing body of evidence linking boldness to a better reproductive success in several species (Ballew et al., 2017; Collins et al., 2019; Smith and Blumstein, 2008), results from my study showed the opposite result. In blackbirds, shyness was coupled with a higher number of fledglings, and I speculate that there could be a relationship between reproductive success and shyness. Shyer blackbirds spent more time in cover and would be less easily detected by predators. This could also lead to lower detectability of parents and chicks at the different stages of breeding. In addition, a higher level of movement by shyer individuals on their territories might improve foraging success by increasing the probability of encountering food items. Higher movement levels may also result in better detection of quality nesting sites. I suggested that shyness is an important characteristic for the breeding success of blackbirds in urban environments. Further studies should explore the links between predator detection, foraging success and shyness in blackbirds.

The results presented here provide field-based insights into the concepts of personality and plasticity of foraging behavioural traits and reproductive success. I speculate about how different factors might influence the variation of behavioural traits in free-living individuals. Specifically, weather conditions influenced the vigilance, aggressiveness, and activity traits of blackbirds. In addition, aggressiveness varied between seasons and time of day, and finally, the number of conspecific encounters influenced aggressiveness in blackbirds. Territorial aggression is expressed at different times in the life cycle. Moreover, there appears to be an advantage to being shy associated with increased foraging activity and reproductive success.

Overall, these factors may reflect behavioural differences in the coping abilities of individuals in different scenarios, and some individuals may express specific behavioural traits that are well matched to inhabiting urban habitat (Mathot and Frankenhuis, 2018, 2018). The general approach taken in this aspect of my research could be a useful baseline for further studies of behavioural traits of free-living animals. These results also lead to several questions concerning the influence of environmental challenges on behavioural traits at the level of intra-and inter-individual. For example, how much of

behavioural variation can be explained by genetic and environmental conditions? How does individual behavioural plasticity explain the adaptation of behaviour in urban areas? Which component of urbanisation most strongly influences behavioural variation of urban adapted birds? How do personality and plasticity mechanisms apply in the daily behavioural responses of free-living birds? How do personality and plasticity of behavioural traits differ between urban and rural blackbird populations?

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Chapter 4:

Risk-taking, neophobia and antipredator behavioural traits in common blackbirds

A male blackbird attacking a morepork model.

4.1 Abstract

Consistency in behavioural traits varies among individuals and can be an indicator of parental investment strategies. However, little is known about variation in combined behavioural responses between reproductive pairs where investment is shared between individuals. In this study, I investigated risk-taking (flight initiation distance), neophobia and antipredator traits in individuals and pairs of brooding blackbirds from 2017 to 2019. I quantified these behaviours in blackbirds to investigate 1) the influence of different factors (sex-age, time, season, year) on various traits; 2) repeatability of behavioural traits; 3) behavioural phenotype correlations (behavioural syndromes); and 4) their fitness consequences on breeding success in blackbirds.

I found that blackbirds were more risk-taking during the breeding season than non-breeding season. I found risk-taking behaviour (FID) for juveniles was moderately repeatable. In addition, risk-taking for males and females was moderately consistent during the breeding season but tended to decrease in the non-breeding season. In addition, blackbirds who were risk-takers (shorter FIDs) produced more eggs per season. While blackbird reproductive success (number of fledged chicks) was not affected by risk-taking behaviour.

My results from the neophobia experiment showed that there were no differences between males and females in their responses to novel objects. Inspection and movements of blackbirds significantly increased in the presence of the novel object, while the nest visit decreased. Depending on the colour of the novel object, the inspection time of the second repeat of the novel object took a shorter time. My results have shown moderate repeatability in inspection and movements within paired blackbirds. In contrast, parental nest visits had a low repeatability estimation. Movements of blackbirds significantly increased around the nests with a greater number of chicks.

I observed the aggressive response of paired blackbirds toward the predator model (nest-defence behaviour = attacks and alarm calling) and post-stress behaviours in paired blackbirds toward a predator model. My results indicated consistent between pair responses, with some highly aggressive pairs and other less aggressive ones. Blackbird pairs show a coordinated response in nest defence behaviour (similar antipredator response between male and female in 80 percent of nests). I also found a significant

relationship between attacks and the age of chicks in the nest. Pairs that had more chicks at the nest presented a higher aggressive response (alarm call). I found that post-stress responses to the predator (latency to feed chicks and the number of post-stress nest visits) were related to breeding parameters. Pairs that had more chicks returned to their nests sooner (shorter latency) after a simulated predator presentation and had more post-stress nest visits. Finally, my results from behavioural syndrome analysis showed that risk-taking blackbirds were more vigilant (chapter 3). I did not find any correlation among other behavioural traits.

These findings demonstrate that risk-taking, neophobia, and antipredator behavioural traits can influence breeding investments in blackbirds. Results from neophobia and antipredator traits support the compatibility of males and females as pairs in response to novelty and predator to protect their investments.

4.2 Introduction

Animals are traditionally believed to be flexible and to adjust their behaviours according to their environmental challenges (McCowan et al., 2015b; Zandberg et al., 2017). However, recent work on animal behaviour has presented a new concept, "animal personality". Personality refers to consistent behavioural differences among individuals across different contexts over time (Dingemanse et al., 2004). Personality has been extensively studied in a wide range of taxa, along with a major number of behavioural traits like boldness, risk-taking, aggressiveness, antipredator, exploration and neophobia (Beletsky, 1983; Fox and Millam, 2007; Holtmann et al., 2017b; Kruuk, 1964). Personality may also be heritable and have fitness consequences (van Oers and Naguib, 2013a). For example, a study on the great tit, *Parus major*, shows that early exploratory behaviour is a heritable personality trait over four generations (Drent et al., 2003b). In addition, studies on blue tits, *Cyanistes caeruleus*, show that consistent variation in neophobia and boldness correlate to breeding success and biomass of broods in the urban environment (Colchester and Harrison, 2016). Another study on this species explains that slow–explorative females have higher nest success (Both et al., 2005). Therefore, variability of behavioural traits may have important ecological and evolutionary implications (Smith and Blumstein, 2008)

A standard way to measure risk aversion is the distance at which animals move away from an approaching predator, including humans, the so-called flight initiation distance (FID)(Weston et al., 2012). In the flight initiation distance, an individual usually minimises the cost of fleeing, walking and running away by not escaping away from the threat until the cost of remaining exceeds the cost of escaping (Blumstein, 2003). The cost of escaping is influenced by several factors such as locomotion energy, leaving a good foraging patch, foregoing an important activity like mating, and increasing the chance of conspicuousness to the predator (Blumstein, 2003; Seltmann et al., 2012; Weston et al., 2012). A study on dunnocks, *Prunella modularis*, revealed FID is a repeatable trait (personality), and birds become risk-takers with increasing age in areas with crowded human disturbance (Holtmann et al., 2017b). Another study on burrowing owls, *Athene cunicularia*, explains that individuals who have nests closer to the road have shorter FIDs than individuals who have nests located further from the road (Carrete and Tella, 2010).

Hence, it is expected that animals vary in their escape decision (FIDs) based on their risk assessment and experience (Evans et al., 2010b).

Additionally, individuals may habituate to a repeated stimulus which is a reduced reaction to the stimulation. Habituation would not be ascribable to fatigue or sensory adaptation (Martin and Réale, 2008). In urban environments, adaptation to human presence means that animals do not see humans as potential predators. This allows the individual to behave normally (Metcalf et al., 2000; Mikula, 2014; Morelli et al., 2018). Another study on this species displays males were less flexible than females in their stress response pattern. Less aggressive penguins habituate quicker than more aggressive conspecifics. Although individuals may habituate to the human approach, unregulated tourist visits at nest sites appear inappropriate and have a negative impact on nesting opportunities (Ellenberg et al., 2009). Therefore, different levels of habituation in individuals may also have fitness consequences and may lead to contemporary evolutionary change in the composition of breeding populations.

Animals can be deterred by (neophobia), attracted to (neophilia), or reluctant to unfamiliar stimuli (Camín et al., 2016). An indicator of an animal's perception of risk, as well as tendency to take a risk, is neophobia. Neophobia, or the uncertainty towards a novel object, food item, or place, is an important factor influencing the foraging behaviour of animals (Echeverría and Vassallo, 2008). Variation in latency to approach novel objects may lead to foraging specialisation since an increase in neophobia will reduce the number of microhabitats that a bird may be willing to explore (the 'neophobia threshold hypothesis')(Greenberg, 1983). For example, a study on wild-caught starlings, *Sturnus vulgaris*, shows that individuals have consistency in their latencies to feed near a variety of novel objects (Boogert et al., 2006). In general, individuals with high behavioural flexibility tend to explore novel objects, places, or situations more than individuals who might avoid novelty; therefore, neophobic individuals tend to remain more specialised (Mettler and Shivik, 2007).

When individuals detect a threat**,** a typical anti-predator response is to first inspect the threat (Carter et al., 2012). Then, individuals may show different levels of other responses. Some individuals may inspect and then approach the predator, while others may flee or find shelter (Magurran, 1986). Understanding antipredator behaviour has motivated behavioural researchers to investigate different aspects of this trait in the

concepts of personality and plasticity (Azevedo and Young, 2006b; Quinn and Cresswell, 2005), benefits driving the interaction among prey individuals (Hilton, 1999), behavioural adjustment (Holtmann et al., 2017b), pair nest-defence strategies, and its influence on life-history traits (Both et al., 2005; Schuett et al., 2011; Vrublevska et al., 2015). For example, a study on dumpling squid, *Euprymna tasmanica*, explains that individual responses to the predator were repeatable as shy individuals avoid the predator while bold individuals attack the predator (aggressive response)(Sinn and Moltschaniwskyj, 2005). In addition, analysis of repeatable behavioural traits like antipredator behaviour provides evidence for a link between antipredator personality traits and fitness consequences. Nest defence behaviour as a response to the predator is thought to be linked to offspring survival. For instance, personality studies on western bluebirds, *Sialia Mexicana*, show that more aggressive males feed their females less frequently during incubation and they have fewer fledged chicks (Duckworth, 2006).

Although personality studies have investigated the effects of individual personality on breeding success and survival, few studies have addressed behavioural similarity within mated pairs and its impact on breeding investments (Both et al., 2005; Burtka and Grindstaff, 2015; Fox, 2007; Laubu et al., 2016). Behavioural traits may signal an individual's quality as a mate and show how individuals' traits match (coordinate) with their mates' traits (Dingemanse et al., 2004). Hence, an effective mating relationship may depend on results from interactions between mates. These results include complementarity or compatibility between genotypes and phenotypes of mates (Burtka and Grindstaff, 2015; Fox and Millam, 2014). Pair bonds, mate choice, parental provision, divorce and nest-defence behaviours have been investigated within the concept of compatibility between mates (Koeninger Ryan and Altmann, 2001). A study on cockatiel pairs, *Nymphicus hollandicus* (monogamous Australian parrot), shows how personality traits of pairs predict compatibility and breeding success. Pairs with higher levels of behavioural compatibility in agreeableness have a greater proportion of fertile eggs than less compatible pairs (Spoon et al., 2006).

Although blackbird behavioural traits have been studied broadly around the world (Grégoire et al., 2003; Groom, 1993; Ibáñez-Álamo and Soler, 2017; Kryštofková et al., 2011; Miranda et al., 2013), there is little research investigating personality and plasticity of behavioural traits in free-living blackbirds. To address variation in behavioural traits

of a blackbird population, I investigated six main questions: 1) Are there significant differences in behavioural traits (risk-taking, aggressive response toward a predator, and neophobia) between sexes and across different age classes of blackbirds? 2); Are there significant differences in behavioural traits across the seasons?; 3) How does human disturbance influence neophobia and aggressive response toward a predator in blackbirds?; 4) How consistent are individual blackbirds across different behavioural traits during breeding vs non-breeding seasons within individuals and pairs?; 5) Are different behavioural traits correlated within individuals, i.e., form a behavioural syndrome?; and 6) How do behavioural traits correlate with fitness, e.g., breeding success? In risk-taking research, I predicted that FID would correlate positively with start distance (indicating a temporal margin safety). I hypothesised that adult blackbirds would have greater FIDs than juveniles due to adults having more experience with human disturbance; hence adults would respond quicker than juveniles. I expected that FIDs of blackbirds in the breeding season would be greater than in the non-breeding season. Individuals would be more responsive around nests to protect their territories. I also expected that risk-taking behaviour would not be a repeatable trait within individuals. Blackbirds' risk-taking behaviour should be flexible to adapt to urban challenges (unpredicted human disturbance, noise disturbance). Finally, I expected risk-taker individuals would have a greater breeding success. Because less risk-taker individuals would search more for food sources and mating opportunity, therefore they might have higher breeding investment and success.

If neophobia is prevalent, then I hypothesised that blackbirds would spend less time inspecting unfamiliar objects near their nest. They may visit the nest less frequently compared with the normal visiting rates to nests. I also expected that blackbirds in the second presentation of the novel object would be less curious and spend less time inspecting the unknown object. I also expected that the repeatability of neophobia responses would be low within individuals while it would be more repeatable within paired blackbirds. Because males and females share parental care; hence as a unit (pair), they would show compatibility in inspecting the objects around the nest as a unit (pair). For example, while the female or male is feeding chicks, the partner would assess hazards around the nest. I also expected that the blackbird response to the novel object would vary depending on the number and age of chicks in the nest. Blackbirds with more chicks

and/or older chicks would be more responsive to the novel object because of their parental investment and the fitness 'value' of older chicks.

In terms of an aggressive response toward a predator (anti-predator behavioural trait), I expected that paired blackbirds would have different intensities of nest defence tactics toward the predator model as their circumstance (number of chicks, and age of chicks) and their behavioural responses would differ from other pairs. However, male and female as a pair would present similar nest defence reactions. Depending on the number of nestlings, pairs with more chicks in their nests would have a stronger response. The anti-predator response would also be higher when chicks are older because chicks are more "valuable" as they are closer to fledgling. After hiding the predator model, I assumed that pairs would need time to recover from the threat and return to normal parental care., i.e., a latency period and those differences will exist between pairs in latency times to feed chicks. I predicted a reduction in the number of visits and an increase in latency to feed chicks in post-traumatic situations. I propose that latency and nest visits would also depend on the number of chicks at the nest. Pairs with more chicks would return to nest duties earlier than pairs with fewer chicks because of the higher cost of failure. Moreover, the repeatability of responses to the predator in pairs was expected to be higher than individuals due to the cooperative nature of nest defence strategies between males and females. Overall, there might be a potential fitness payoff for parents, selection acts on future, as yet, uncommitted investment, rather than the investment made in the past. Further, while parents might perceive a greater risk to leaving chicks of larger broods unattended, the other side of the parent-offspring communication underpinning begging is that larger broods are likely both hungrier and more vociferous

Finally, I also predicted a link between behavioural traits and evidence of behavioural syndrome. Risk-taker blackbirds were expected to be less neophobic and more aggressive (toward the predator). I also anticipated that neophobia and antipredator behavioural traits would not correlate with risk-taking traits and behavioural traits recorded from daily foraging (chapter3: movement, vigilance, aggressiveness -toward intraspecific, shyness). This is because the type of challenge or stress in antipredator and novelty context might differ from the daily challenges of urban blackbirds. In neophobia and antipredator experiments, male and female responses would be cooperative. In

addition, the level of danger in the antipredator experiment is high; therefore, I expected an intense and similar response from a paired blackbird.

4.3 Methodology

4.3.1 Study area and species

The study area is approximately 15 ha and is located on the North Shore of New Zealand's largest city: Auckland. Auckland is located in a sub-tropical climate zone. The study area is composed mainly of open lands (lawns), bushes, green walls, and buildings and it is a low-density urban area. The low vegetation surroundings provide a range of potential nesting and brood-rearing locations. Average summer daytime air temperatures vary from 22°C to 26°C and rarely exceed 30°C. Winter daytime average air temperatures vary from 12°C to 17°C. The regular annual sunshine is also about 2000 hours in most areas. Winters are the most unsettled time of the year and are subject to frequent rainfall. Storms of tropical origin in summer and autumn bring high winds and heavy rainfall from the east or northeast (Sturman and Tapper, 2006).

My study area has a large population of common blackbirds, *Turdus merula*, with approximately 6.7 pairs per hectare. Pairs are socially monogamous and stay on their territories throughout the year. Male blackbirds are all black with a yellow/orange bill and eye-ring. Female blackbirds have mainly dark brown plumage (Hatchwell et al., 1996d). The male starts singing a melodic and complicated song in the breeding season in the study area (from late August to late December). The female concentrates on nest building and incubation, while the male does not assist in this activity. However, males provide food for the female when the female sitting on the nest. Females generally lay three blue-green eggs and incubate for 13-14 days. Chicks are blind and naked when hatched. Both male and female feed the chicks. Chicks are fledged at 13-15 days and become independent at 28-31 days. Depending on the number of fledged chicks, the female will decide whether both the male and female can look after fledged chicks for the next two weeks(Ibáñez-Álamo and Soler, 2017). In some instances, the male can look after the chicks while the female starts a new breeding cycle (Faivre et al., 2001; Kentish et al., 1995; Niethammer, 1970; Tomia, 1993).

I collected data over three years (breeding seasons and non-breeding seasons) from 2017 to 2019. I investigated an individually colour-banded population of common blackbirds (hereafter blackbirds).

4.3.2 Data collection

4.3.2.1 Risk-taking

In this experiment, the response of an individual blackbird to a human approach was measured by flight initiation distance (FID) as a measure for risk-taking or boldness (Rodríguez-Prieto et al., 2011). While an individual blackbird was foraging on the ground, I identified a focal bird from its colour band and observed it for a minute to make sure the bird was foraging normally. Then, I started approaching the focal bird from a distance between 15 to 35 meters (start distance) at a consistent speed in a straight line (1 meter per second, I practiced approaching the bird at a consistent speed by walking in a specific time). When the focal blackbird decamped (either by flight or by foot), I stopped approaching. Then I used a rangefinder to measure the distance between my location and the point at which the blackbird decamped (FID) (+/- 1 meter, Bushnell Sport 450, all FID under one meter considered as 0.5 m) (Carrete and Tella, 2010; Holtmann et al., 2017b; Weston et al., 2012). I also recorded data related to the sex and age of focal blackbirds and the date of the experiment.

Figure 4.3.1. The novel object used in this research.

4.3.2.2 Neophobia

I conducted a novel object experiment during the 2018 breeding season when paired blackbirds had their chicks at the nests and nestlings were 3-10 days old. The novel object experiment was carried out between 0700 and 1700 hours. The experiment included presenting a control and a novel object randomly. As a novel object, I attached shiny

bright streamers (pool: red, silver, blue, pink) to a colourful dog-ring toy (Figure 4.3.1). I used different colours to present a novel object in each trial (a novelty in colour). I randomly selected the colour of the novel object in each repeat of the novel treatment. Each pair were exposed to two different random colours that were selected from the pool of colours, as novel object 1 and novel object 2. Then, the novel object was hung on a green pole and set within 2 meters of the focal nest when pairs were not around the nest. The pole without the novel object was used as a control as the birds were already familiar with this object from previous experiments. Blackbirds did not behave aggressively towards the pole and fed chicks normally and without replacement. During the novel object experiment, I attached the object to the pole for 45 minutes and recorded the blackbird behaviour. Each treatment was repeated two times (two controls, two novel objects) with a gap of a minimum of 5 hours and a maximum of 12 hours between each trial.

I recorded three parameters from both control and novel treatments. I recorded the number of nest visits within 45 minutes, the time (minutes) that the focal blackbird spent within 2 meters of the nest in the first encounter with the novel object/pole (hereafter inspection), and the number of movements (hereafter movement) that the focal blackbird had within 2 meters of the nest in the first encounter with the novel object/pole. Additionally, I recorded blackbird and pair identities, the number of chicks at the nest, the number of humans passing within 10 meters of the nest, and the chicks' age (day).

4.3.2.3 Antipredator behavioural trait: aggressive response toward the predator

I conducted a simulated predator exposure with a taxidermy owl (morepork, *Ninox novaeseelandiae*) to assess antipredator behaviour intensity. Like other avian species, blackbirds both alarm-call and attack when they have encountered a threat stimulus. Morepork is a small brown owl found throughout New Zealand (Figure 4.3.2). The nest defence experiment was carried out when pairs had nestlings between 4 to 14 days old and between 0800 and 1700 hours. Before starting the model presentation, a green pole was placed at least two meters away from the target nest during the entire experiment. The focal nest was observed for 30 minutes. This part allowed me to observe male and

female normal behaviour and checked the way they fly in the nest to feed their chicks. After normal nest observation, the owl was attached to the pole for 15 minutes and behavioural responses were recorded. After 15 minutes, the model was hidden, and focal pairs were observed for an additional 30 minutes. As a control, I used a non-predatory species of similar size to the owl, a taxidermy New Zealand wood pigeon (kererū, *Hemiphaga novaeseelandiae* (Figure 4.3.2)). The control model ensured that blackbirds were reacting to the presence of a morepork and not to just to the presence of a large bird near the nest.

Blackbirds typically exhibited two main responses: aggression/alarm and normal behaviour. An aggressive response was defined by counting the number of attacks and hovers (hereafter attacks) and alarm calls displayed by individuals. During non-aggressive responses, the blackbirds did not attack or engage or alarm call. I also recorded the blackbird's behaviour after removing the model as a post-stress response (30 minutes). Post-stress responses included a delay in the feeding time of the chicks (hereafter latency) and the number of nest visits (hereafter post-stress visit). Each model (morepork/ kererū) was repeated on two occasions. Additionally, I recorded the number of chicks in the nest, the age of the chicks, and the number of people that walked within 10 meters of the nest.

Figure 4.3.2 The control (Kererū, taken by Enzo M R Reyes) and the predator (Morepork) species were used in this research.

4.4 Statistical analysis

4.4.1 General behavioural variation assessment

All statistical analyses were conducted with R version 4.0.4 (R Core Team 2021). I used a generalized linear mixed model (GLMM) using packages "*lme4*" and "*lmerTest*" to investigate the impacts of different explanatory factors on risk-taking, neophobia and antipredator traits (Harrison et al., 2018; Kuznetsova et al., 2017).

In the risk-taking experiment, I included sex, age, trial number, start distance, season and year as fixed factors and individual identification (ID) as a random factor. The response variable was FID. For neophobia, I ran separate analyses for the response variables inspection time, nest visits and movements. Fixed effects included the number of chicks in the nest (breeding parameter), age of chicks, sex, treatment, the number of repeats, the number of people passing within 10 meters of the nest during the experiment and the time (morning/afternoon). To find out if the blackbird response was influenced by colours depending on the repeat (habituate or sensitive to a specific colour), I also included a two-way interaction term between the number of repeats and the colour of the novel object. I included individual ID and pair ID as the random variables. In the aggressive response to the predator (aggressiveness), I included the aggressive responses attack and alarm calls. I also separately analysed the post-stress response variables included post-stress visits and latency. Fixed effects were sex, the number of chicks (the breeding parameter), the chicks' age, treatment type (kererū or morepork), and the number of people passing within 10m. Individual identification and pair identification were included in the models as random effects.

A GLMM with gaussian distribution was fitted for: FID (risk-taking), inspection (neophobia) and latency (post-stress situation). I also fitted a GLMM with Poisson distribution for : nest visits (neophobia), attacks (aggressiveness) and post-stress nest visits (post-stress situation). And a GLMM with a binomial distribution was fitted for alarm call (yes or no). I used the *lme4* package to fit GLMMs. (Bates, Maechler, Bolker, & Walker, 2015). I used the "*lmer Test*" package for quantifying p-values of fixed effects via Satterthwaite approximation of degrees of freedom (Kuznetsova et al., 2017). Accordingly, for all response variables, I ran several models with different combinations of fixed factors. To select the final model, I performed backward step removal of fixed

factors, starting with the highest p-value. I first fit all the factors and ran the full GLMM model and calculated the AIC. I then removed the factor with the highest non-significant p-value and ran the reduced model. I compared the new AIC value with the previous model, if the AIC was lower, I continued the process and removed another factor. If the AIC of the reduced model was higher, then I stopped the model selection. Finally, the model with the lowest AIC value was selected (refer to Appendix : section 7-1, 7-2 and 7-3). I only presented the final model for response variables related to risk-taking, neophobia and antipredator traits.

4.4.2 Repeatability

I ran repeatability analysis using the package "*rptR*" to estimate consistency of risk-taking trait, neophobia and antipredator behavioural traits (Stoffel et al., 2017). I applied "*rptGaussian*" function to estimate the repeatability of risk-taking, FIDs, of males, females, and juveniles. I also assessed the repeatability of risk–taking trait within male and female a cross breeding and non-breeding seasons. Bird ID was considered as a random variable. I also investigated whether responses to the novel object were consistent in both individuals and blackbird pairs. Response variables included inspection, the number of nest visits and the number of movements around the nest when the novel object was presented. Individual and pair identifications were included as the response factors. Finally, I tested the consistency of antipredator response (aggressiveness) and post-stress behavioural traits within individuals and pairs. I estimated the repeatability of the aggressive responses of paired blackbirds (number of attacks, alarm call) and post-stress responses in individuals and pairs. Individual and pair identifications were considered as random variables in the repeatability model.

4.4.3 The link between traits and reproductive parameters

I conducted a "linear regression analysis" (*lm*) to investigate the influence of risk-taking on breeding parameters (the number of eggs and fledged chicks per season). I used the "*plyr*" package to calculate average behavioural types using the "*ddply*" function and conducted a linear regression between response variables (breeding measurements) and predictor variables (behavioural types). I used the "*ggplot*" function from package "*ggplot2*" to present the significant linear relationship between breeding characters and response variables of traits (Wickham, 2006).

4.4.4 Behavioural syndrome

To determine the strength of correlation between behavioural traits (behavioural syndrome) recorded from observational data, I applied a "Spearman rank correlation" using "*ggpubr*" package, and a graph presented significant results. I assessed behavioural syndrome in three categories. First, I investigated the relationship between risk-taking trait and behavioural traits from the forging context (chapter 3: movement, shyness, aggressiveness [toward conspecifics] and vigilance), neophobia and aggressive response toward the predator. Second, I looked for behavioural syndrome between neophobia and behavioural traits from forging context (chapter 3: movement, shyness, aggressiveness [toward conspecifics] and vigilance), and aggressive response toward the predator. Third, I investigated the relationship between aggressiveness (response to the predator) and behavioural traits that were recorded during daily blackbird foraging (mentioned earlier).

4.5 Results

4.5.1 Risk-taking

4.5.1.1 General behavioural variation assessment

From 2017 to 2019, I recorded FIDs from 54 blackbirds that ranged from one to 6 records for each individual per year. FID was on average 9.0 m (SD = 4.8) and ranged from 2 m to 28 m (N = 337 FID records). In the best fit model for FID, start distance and season were included. Results showed that FIDs varied significantly between the breeding (mean ± SE: 8.1 ± 0.4, N = 126 records) and non-breeding seasons (mean ± SE: 9.5 ± 0.4, N = 211 records). Blackbirds were more risk-taking in breeding season (Figure 4.5.1.A, Table 4.5.1). In addition, FIDs increased significantly in longer start distance (Table 4.5.1 and Figure 4.5.1.B). There was no significant difference in FIDs among males (mean ± SE: 9.0 ± 0.3, N = 220), females (mean ± SE: 9.3 ± 0.5, N = 75) and juveniles (mean ±SE: 8.3 ± 0.7, N = 42). Moreover, other factors, such as, year, or the number of repeats, did not influence variation of FID in individual blackbirds and were not included in the best fit model.

Table 4.5.1. Results from the best Generalised linear model for flight initiation distance (risk-taking behaviour, AIC = 1944.5) A significance level of $p \leq 0.05$ is shown by an asterisk (*).

Response variable	Explanatory variable	Estimate	SE	z	*p*
FID	Intercept	-0.19	1.16	-0.17	0.86
	Season: non-breeding	1.40	0.47	3.08	0.002*
	Sex: male	0.44	0.05	7.79	≤ 0.001*

4.5.1.2 Repeatability

First, I estimated repeatability of FIDs within males, females, and juvenile separately. Results showed that FIDs in juveniles were moderately repeatable (R = 0.45, p = 0.009, CI = [0.18, 0.63], N = 8 individuals, 48 FIDs). Repeatability of FID within female blackbirds (R = 0.29, SE = 0.15, CI = [0.06, 0.52], p = 0.001*, N = 75, 13 females) was greater than males (R = 0.14, SE = 0.07, CI = [0.01, 0.22], $p \leq 0.001$*, N = 218, 28 males). Repeatability of FID for blackbirds in breeding seasons was higher than ones in non-breeding seasons

for males and females (Table 4.5.2). FIDs in both males and females were moderately repeatable in breeding season.

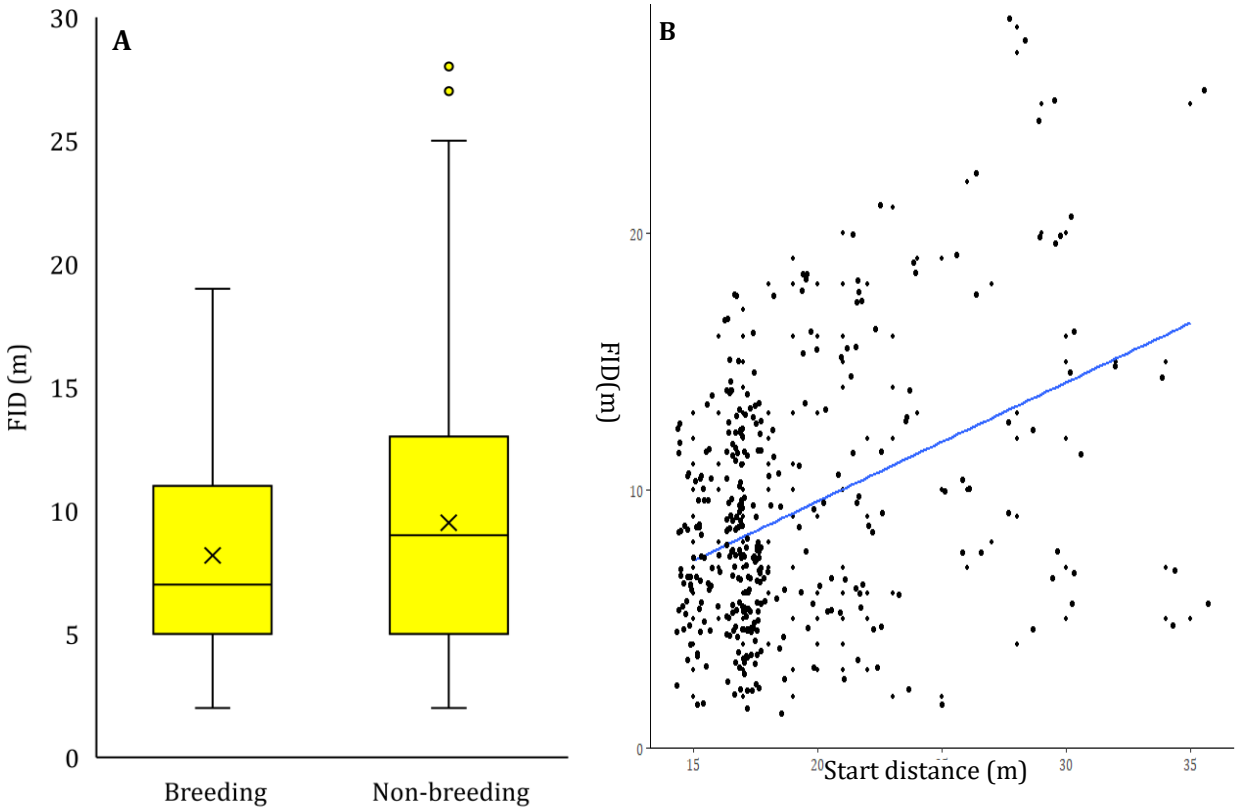

Figure 4.5.1. Variation of FIDs in blackbirds. A) Variation of FIDs between breeding (N = 126 records) and non-breeding seasons (N = 211 records). B) Relationship between FID and start distance (N= 337)

Table 4.5.2. Repeatability (R) of FID for blackbirds within non-breeding and breeding seasons for males and females. CI: 95% confidence interval; p: significance of repeatability; N: observations (individuals). A significance level of p ≤ 0.05 is shown by an asterisk (*).

	Season	R	SE	CI	*p*	*N*
Male	Non-breeding	0.14	0.09	[0.06, 0.33]	0.01*	143 (27)
Female	Non-breeding	0.31	0.15	[0.05, 0.53]	0.02*	49 (11)
Male	Breeding	0.27	0.15	[0.07, 0.51]	0.01*	69 (19)
Female	Breeding	0.43	0.23	[0.02, 0.76]	0.04*	25 (10)

4.5.1.3 The link between breeding parameters and risk-taking trait

Linear regression analysis from 91 blackbirds (included same individuals who breed over three years) showed that the number of eggs per season related to the risk-taking trait in blackbirds (LM: ES: -0.28, SE = 0.08, z = -3.61, p = 0.001*). Blackbirds that had shorter FIDs (risk-takers) had more eggs per season (Figure 4.5.2). However, there was no significant relationship between number of fledged chicks and risk-taking (LM: ES: -0.13, SE = 0.08, z = -1.66 p = 0.10).

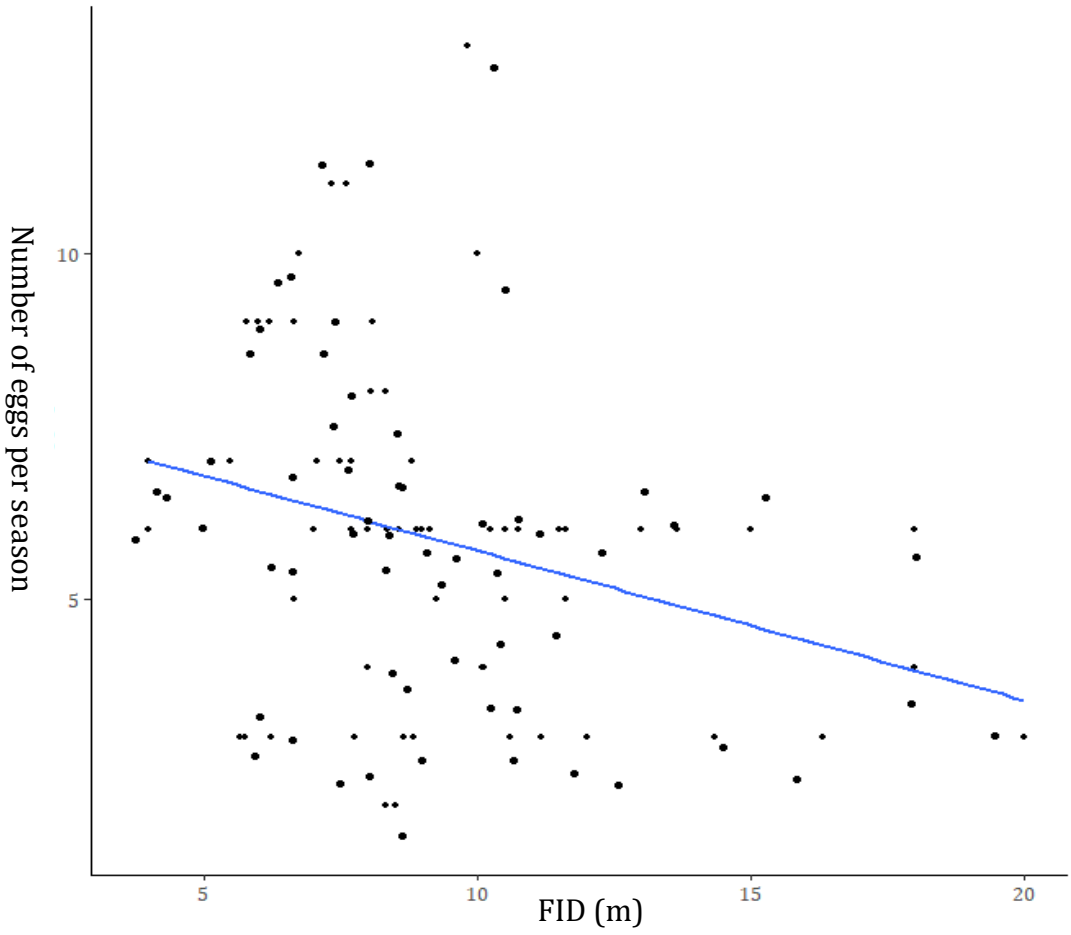

Figure 4.5.2. Linear regression presents relationship between FIDs and the total number of eggs per season in 91 individual blackbirds

4.5.2 Neophobia (novelty)

4.5.2.1 Behavioural variation assessment

The neophobia experiment was carried out across 28 active nests (56 individuals) in 2018. In ten nests, during a complete set of the experiment (four trials: two control treatments and two novel treatments), one of the parents (male or female) was absent in

few trials. In addition, few nests failed and lost their chicks before completing the experiment; therefore, the data was unbalanced. Overall, 100 control and 103 novel trials were recorded. Results from the best fit models related to selected parameters (neophobia response variables) are presented in Table 4.5.3. In the best fit model for the inspection time, treatment, chick age, interaction between colour and repeat were included (Table 4.5.3). Blackbirds spent a significantly longer time around the nest to inspect the novel object compared to the control treatment (Figure 4.5.3.A).

Table 4.5.3. Results from the best Generalised linear model on neophobia responses in blackbirds. $p \leq 0.05$ required for a significance level, shown by an asterisk (*).

Response variable	Explanatory variable	Estimate	SE	z	*p*
Inspection	Intercept	2.00	0.56	3.57	≤ 0.001*
	Treatment: control	-1.27	0.35	-3.67	≤ 0.001*
	Colour: blue	-2.67	0.59	-4.49	≤ 0.001*
	Colour: pink	0.78	0.69	1.14	0.26
	Colour: red	0.35	0.50	0.70	0.48
	Repeat: repeat 1	2.60	0.54	4.81	≤ 0.001*
	Age of chicks	-0.13	0.08	-1.76	0.08
	Colour*repeat	-3.08	0.77	-3.99	≤ 0.001*
Movement	Intercept	-0.88	0.56	-1.57	0.12
	Treatment: control	-0.80	0.10	-8.18	≤ 0.001*
	Age of chicks	0.17	0.04	3.74	≤ 0.001*
	Number of chicks	0.38	0.18	2.11	0.03*
Nest visit	Intercept	0.56	0.22	2.15	0.01*
	Treatment: novel	-0.33	0.08	-3.91	≤ 0.001*
	Number of people	-0.03	0.01	-2.14	0.03*
	Number of chicks	0.12	0.08	1.51	0.12

The two-way interaction between inspection time and repeat was significant. This interaction indicated inspection time depending on the colour of the novel object varied. Inspection duration in the second repeat of the novel object was significantly shorter when compared to the first presentation of the novel object (novel 1: mean ± SE = 2.0 ± 0.1 (min), N = 54; novel 2: mean ± SE = 1.3 ± 0.3 (min), N = 49; Figure 4.5.4, Table 4.5.3). The inspection duration of the first presentation for one nest was much longer than others (15 minutes: outliner in Figure 4.5.4). Besides, I also ran the best fit model without the data from that nest (15 minutes inspection time) to make sure the significant decline of inspection duration not only affect by data from one nest. The new arrangement of data also showed a significant decline in the second repeat of the novel object. Therefore, I kept the data from the mentioned nest. The inspection time also varied depending on the colour of the novel object (mean ± SE: blue = 1.2 ± 0.4, N = 15; red = 1.3 ± 0.2, pink: 2.0 ± 0.4, N = 7; N = 42; silver: 2.2 ± 0.5, N = 39). The shortest inspection time belonged to the blue and red objects, while the longest inspection was related to the silver and pink objects. The variation of inspection between blue and silver was noticeable (Table 4.5.3).

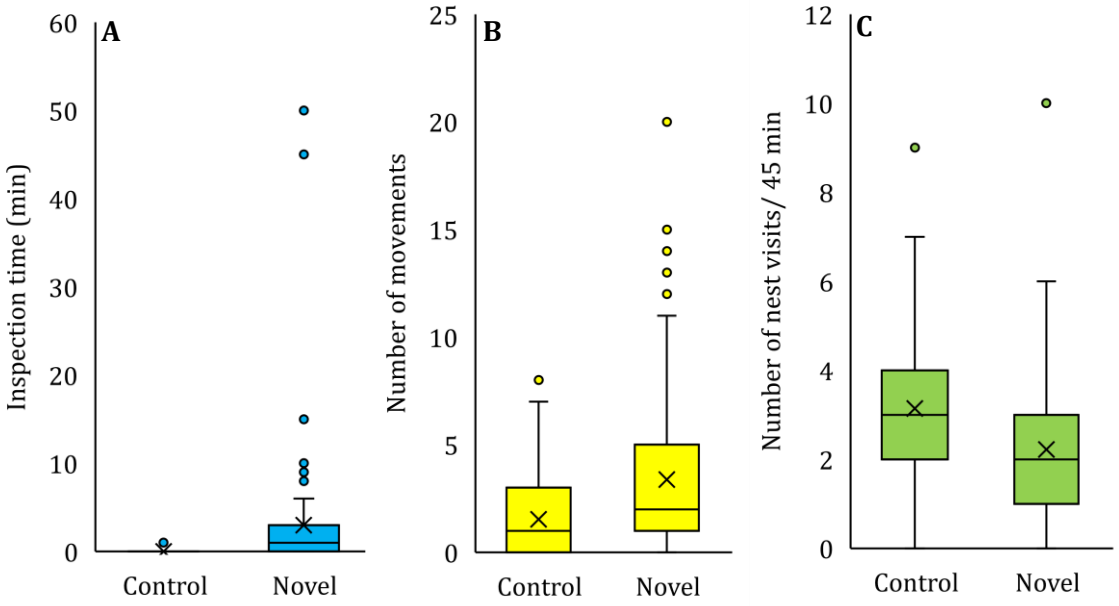

Figure 4.5.3. Results showing the variation of A) inspection time B) movements C), nest visits around the nest between control (N = 100) and novel presentations (N = 103).

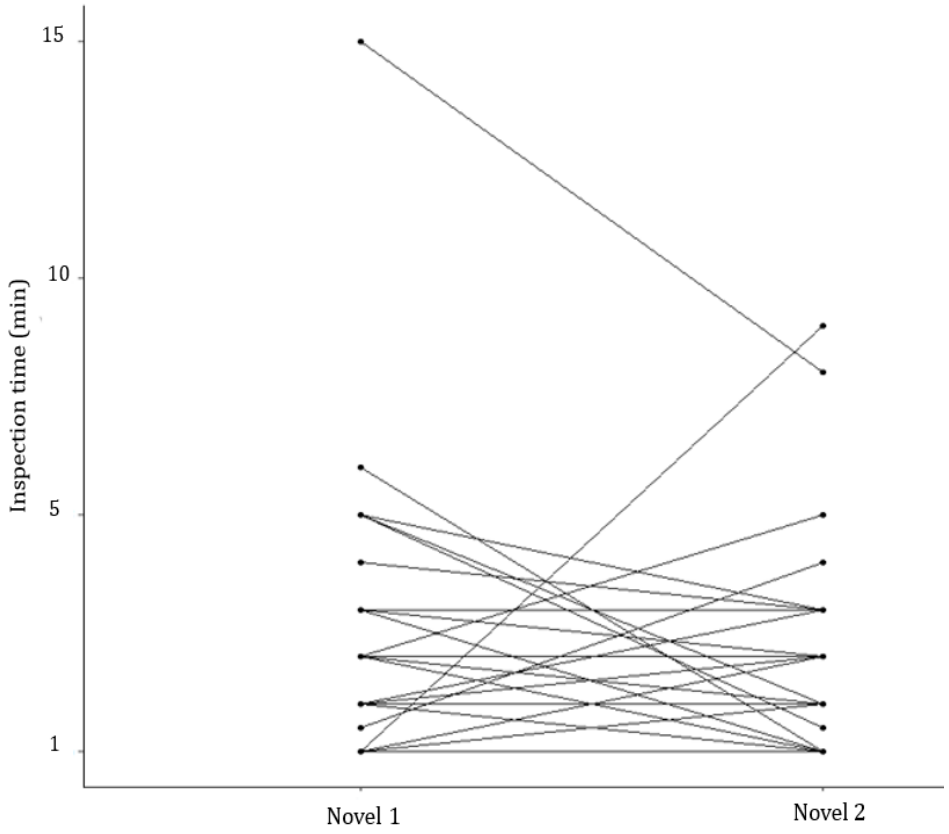

Figure 4.5.4. Inspection time of the novel object between first repeat and second repeat (novel1, novel2) of neophobia experiment (Number of nests = 50 individuals).

Blackbird movements in the novelty treatment increased 1.5 times compared to the control treatment (Figure 4.5.3.B). In this model, the blackbird movement significantly increased around the nests with a greater number of chicks (Figure 4.5.5.A). Different ages of nestlings were associated with changes in movements of male and female blackbirds around the nest and fluctuated across different ages of chicks at the nest (Figure 4.5.5.B). Blackbird's nest visits declined in the presence of the novel object (number of visits in 45 minutes: control treatment: 3.1, novel treatment: 2.2, Figure 2.5.3.C). Due to more people (visitors) passing around the nest, nest visits marginally declined when the novel object was near the nest. The number of chicks did not influence the nest visit model, although this factor was included in the best model with the lowest AIC value. In the presence of the novel object, blackbirds also visited their nest fewer times when more people were around the focal nest.)

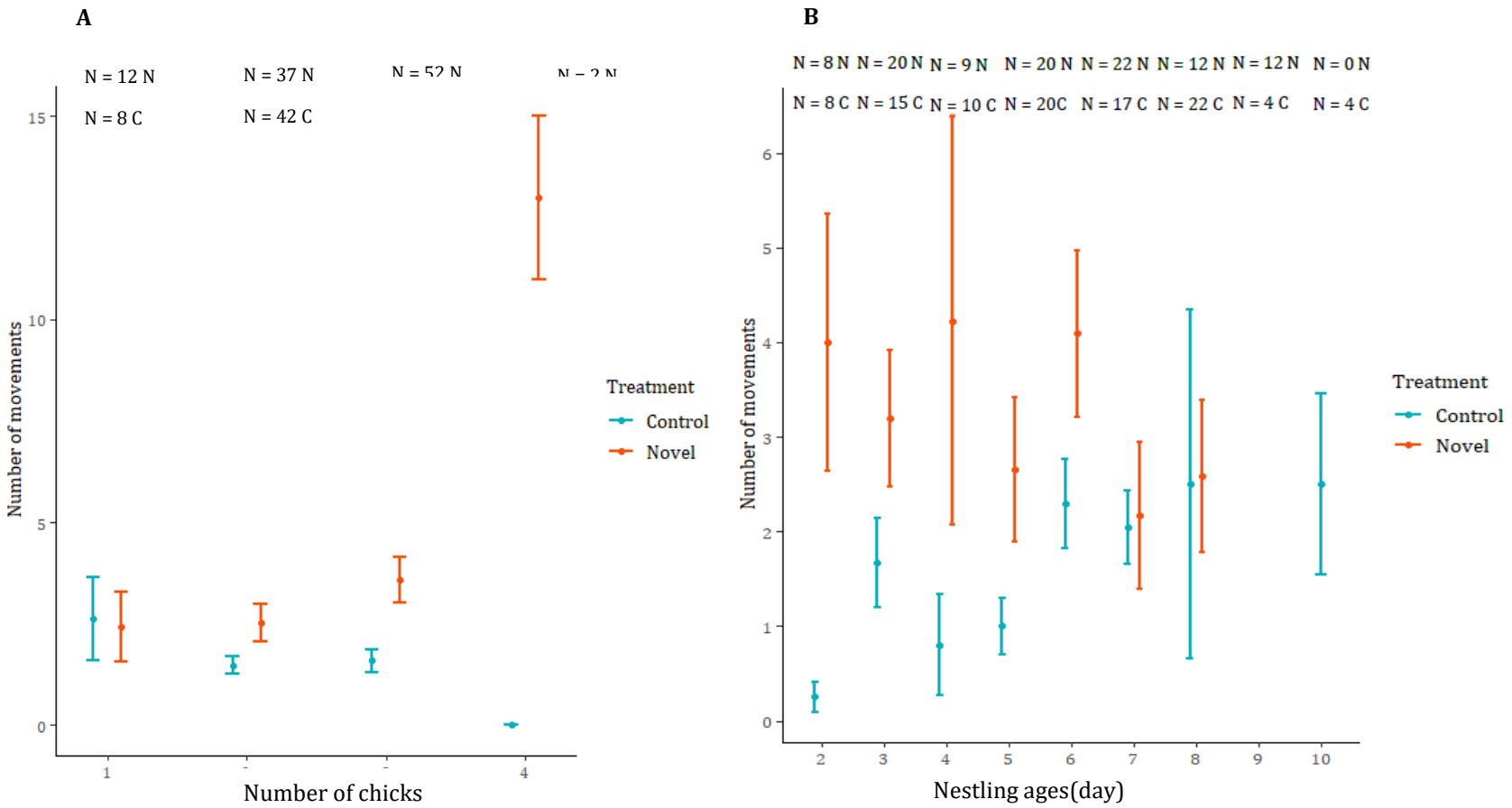

Figure 4.5.5. Variation of paired blackbird's movement in response to the novel object. A) Variation of movement around the nest with different numbers of chicks at the nest (N = 103 novel, N =100 control). B) Variation in movement around the nest in control and novel treatments across different nestling ages (N = number of novel trials, C = number of control trials).

4.5.2.2 Repeatability

The repeatability of inspection time between pairs was high (R = 0.57), while the inspection was not repeatable in individuals. In addition, the number of movements within pairs was also moderately repeatable (R = 0.47), while it was not repeatable for individual blackbirds (R = 0.07). The lowest repeatability estimation for both pairs and individuals were reported for the number of nest visit responses (R = 0.1, R = 0.02), (Table 4.5.4).

Table 4.5.4.Repeatability estimations (R) of the neophobia behavioural trait within the individual (28) and blackbird pair (56). CI: 95% confidence interval; p: significance of repeatability. A significance level of $p \leq 0.05$ was used and is shown by an asterisk (*).

Gaussian		**R**	**SE**	**CI**	***p***
Inspection	Individual	0.01	0.05	[0.00, 0.16]	1.00
	Pair	0.57	1.00	[0.41, 0.72]	0.004*
Poisson		**R**	**SE**	**CI**	***p***
Movements	Individual	0.07	0.10	[0.00, 0.35]	0.25
	Pair	0.40	0.13	[0.13, 0.60]	≤ 0.001*
Nest visits	Individual	0.02	0.09	[0.00, 0.29]	0.44
	Pair	0.10	0.09	[0.00, 0.28]	0.22

4.5.3 Antipredator behavioural trait: aggressive response toward the predator

4.5.3.1 Behavioural variation assessment

The experiments were carried out at 70 active nests from 2017 to 2019. A total of 479 trials recorded blackbirds' responses to the models (morepork and kererū). In this experiment, the numbers of trials per treatment (control and predator) were not balanced. Because in some nests, one of the parents (male or female) was absent during the experiment, and some nests failed before completing all series of experiments. When I did the experiments, I did not find any aggressive response (alarm and attack) to the pole alone located near the nest. Blackbirds did not attack the pole and there was no change in chick feeding rate (non-aggressive). Therefore, in further analyses, I only included kererū (control) and morepork (predator) stimulus. When I presented the predator stimuli, different nest defence strategies were observed from blackbird pairs (Table 4.5.5). Interestingly, 34 (48.6%) pairs ignored the model and fed chicks (non-aggressive response, while 15 pairs (21.4%) showed the strongest nest defence; they alarm called and attacked the model (aggressive response, Figure 4.5.6). Ten percent of responses were related to both male and female alarm calling. Overall, in 80 percent of all nests, male and female as a pair responded similarly toward the predator (both male and female ignored or alarmed or attacked).

The number of attacks varied between a minimum of 0 and a maximum of 125 attacks toward the models in the 15 minutes of the model presentation. Results from GLMM showed that the number of attacks in morepork trials (mean ± SE: 8.2 ± 1.1, N = 253) was significantly more than kererū trials (mean ± SE: 1.7 ± 0.5, N = 226) (Table 4.5.6). I also found significant moderate variation in the number of attacks across different chick ages. Generally, the number of attacks increased from 4 to 9 days of age and then declined (Table 4.5.6 and Figure 4.5.7). The number of attacks by male blackbirds (morepork: mean ± SE: 9.7 ± 1.8, N= 128 trials; kererū, mean ± SE: 2.0 ± 0.7, N = 115 trials) was higher than females (morepork: mean ± SE: 6.7 ± 1.4, N = 125 trials; kererū: mean ± SE: 1.4 ± 0.50, N = 111 trials), but it was not significant, and I did not include in the final attack model.

Table 4.5.5. The overall result from exposing the predator model to mated blackbird pairs. Seven scenarios were observed in response to the predator model from 2017 to 2019.

		Scenario 1	**Scenario 2**	**Scenario 3**	**Scenario 4**	**Scenario 5**	**Scenario 6**	**Scenario 7**
Year	Total nests	Male: Normal Female: Normal	Male: Normal Female: Alarm	Male: Alarm Female: Normal	Male: Alarm Female: Alarm	Male: Alarm-Attack Female: Alarm	Male: Alarm Female: Alarm- Attack	Male: Alarm-Attack Female: Alarm-Attack
2017	16	8	0	2	1	1	0	4
2018	26	12	0	1	3	4	1	5
2019	28	14	0	2	3	1	2	6
Total	70	34 (48.6%)	0	5 (7.1%)	7 (10%)	6 (8.6%)	3 (4.3%)	15 (21.4%)

Figure 4.5.6 Aggressive response of blackbird toward a morepork model: hover and attack.

Table 4.5.6. Results from the best GLM model of response variables to predator simulation in blackbirds included antipredator responses (attack and alarm) and post-stress responses (latency to visit nest and post-visit).

Response variable	Explanatory variable	Estimate	SE	z	*p*
Response to the predator model					
Attacks	Intercept	-8.24	1.47	-5.60	≤ 0.001*
	Treatment	-1.60	0.06	-28.40	≤ 0.001*
	Age of chicks	0.09	0.01	7.72	≤ 0.001*
Alarm call	Intercept	1.08	0.43	2.48	0.01*
	Treatment	-0.50	0.20	-2.56	0.02*
	Number of people	-0.01	0.01	-1.73	0.08
	Number of chicks	-0.55	0.16	-2.69	0.007*
Post stress response					
Latency	Intercept	35.64	4.68	7.62	≤ 0.001*
	Treatment	-1.34	1.07	-1.25	0.21
	Sex	2.24	1.19	1.88	0.06
	Age of chicks	-0.55	0.30	-1.87	0.06
	Number of chicks	-4.71	1.33	-3.55	≤ 0.001*
nest-visit	Intercept	0.03	0.20	0.15	0.88
	Treatment	0.14	0.06	2.15	0.03*
	Number of people	-0.01	0.00	-1.81	0.07
	Age of chicks	0.03	0.02	1.62	0.11
	Number of chicks	0.26	0.07	3.52	≤ 0.001*

The number of blackbirds that alarm called when presented with the model was significantly higher for the morepork treatment (Table 4.5.6, Figure 4.5.8.A). In addition, pairs, who had one or two chicks, alarm called more noticeably when a predator model was near their nests compared to pairs that had three or four chicks at their nests (Table 4.5.6, Figure 4.5.8. B and C).

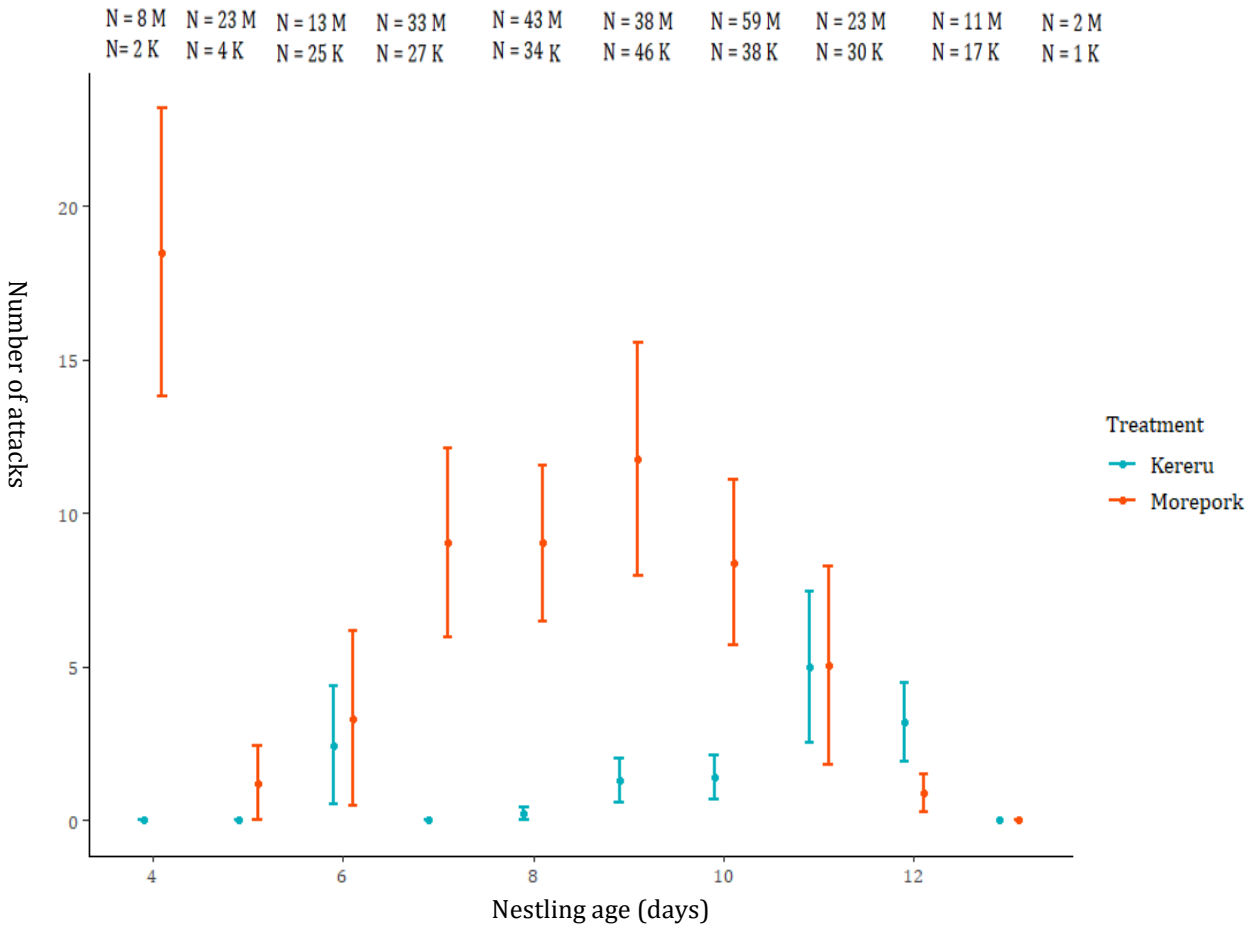

Figure 4.5.7. Variation in the number of attacks on the morepork (red) and kererū (blue) treatments across different nestling ages, M = number of morepork trials and k = number of kererū trials.

Regarding post-stress responses, there was no significant variation in latency to visit the nest between morepork and kererū treatments (morepork: mean ± SE: 20.6 ± 0.9, N = 253 trials; kererū: mean ± SE: 18.9 ± 0.87, N = 226 trials; Table 4.5.6). In addition, there were no significant differences between males (morepork: mean ± SE: 21.2 ± 1.3 (min), N = 128; kererū: mean ± SE: 20.5 ± 1.3 (min), N = 115) and females (morepork: mean ± SE: 20.0 ± 1.3, N = 125; kererū, mean ± SE: 17.3 ± 1.1, N = 111), indicating that both females and males did not have different latency times (Table 4.5.6). This model revealed that pairs that had more chicks at the nest came back to the nest earlier than pairs who had fewer chicks (Table 4.5.6, Figure 4.5.9.A).

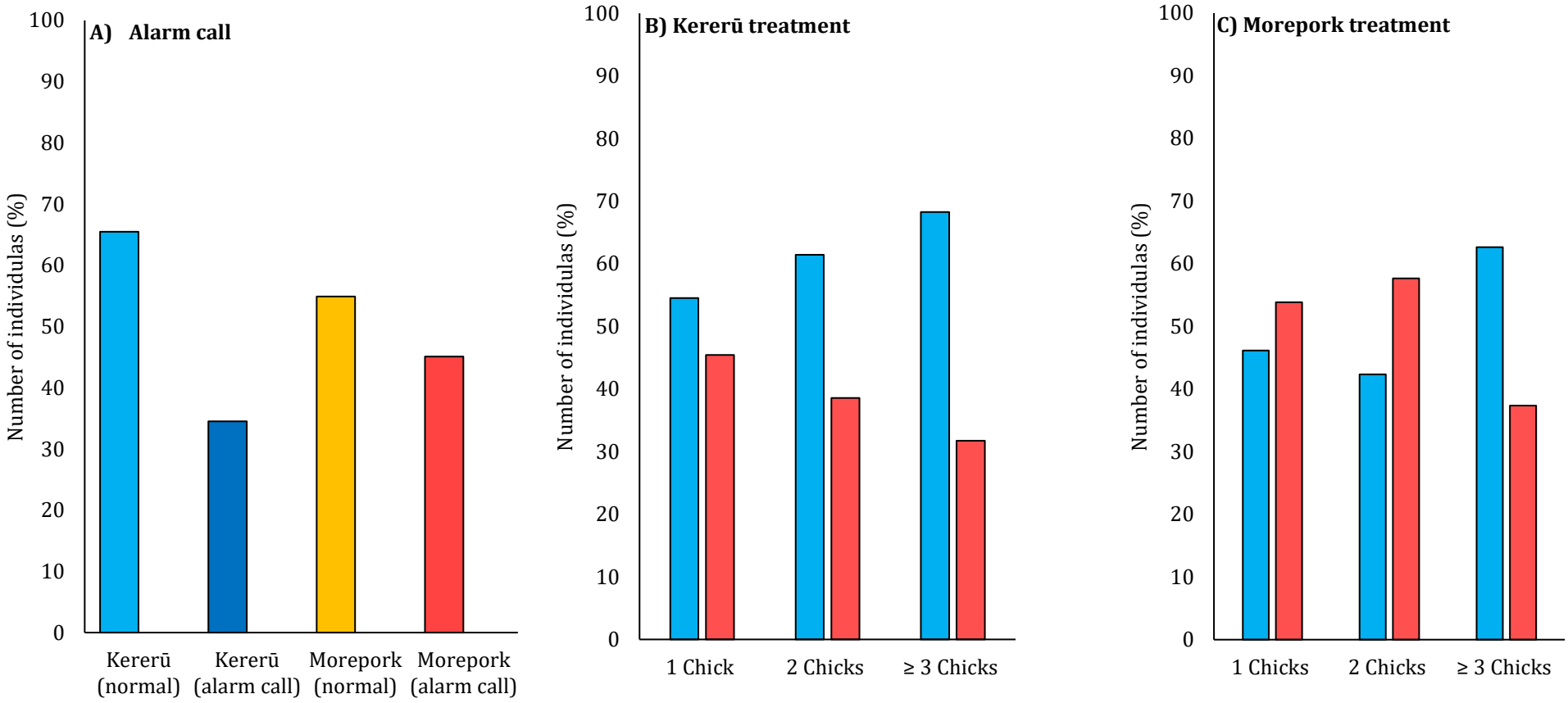

Figure 4.5.8. The percentage of blackbirds that alarm called. A) The percentage of blackbirds that alarm called (red) and did not alarm call (blue) when morepork and kererū were presented near the blackbirds' nests (Number of trials: kererū: 226, morepork: 256). B) The percentage of blackbirds that alarm called (red) and did not alarm call (blue) when the models were presented across different number of chicks at the nest (Number of trials : A) kererū: 1 chick = 11, 2 chicks: 70, ≥ 3 chicks= 145; B) morepork: 1 chick: 13, 2 chicks: 85, ≥ 3 chicks: 158)

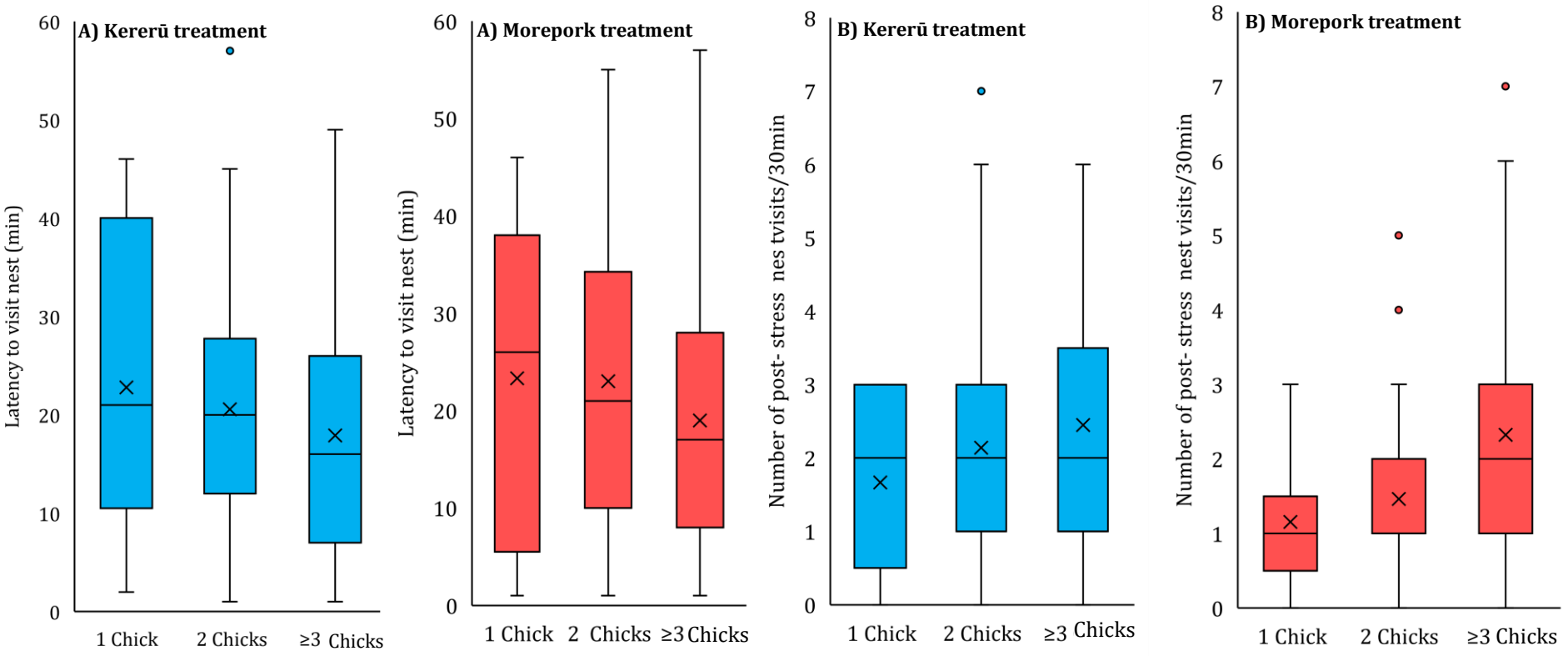

Figure 4.5.9. Variation of latency and nest visits regarding the number of chicks. A) Variations in latency to visit nest related to different number of chicks (Number of trials: morepork: 1 chick = 13, 2 chicks = 89, 3 chicks = 154; kererū: 1 chick = 9, 2 chicks = 72 , 3 chicks = 145). B) Variation in the number of post- stress visits by blackbird pairs related the number of chicks at the nest (Number of trials: morepork: 1 chick = 13, 2 chicks = 89, 3 chicks = 154; kererū : 1 chick = 9, 2 chicks = 72 , 3 chicks = 145)

The number of post-stress visits in the morepork presentation was slightly lower than the kererū presentation (morepork: mean ± SE; 2.0 ± 0.09 N = 253, kererū: mean ± SE; 2.3 ± 0.09, N = 226), but there was no significant difference. The number of post-stress visits increased slightly with more chicks in the nest in both treatments (Table 4.5.6 and Figure 4.5.9.B). In this model, sex, age of chicks, number of people, did not influence the model.

4.5.3.2 Repeatability

I tested whether responses to the predator model (attacks and alarm calls) and post-stress responses (latency and post-stress visits) were repeatable in individual and paired blackbirds (Table 4.5.7). I excluded individuals who confronted once to the predator model (7 individuals). Overall, results showed that repeatability estimations were high within pairs and response variables were not repeatable in individuals. Alarm calling and attacks in pairs were highly repeatable (alarm call = 0.88, $p \leq 0.001$*; attack: R = 0.82, $p \leq 0.001$*, Table 4.5.7). Latency and post visits were moderately repeatable in pairs (Table 4.5.7). Response variables were not repeatable within individuals (Table 4.5.7).

Table 4.5.7 Repeatability (R) of antipredator and post-stress responses within individuals and pairs across study years. CI: 95% confidence interval; *p*: significance of repeatability (253 experiments from 41 pairs, 82 individuals). A significance level of $p \leq 0.05$ is shown by an asterisk (*).

Gaussian variable		**R**	**SE**	**CI**	***p***
Latency	Individual	0.001	0.01	[0.00, 0.04]	0.50
	Pair	0.20	0.07	[0.07, 0.30]	≤ 0.001*
Poisson variable		**R**	**SE**	**CI**	***p***
Attacks	Individual	0.11	0.36	[0.05, 0.97]	≤ 0.001*
	Pair	0.82	0.26	[0.23, 0.90]	≤ 0.001*
Alarm call	Individual	0.00	0.01	[0.00, 0.02]	1
	Pair	0.87	0.07	[0.75, 0.97]	≤ 0.001*
Post- stress nest visit	Individual	0.03	0.04	[0.00, 0.12]	0.31
	Pair	0.23	0.10	[0.01, 0.30]	0.01*

4.5.4 Behavioural syndrome

Spearman rank correlation analysis showed that there was a moderate negative correlation between risk-taking and vigilance traits (Table 4.5.8, figure 4.5.10). I did not find any correlations among the other behavioural traits.

Table 4.5.8. Behavioural type correlation between selected behavioural traits.

Category	Behavioural traits (chapter 3)				Neophobia	Aggressiveness
	Aggressiveness	Activity	Shyness	Vigilance	Inspection	Attack
Risk-taking						
FID	0.25	0.69	-0.03	-0.42	0.54	-0.16
P value , N	0.14, 34	0.70, 34	0.84,34	0.01*, 34	-0.12, 24	0.39, 28
Aggressiveness						
Attack	0.05	0.18	0.26	0.03	0.06	
P value ,N	0.78, 26	0.37, 26	0.19	0.86, 26	0.63, 52	
Neophobia						
Inspection	0.21	0.14	0.17	-0.10		
P value, N	0.32, 23	0.49, 23	0.43, 23	0.64, 23		

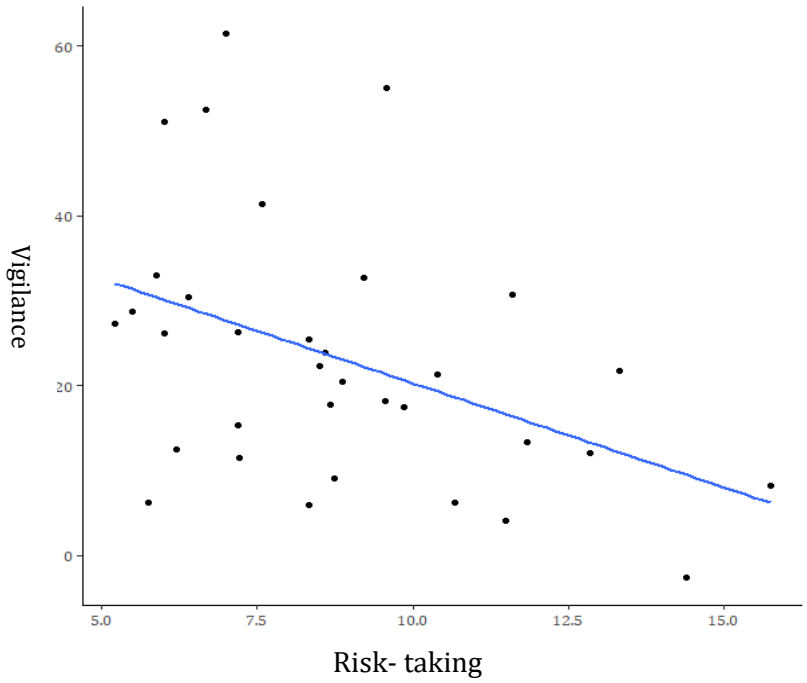

Figure 4.5.10 Correlation between flight initiation and vigilance in 34 individual blackbirds.

4.6 Discussion

4.6.1 Risk-taking

I investigated the variation in risk-taking behaviour in blackbirds and explained the factors that might influence it. Flight initiation distance is a standard experiment for assessing individual's risk-taking (Frid & Dill, 2002; Blumstein, 2006). In my results, increasing start distance was positively related with FIDs. There was also a significant seasonal difference in FID between individuals with shorter distances in the breeding season. I also found that blackbirds with shorter flight initiation distances (risk-takers) had more eggs per season and there was no association with the number of chicks and FID.

Human "predators" have been frequently used in FID studies (Blumstein et al., 2005; Cooper Jr and Frederick, 2007). Wild animals normally treat humans as potential predators (Beale and Monaghan, 2004; Frid and Dill, 2002). In contrast, in urban areas, the presence of a humans may not be perceived as a potential threat by urban birds, as humans even feed them on occasion (habituation to human presence). In addition, in urban areas, the density of established territories is high (Uchida et al., 2016). A study on brush turkeys showed that there is no correlation between FIDs and start distance in individuals in lawn and street urban areas. Because individuals in urban areas have higher level of experience of human disturbance than those in natural environments (Hall et al., 2020). A study on 68 bird species in Australia, demonstrates a significant positive relationship between FID and start distance (Blumstein, 2003). It means individuals dynamically assess risks and have a temporal margin of safety: as starting distance increases (higher level of risk), individual flies at the greater distance (Blackwell et al., 2014; Cooper Jr and Frederick, 2007). I found similar results and there was also a positive association between start distance. I suggest that a human approaching a bird as a proxy of risk-taking will vary in its perceived threat by blackbirds within a range from 15 to 30 m. Blackbirds that flew at longer start distances assessed a higher level of threat (risk-averse). In addition, the variation of flight initiation distances relating to the start distance indicated a temporal margin of safety for blackbirds. I recommend future studies consider other parameters such as the number of birds that forage around the focal bird, the distance of focal bird to the vegetation, and the human population density at the focal bird foraging site.

Sex may also influence risk-taking behaviour due to life history variations between males and females and metabolic rate differences between sexes of many species (Lagos and Herberstein,

2017). On the one hand, males are usually looking for or attracting mates, display elaborate colours; hence, they may face a higher predation risk (Zuk and Kolluru, 2015). On the other hand, other studies show, that it is energetically costly for females to produce eggs, incubate, and rear chicks (Tinbergen and Dietz, 1994). These energy demands may be similar overall, but they vary in when they occur during the breeding cycle. To meet energy demands, females need to forage intensely for food, which may make them less vigilant and risktaker (Dukas and Kamil, 2000; Martin and Badyaev, 1996). Females in Eurasian blackbirds forage more than males and forage closer to the ground during the breeding season; hence females are more risk-takers than males and suffer higher predation risk (Post and Götmark, 2006b). However, I found no significant difference in FIDs between males and females in blackbirds. My explanation for this result is that male and female blackbirds forage on their territories equally in the non-breeding season. Although males and females have different breeding activities (male: singing, female: nest building, incubation), the level of the risk assessment would be similar in both males and females as they were exposed to the same levels of human disturbance in urban areas. Both male and female blackbirds have high energy demands during the breeding season (e.g., mating, singing, building the nest, grading the territory, egg-laying and feeding chicks). These high energy demands during the breeding season can lead to an increase in the frequency of high-risk situations and stay longer time in that situation (foraging), hence blackbirds presented shorter FIDs during the breeding season (risk-taker).

Flight initiation distance presents an estimate of the risk that an individual is willing to take in the wild to achieve benefits, e.g., food and mate and breeding success (Blumstein, 2006). Reproducing at a higher rate requires additional resources and high risk-taking (Møller, 2014). As a result, individuals have to trade-off between survival and reproduction (Cooper and Frederick, 2007; Kawecki and Stearns, 1993; Travis, 1994). At the intraspecific level, individuals within a population, life-history traits are positively associated with risk-taking and risk-taker animals have greater breeding investment (Cooper (Jr.) et al., 2015; Kawecki and Stearns, 1993; Rodriguez-Prieto et al., 2009). The trade-off between risk-taking behaviour and breeding characteristics have been addressed in several studies. Human approach experiments in Eurasian curlews, *Numenius arquata*, show that hatch success in parents with intermediate FIDs is higher than individuals with short and very short and very long FID (de Jong et al., 2013). A study on barn swallows, *Hirundo rustica* and house sparrows, *Passer domesticus* shows that birds with shorter mean FIDs have large annual fecundities compared with birds with longer FIDs (Møller and Garamszegi, 2012). Similar results have been reported in other taxa:

risktaker females in the grey seal, *Halichoerus grypus*, produce heavier pups (Bubac et al., 2018) and bolder males and females in the black-browed albatross *Thalassarche melanophrys* have higher breeding success (Patrick and Weimerskirch, 2014c). I suggest that risk-taking behaviour has a potential influence on breeding investment of blackbirds, with individuals taking greater risks to achieve future fitness return.

Studies have revealed high repeatability of risk-taking behaviour in many species such as common eider, *Somateria mollissima* (Seltmann et al., 2012b), barn swallows *Hirundo rustica* (Møller, 2014) and burrowing owl, *Athene cunicularia*, (Carrete and Tella, 2010). Repeatability provides evidence that among-individual variation is caused by factors inherent to the individual (Rodríguez-Prieto et al., 2011). In contrast, behaviour may be extremely flexible, which is indicated by low repeatability (Bell et al., 2009). Other studies have also demonstrated low repeatability for American robin, *Turdu migratorus*, and Iberian wall lizards, *Podarcis hispanicus* (Eason et al., 2006; Rodríguez-Prieto et al., 2011). In my study, I found risk-taking behaviour (FID) within juveniles was moderately repeatable. In addition, risk-taking within males and females was moderately consistent during the breeding season and tended to decrease in non-breeding season. In non-breeding seasons, individual blackbirds concentrate on foraging, and they are not as vigilance and risk-taking as breeding season . These results highlight the potential seasonality of risk-taking personality in adults and evidence of personality in individuals' earlier ages (juveniles). It suggests that animal react depending on circumstances. I also suggest that during non-breeding seasons urban birds might adjust to the urban challenges with a high level of flexibility (plasticity), which allow them to thrive in urban conditions (Vines et al., 2016). Finally, I recommend that future studies on risk-taking behaviour consider other parameters such as distance to the vegetation or refugee, food availability, particular predator, group size, age and human density of areas. Investigating these factors will reveal shifts in fear behaviour in urban areas, which may have potential conservation decision-making in different environments.

I only found a negative correlation between risk-taking and vigilance. I didn't find any correlation among other behavioural traits. Similar to my result, research on woodchucks, *Marmota monax*, and red squirrels, *Sciurus vulgaris*, shows a negative correlation between flight initiation and vigilance traits (Lippmann,2003; Uchida et al., 2019). A reduction in vigilance to human presence in urban areas covary with an enhance of risk-taking behaviour. In nature, humans normally are considered as a real threat (top predator), while in urban areas,

humans build a different relationship with animals (not a real danger), for example, humans feed birds and birds nesting near buildings(Møller et al., 2015; delBarco-Trillo, 2018). Therefore, birds in urban areas tolerate human presence, optimise their predator avoidance and achieve advantages of being in urban environment. Adaptation to human disturbance helps individuals to minimise energy expenditure and avoid costs of unnecessary escapes by increasing vigilance and risk-taking behavioural traits.

4.6.2 Neophobia

My results confirmed the presence of neophobia in blackbirds by revealing a significant difference in blackbird responses between control and novel object treatments. Both male and female blackbirds showed neophobic responses when confronted with a novel object. In my research, the sex of the bird did not explain the differences in behaviour for any response variable (inspection, movements, and number of nest visits). Research on common blackbirds and wild-type zebra finches, *Taeniopygia guttata,* shows that neophobia does not vary between sexes (Miranda et al., 2013a; Schielzeth et al., 2011). Consistent with the results from other studies on blackbirds, common ravens, *Corvus corax*, and caracara, *Milvago chimango* (Biondi et al., 2010; Heinrich, 1995; Miranda et al., 2013a), my results showed that there was an effect of the trial number (repeat) and colour on the inspection time. I suggest that individuals will become less sensitive to repeated exposure to novel objects (habituation). In addition, the decline in neophobic across repeated trials could be because of gaining experience with objects, reducing exploration and avoidance from the objects. Additionally, my results revealed that in the presence of the novel object, blackbirds that had a greater number of chicks in their nest responded more intensely than birds with fewer chicks. Some studies have revealed that assortative mating pairs at extremes of aggression and exploratory axes have the highest reproductive success (Both et al., 2005). In blue tits, variation in neophobia trait was related to total offspring biomass (Colchester and Harrison, 2016). Although I didn't find this type of relationship between neophobia response and breeding success, my results revealed evidence of a link between stronger a neophobic trait in pairs and greater breeding investment.

I also found consistent variation in the inspection of the novel object and the number of movements around the object within pairs. While the number of nest visits was not repeatable. Similar studies show repeatability of neophobia within individual blackbirds (Miranda et al., 2013a), blue tits, *Cyanistes caeruleus*, (Colchester and Harrison, 2016), great tits (Both et al., 2005), and zebra finches, *Taeniopygia guttata*, (Coleman and Mellgren, 1994; Schielzeth et al.,

2011). Although those studies show repeatability of neophobia within individuals, my research reveals high repeatability of neophobia (inspection, movement) within pairs. My results show a compatible and likely cooperative neophobic response in paired blackbirds.

In my study, the response of blackbirds varied between blue and silver novel objects. Investigating the influence of colour on animal response has been studied in several species. For example, northern bobwhites, *Colinus virginianus,* individuals avoid eating red food while, they do not avoid blue food (Mastrota and Mench, 1995). Generally, red can be a sign of danger, while blue is not a warning sign. However, I didn't find significant variation between responses to red and blue in blackbirds. Greenberg (1983) showed that birds' neophobic response is stronger towards brighter coloured objects than dull coloured ones. And visual experiences of different colours varied in different species depending on the memory of discrimination (Lecuelle et al., 2011). In this study, I had limitations in selecting colours, and all shiny things were bought randomly. Although I could not explain the mechanism that blackbirds responded to the different colours, there was likely a result of the blackbirds' neural discrimination of different colours. And potentially associations between threats and colour. These results presented optional future studies on the effect of novelty on colours in neophobic responses of individuals

4.6.3 Antipredator behavioural trait

In the antipredator experiment, both males and females contributed to nest defence in the majority of nests that reacted to the models. The result from the antipredator experiment showed that pairs presented two main tactics. Approximately 21% of the total pairs ignored the presence of the predator model. While 49% of paired blackbirds showed strong parental nest defence towards the predator model (alarm and attack). In 30% of pairs, males and females differed in their responses to the predator model. Overall, 80% of pairs displayed similar nest defence responses to the predator model.

I found that blackbirds' responses differed significantly for morepork and kererū. Some pairs responded aggressively to the kererū model, while some did not respond aggressively. The number of attacks toward the kererū was significantly lower than ones toward the morepork. Similar observation of antipredator response have been recorded in Siberian jay, *Perisoreus infaustus*, redwing, *Turdus iliacus*, and in fieldfare, *Turdus pilarfrom* (Eggers et al., 2005; Ibáñez-Álamo and Soler, 2017; Meilvang et al., 1997). Two general hypotheses have been proposed to

explain these results. First, recognising a predator in some avian species such as pied flycatcher, *Ficedula hypoleuca*, and seychelles warbler, *Acrocephalus sechellensis,* appear to be innate (Curio et al., 1978; Veen et al., 2000). While in some other avian species, e.g., great tit, *Parus major,* a specific learning process is needed (Kullberg and Lind, 2002). Curio et al. 1978 explain that blackbirds learn to discriminate predators. Hence, I assumed that the absence of experience might lead to poor recognition of the predator and kererū. There was the possibility that blackbirds learned incorrectly to recognise the kererū as a predator. The second theory suggests that aggressive territorial behaviour can be related to territorial birds' anxiety levels to any species near their nests (Cramp 1988). This theory explains that aggressive territorial behaviour can be related to the variation of aggression within individuals. Individuals with a higher level of aggressiveness would present a more intense aggressive reaction to any species near their nest. My results were partially consistent with the second theory because I also observed that blackbirds who alarmed and attacked the morepork model also presented similar aggressive responses (lower intense) toward the kererū model. Overall, I suspect that blackbirds learn to recognise avian predators (the size and shape of the predator) and the level of aggression in individual blackbirds varies; more aggressive blackbirds respond aggressively to any large bird.

My results showed similar responses of males and females to the risk of nest predation and post-stress responses. Similar to this finding, a study of blackbirds shows a coordinated antipredator response to the nest-defence behaviour in blackbirds (Ibáñez-Álamo and Soler, 2017). Blackbirds displayed high levels of cooperative antipredator tactics as a pair or parent. Krys tofkova et al. 2011 shows that male and female blackbirds responded similarly to the threat posed by a magpie in terms of the time that they spend hidden, while males do significantly more nest defence in comparison with females. The similarity of antipredator response between sexes is that male and female blackbirds in my study further demonstrate the comparable parental duties of blackbird parents.

Antipredator responses increased in blackbirds between days 4 to 8 of nestling age. At this stage, nestlings were more vulnerable and needed more parental care. By the end of the nesting period (between days 8 – 12), paired blackbirds were less aggressive and attacked the predator model less, likely because the development of nestlings was almost completed. Contrary to my expectation, there was no relationship between the number of nestlings and the number of attacks, perhaps because the majority of birds had three egg clutches. However, pairs with

more chicks tended to alarm call more often to predators, an important tactic but less risky. This has been observed in other studies of antipredator behaviour in birds where the antipredator response can lead to injury or death for parents when birds attack the predator (Brunton, 1990). In blackbirds, if one of the parents were injured or killed by a predator, the remaining partner may be unable to feed the chicks; therefore, chicks would die. In addition, alarm calling as an antipredator response can disturb a predator during the day by revealing the predator's location. Then, other birds around the focal nests would be vigilant or aggressive toward the predator (Kullberg and Lind, 2002). As I observed in the experiments, other bird species whose territories were close to the focal blackbirds also approached close to the predator model. They alarm called and even attacked the predator model. Therefore, the first effective response to a predator may be alarm calls. Additionally, post-stress responses (latency and post-visit) revealed the importance of parental care after a stressful encounter in blackbirds. A study on Siberian jays, *Perisoreus infaustus*, showed that pairs in the presence of a predator around the nest reduce visit rates. In contrast, when a predator is less active, pairs allocate more feeding effort (Eggers et al., 2008). Blackbird pairs that had more chicks invested more in their breeding effort; hence when the predator was hidden, they fed their nestlings earlier and more than pairs that had fewer nestlings. My results also show that attack and alarm calls were highly repeatable within pairs of blackbirds, while latency and nest visit was not repeatable in the post-stress situation. This result suggests a coordinated response in paired blackbirds in a high-risk situation.

In conclusion, my results show how blackbirds respond to different levels of a potential threat (the novel object (harmless thing), human (a daily risky situation, not a high level of threat) and predator (a high-risk situation). Breeding parameters influenced their response to objects and species around them. I found that blackbirds are risk-takers in the breeding season.

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Chapter 5:

Responses of male blackbirds to songs of familiar and unfamiliar conspecifics

A male blackbird on his singing location.

5.1 Abstract

Territorial behaviours have an important role in territory stability and social dynamics. Singing by male birds plays a critical role in female attraction, territorial defence and advertising male quality. Singing can act as an aggressive signal; birds may use song to assess fighting ability and to determine the probability of attack or invasion by conspecific rivals (Bard et al., 2002). In addition, territorial behaviours include both long-range signalling and short-range confrontations (Stamps & Krishnan, 1997), and warn conspecifics against approaching too close. Playback experiments provide a robust and practical approach to investigate how different individuals behave in response to an aggressively signalling conspecific.

In this study, I carried out two types of field playback experiments, one in 2018 and another in 2019. In the first playback, I investigated the response of an urban population of blackbirds to different conspecific songs. I aimed to determine if blackbirds display different responses to playback songs from males of varying levels of aggressiveness. As part of this experiment, I investigated the effect of anthropogenic disturbance on the response of blackbirds to the playback. I also investigated if there was a correlation between male responses and parental care/breeding success in male blackbirds. In the second playback experiment, I investigated whether male blackbirds discriminate between the songs (a long-range signal) of neighbours and strangers and vary their response accordingly.

My findings demonstrate that individuals show the same response to songs from aggressive and non-aggressive male blackbirds. Interestingly, male blackbirds close to the road demonstrated a significantly stronger aggressive response towards all playbacks. In addition, there was a positive correlation between the response of the male blackbird to playbacks and the parental care he provided to his offspring (nest visits) during chick-rearing. The results from the second playback showed that male blackbirds respond strongly to dawn songs irrespective of the source of the song (neighbour or stranger). Furthermore, the response to daytime songs from stranger blackbirds was significantly stronger than to songs from neighbouring blackbirds, supporting the 'dear enemy' hypothesis. Male blackbirds were able to evaluate songs of different complexity, and from different sources, and discriminate between stranger and neighbour signals.

5.2 Introduction

Song plays an important role as a sexually selected trait in many bird species (McGregor et al., 1981). Signals produced by a sender in a song context have been shown to convey information (Ballentine et al., 2008; Searcy et al., 2006, 2000); this information involves sexual attributes of the sender such as motivation, status and the quality of the sender (Dabelsteen and Pedersen, 1990a; Hurd, 1997; Janicke et al., 2008; Rohwer, 1977). Hence, songs can also indicate substantial variation among singing males. These variations can be associated with age, time of day or season, mating status, reproductive ability of mates, acoustic habitat characteristics and behavioural traits of mates (Garamszegi et al., 2008; Jacobs et al., 2014; Naguib et al., 2016; Snijders et al., 2015). For example, song characteristics vary with age in the willow warbler, *Phylloscopus trochilus*, where male song repertoires increase across years (Gil et al., 2001). Male blackbirds respond more aggressively to dawn songs than daytime songs; because dawn songs are faster and have a high number of twitters (Dabelsteen and Pedersen, 1990a). In song sparrows, *Melospiza melodia*, males with greater repertoire sizes have higher reproductive success and longevity (Gil et al., 2001). Fast explorers in great tits, *Parus major,* have higher dawn and daytime song rates before egg-laying (Naguib et al., 2010). Therefore, many factors can impact on characteristics of the song in individuals, which also reflect the inter-and intra-individual variation in their behavioural traits.

In many species, differences in personality traits influence the performance of individuals during their lifetime; these activities include foraging behaviour, mating decisions, dispersal and reproduction (Amy et al., 2010). Personality can determine how individuals cope with challenges and make decisions in response to different stimuli (Polverino et al., 2016). Personality can also influence mate choice because certain behavioural traits predict individual qualities that impact the breeding success (Colchester and Harrison, 2016; Fox and Millam, 2014). Additionally, singing in birds does not only convey information to females and rivals but also attracts predators. Therefore, a singing male takes a risk while singing, exposing himself to predation risk (Bradbury and Vehrencamp, 1998; Parker and Tillin, 2006). Hence, it can be expected that song in birds reveals personality characteristics such as aggressiveness, boldness and risk-taking, related to a stressful or adventurous situation.

Songbirds use their songs to attract their mates and repel rivals (Hill et al., 2018). When a bird is singing, this signal delivers information to specific individuals (Beecher et al., 1996). One of the essential requirements for such vocal interactions is the ability to distinguish individuals based on their vocalisation (Skierczynski et al., 2007). A playback study shows that robins respond more strongly to the songs of non-neighbours than neighbours (Brindley, 1991). Bird vocalisation research has also shown that neighbour–stranger recognition is essential in shaping the strength of a territory owner's response during simulated territorial intrusions (Richards, 1979). By identifying the established neighbours (their song), territorial birds may reduce the costs of unnecessary repeated aggressive interactions since neighbours may pose little threat to the territorial bird compared to interactions with strangers (Bee and Gerhardt, 2001; Hardouin et al., 2006). This form of social recognition is known as the "dear enemy phenomenon" (Wilson, 1975). A study of ortolan bunting, *Emberiza hortulana*, found differences in the frequency of shared song types that enable the focal bird to discriminate between neighbour and stranger song. Hence, songs may be expressed in a sophisticated manner by the sender (Deeming, 2008), and individuals (receiver of the signal) evaluate and recognise songs.

Bird song studies have shown that the characteristics of songs might differ depending on the time of day (Avey et al., 2008). During the breeding season, the dawn song may have a crucial function for the territory owner in defence of a territory (Hill et al., 2018). Dawn songs play roles in mating activity (Dalziell and Cockburn, 2008), guarding performance (Otter et al., 1997) and male quality (Buchanan and Catchpole, 2000). In comparison, the daytime song is often used for female attraction and long-distance territory advertisement (Liu, 2004; Liu and Kroodsma, 2007). The broadcast of songs is most intensive during dawn, when song activity is at its peak. For example, the dawn chorus of field sparrow, *Spizella pusilla*, is more complicated than daytime songs (Nelson and Croner, 1991). In winter wrens, *Troglodytes troglodytes*, the number of songs produced is highest during dusk (Schmidt and Belinsky, 2013). In the song sparrow, *Melospiza melodia*, the rate of switching song types at dawn is higher than at daytime (Beecher et al., 1996). Hence, in many species, songs that are sung at dawn are more elaborate and variable than songs during the day, and it has been suggested that this plays an important role in social interactions among males (Liu, 2004; Spector, 1992).

In common blackbirds, males sing during the breeding season (dawn, daytime, and dusk) to defend their territories and threaten or attack rival males (Dabelsteen, 1984). Males have a large repertoire of stereotypic songs with diverse song types (Dabelsteen and Pedersen, 1992; Hall-Craggs, 1962; Mendes et al., 2011). A song typically starts with a motif, followed by a twitter section (Hesler et al., 2011). The motif or whistle has a relatively low frequency (1.5 – 3 kHz), is long-ranging, and has three to five simple elements that end with a twitter (Dabelsteen and Pedersen, 1985; Rasmussen and Dabelsteen, 2002). The twitter part has more complex elements, a much higher frequency (approximately 10 kHz), lower amplitude and shorter transmission range (Dabelsteen, 1984b). Studies of blackbird song have revealed information about the role of song in species recognition (Dabelsteen and Pedersen, 1985), aggressive tendencies (Dabelsteen, 1981; Ripmeester et al., 2007), habitat characteristics (Ripmeester et al., 2010), song complexity (Dabelsteen and Pedersen, 1990b) and in an intra- and inter-sexual context (Rasmussen and Dabelsteen, 2002). However, it remains unclear whether songs in blackbirds deliver information about behavioural traits, such as aggressiveness or fear, parental care, and male quality (breeding success). There is also no research investigating the dear enemy hypothesis in blackbirds.

In this research, I assessed the responses of male blackbirds to different types of songs by designing two playback song experiments. I examined whether individuals have different responses to playback songs from males of varying levels of aggressiveness. Aggressiveness (or lack thereof) is a natural response to a stressful situation (like predator exposure). In Chapter 3 I assessed the aggressiveness of blackbirds in response to a predator. I used those data to identify males of varying degrees of aggressiveness and selected their songs for playback experiments in this chapter. Here, I investigated five more questions: 1) Do males respond differently to the songs from aggressive and non-aggressive males? 2) How do human disturbances (e.g., distance from a road) impact the intensity of male response to stranger songs? 3) Do males with different aggressiveness levels respond differently song playbacks? 4) Are there any correlations between the intensity of the male response and breeding success? and 5) Does parental care correlate with the strength of the male response to the blackbird songs? I expected that the blackbird song would contain characteristics that correspond to individual variation in aggressiveness; characteristics that other males can use to determine the level of aggression by the signaller. Therefore, male blackbirds should respond differently to songs from males with different levels of aggressiveness. I also expected that males with different aggressiveness levels would

respond differently to the songs of stranger blackbirds; more aggressive males would respond more strongly to the playback song than less aggressive males. I also expected that the male response to the playbacks would be affected by anthropogenic impacts; males closer to the road would be more sensitive (aggressive) and would respond strongly to stranger song. The density of birds would be high near the road; because being near the road appears to have an advantage for nesting blackbirds (breeding success, chapter 3). Therefore, competition and aggression would be high in individuals who live near the road. Finally, I expected the male response would also predict male quality; more aggressive males provide more parental care and attention to the nest and have higher numbers of fledged chicks .

In the second playback experiment, I investigated the blackbird's ability to distinguish between songs from neighbours and strangers (dear enemy hypothesis). I addressed song discrimination with two questions: 1) Do blackbirds discriminate songs from neighbours, local strangers and distant strangers from Europe?; 2) How does the response of male blackbirds vary for dawn and daytime songs? I predicted that male blackbirds could discriminate between songs from neighbours and strangers. Males would respond more strongly to dawn songs from European blackbirds, New Zealand strangers and neighbours, respectively. The stranger blackbirds' territorial status was unknown; therefore, a song from a stranger would be a serious threat to the territorial male blackbird and require a stronger response . I assumed that the dawn chorus would be more complicated and would mediate social interactions among territorial males, while daytime songs in blackbird might act as a general territorial advertisement. Therefore, the strength of reaction to these songs would be different depending on the source of the song (neighbour or stranger).

5.3 Methodology

5.3.1 Species and field site

I conducted two playback experiments at Massey University Albany Campus, located in an Auckland suburban area (36.733982°S, 174.701416°E). Common blackbirds, *Turdus merula,* are a medium-sized thrush, belonging to the Turdidae family. The blackbird is native to the Middle East, Europe and the northwest of Africa. This bird was introduced by English immigrants to New Zealand between 1867 and 1879 (Hatchwell et al., 1996). Although they are originally a forest species, blackbirds are common in New Zealand in urban and suburban areas, parkland, farmlands, woodland, orchards, bush edges, and native forest (Heather and Robertson, 2000). Male blackbirds were colour-banded with permission given by the New Zealand Department of Conservation and Massey University Animal Ethics Committee (AEC/17 (Amended 01/14)). I carried out the song discrimination playback in 2019 and responses to aggressiveness of signal playback in 2018.

5.3.2 Song recordings

All recordings were taken from colour-banded males during dawn chorus and during the daytime in the breeding seasons of 2017 and 2018. The dawn songs were recorded before sunrise between 4:00 to 6:00 local time, within the male territories. Daytime songs, by definition, were recorded after sunrise between 0800 and 1600 hours, local time. Song recordings were made using a directional shotgun microphone (Sennheiser ME66, Sennheiser, Germany) connected to a Marantz solid-state digital recorder (Marantz Professional PMD 661, Marantz Professional, Cumberland, RI, U.S.A.) with 24-bit sampling precision and 48 kHz sampling rate. I created a pool of blackbird songs to use for the playbacks. Each song has associated metadata, including male identity, time of singing, location of focal male and date of recording.

5.3.3 Aggressive behaviour assessment

I measured the aggressiveness of 20 male blackbirds towards a predator, using a taxidermied avian predator model, a morepork, *Ninox novaeseelandiae*, (chapter 3). I carried out the experiment in the breeding season of 2017 near the blackbirds' nests when pairs had chicks older than five days. I presented the predator model and recorded male and female responses. The highest response of individuals to the model included attack and

alarm calling and the lowest response was ignoring the predator. In this study, I used the response of male blackbirds to the predator model as a proxy of aggressiveness. I selected songs from the most aggressive and least aggressive males for a pool of songs in this experiment. The selected pool song included songs from 15 males (N = 8 non-aggressive males; N = 7 aggressive males).

Figure 5.3.1. Recording blackbird song during the breeding season (taken by Emad Shariat).

5.3.4 Playback 1: songs from differentially aggressive males

I designed a playback experiment to test the response intensity of male blackbirds to the songs from differentially aggressive males (chapter 3). I tested if song parameters varied between aggressive and non-aggressive male blackbirds. Song measurements included song duration (the duration of a complete song, motif plus twitter), the interval between

songs, the lowest frequency of songs (Hz), the highest frequency of songs (Hz), and bandwidth (the difference between low frequency and high frequency, Hz). All songs were measured in Raven Pro 1.5 software (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.). I applied non-parametric Mann-Whitney U tests to compare the songs between the two types of males. Results showed that low frequency, high frequency, and bandwidth varied significantly between songs from aggressive and non-aggressive males (Table 5.31).

Table 5.3.1. Description of song measurements between aggressive and non-aggressive males (N = 8 non- aggressive males; N = 7 aggressive males; mean ± SD) and the results from a Mann-Whitney U test for song measurements in common blackbirds. $p \leq 0.05$ required for a significance level, shown by an asterisk (*).

Parameter	No. of songs	Non-aggressive male songs	No. of songs	Aggressive male songs	W	*p*
Song interval (s)	120	3.4 ± 0.1	37	3.4 ± 0.2	2139	0.7
Song duration (s)	349	2.6 ± 0.1	262	2.6 ± 0.1	43833	0.3
Bandwidth (Hz)	349	1801.9 ± 53.0	262	1896 ± 51.1	38772	0.001*
Low frequency (Hz)	349	1376.4 ± 11.0	262	1446.17 ± 15.8	37019	≤ 0.001*
Max Frequency (Hz)	349	2429.9 ± 27.0	262	2547.71 ± 26.8	35794	≤ 0.001*

Playbacks were performed during the breeding season between September and October 2018. All playbacks were completed before eggs hatched. I tested three different types of playback treatments per territorial male blackbird. Each male blackbird was subjected to six trials in a random order (two repeats of song types per territorial male): (1) two random songs from the most aggressive males, (2) two random songs from the non-aggressive males, and (3) two songs from the native tūi, *Prosthemadera novaeseelandiae novaeseelandiae* (control song). Selected songs were not songs from the focal male's neighbours. A minimum one-day gap was allowed between each treatment (6 days = 6 playback songs).

Playbacks were carried out in the morning after sunrise between 0600 and 1400 local hours. Before the playback, I specified the location of the speaker by placing markers at 5, 10, 15 and 20 meters around the speaker location in each male territory. The experiment was started by placing a UE Mega Boom speaker (Ultimate Ears) one to two meters above

the ground within the centre of the male's territory, close to the focal bird's nest or where the focal male usually sang. I observed the focal male one minute before beginning the playback experiment. Subsequently, the song was played to the focal male with 4 minutes of a randomly selected song. Measured responses to playback included the minimum distance between the bird and speaker during the playback (hereafter min distance, in meters), latency to reach the minimum distance (hereafter min.dis.latency, in seconds), response duration (seconds), time that the focal male spent within 5 meters of the speaker (within 5 m, seconds), the number of flyovers of the speaker (hereafter no. of flights) and the number of calls during (hereafter no. of calls) the playback. Data collected directly in field .

Additionally, I collected other parameters related to male parental care, including the number of nest visits within 30 minutes during chick-rearing stage and the number of fledged chicks per nest (chapter 2). Human disturbance parameters included the distance of the nest from the road (chapter 2). Individual behavioural traits included the male's aggressiveness score (chapter 4). I conducted 120 playback trials for 20 territorial male blackbirds.

5.3.5 Playback 2: song discrimination

This experiment tested whether male blackbirds discriminated between dawn and daytime songs from their neighbours and strangers. For the playback experiment, I checked pairs breeding behaviour in their territories, and I selected ten males whose female built their nest but didn't start to lay eggs . Then, I collected information regarding the identity of their neighbours to select neighbour songs. I selected songs from the known neighbouring males that remained unchanged around the focal male territory. Stranger songs were also randomly chosen from songs recorded from the farthest territorial males in the same population. I randomly selected two dawn songs and two daytime songs from neighbours and strangers to create a pool of songs for each territorial male. In addition, I wanted to know if blackbirds can recognise songs from more distantly related blackbirds. I did not use blackbird songs from the United Kingdom because these might be the source of the NZ population (Gurr, 1954). The dawn songs of European blackbirds were downloaded from https://www.xeno-canto.org/. Songs from European blackbirds were recorded in France, Germany, and Poland. For each focal male, I randomly selected two dawn songs and added them to the pool. Overall, ten songs (two dawn and two daytime songs from neighbours,

strangers and two European blackbird dawn songs) were selected as playback songs of each focal male. In this experiment, I used a chaffinch song as the control treatment.

I used *Audacity* software to create playbacks and adjust the volume levels for the field speaker (D. M. Mazzoni, http://audacity.sourceforge.net). A DSE Sound Level Meter was also used to set average playback amplitude at approximately 85 Db, measured at a distance of one meter from the speaker. Speaker amplitude was determined by adjusting volume levels for field speakers (in urban areas) to match song amplitude levels at a one-meter distance. All selected playbacks were adjusted for the same duration (180 seconds). Each trial contained four sections: 1. one-minute silence; 2. three minutes of blackbird or chaffinch song (randomly chosen); 3. another one-minute silence; 4. a contingent playback song. If the second section was a chaffinch song (control 1), the fourth section would be a blackbird song or vice-versa (a chaffinch song that was played in section four, named control 2) . Overall, a playback trial took 8 minutes.0

Playbacks were conducted from 5 August until 5 October 2019, between 07:00 and 17:00 local time and only during suitable weather conditions. Before the playback, I specified the location of the speaker and 5 meters around the speaker in each male territory. A UE Mega Boom Speaker (Ultimate Ears) was positioned one meter above the ground and as close as possible to the nest site location (if possible) or singing location of the focal blackbird. A playback was broadcast when a focal male was observed in his territory while foraging. The blackbird behaviour was observed for one minute, and then the playback was played, and the male responses were recorded. I recorded the responses of the focal male to the playback as follows: response duration, min.dis.latency, min distance, within 5 m, time that focal male started foraging when the playback song was played (hereafter normal forage. time, in second), and the normal foraging distance of blackbirds when the playback song was finished (hereafter normal forage distance, in meter). All responses were collected and recorded in the field. In total, I conducted 200 trials for ten individuals, including 10 playback experiments per male (100 blackbird song playbacks, 100 chaffinches song playbacks).

5.4 Statistical analysis

All analyses were conducted in R version 4.10 (R Core Team, 2021). I applied a Spearman's rank correlation between response variables within each experiment. Results showed the majority of response variables were significantly correlated with each other in both experiments. To remove the issue of correlation between variables, I applied Principal Component Analysis (PCA). I ran a PCA from the package "*factoextra* " to reduce the set of response variables into an single principal component (PC1) (Kassambara and Mundt, 2017). I applied this analysis for both playback experiments. Further analyses were carried out on PC1.

I applied a Generalized Linear Mixed Model (GLMM) using the packages "*lme4*" and "*lmerTest*" to investigate the effects of songs from differentially aggressive males (Harrison et al., 2018; Kuznetsova et al., 2017). Fixed factors were playback treatment (songs from aggressive males, non-aggressive males), the focal male aggressiveness score, the nest distance from the road, and the number of nest visits by the focal male during chick rearing stage. In this model, male identification (ID) was included as a random factor. The models were fitted using the "*lmer*" function for Gaussian distributed data. I used the "*lmerTest*" package for quantifying p-values of fixed effects via Satterthwaite approximation of degrees of freedom (Kuznetsova et al., 2017). I adjusted contrasts associated with factor treatment, so it has one contrast that compared the response to control song versus response to blackbird song (C-vs-Tr) and response to song from aggressive males versus song from non- aggressive males (NonAgs-vs-Ag). I also included interactions between the playback treatment and other fixed factors; the interactions mean that the effects of treatment depended on the other fixed factors. To make the fixed main effects of treatment more sensible, I also used mean-centred distance to the road, mean-centred nest visit, and adapted male aggressiveness. Male aggressiveness variable means that nonaggressive male was baseline and aggressive was the effect. I fit the different interactions between fixed factors and treatment and calculated the AIC. Then, I compared the AIC values, a model with the lowest AIC value was selected as the best model (refer to appendices, section 7.4).

To investigate if blackbirds can discriminate between songs from neighbour and stranger blackbirds, I ran two GLMM analyses: one for the response of blackbirds (PC1) to the dawn songs (neighbour, stranger, and European blackbirds) and the second one for the

response of blackbirds (PC1) to the daytime songs from different sources (neighbour, strangers). In these models, PC1 was the response variable, playback type (neighbour, stranger, European blackbirds, and control) was a fixed factor, and the male identification was a random factor. In addition, I applied Tukey post-hoc tests to explore which types of playbacks were significantly different from each other. All tests were two-tailed with a significance threshold of 0.05.

5.5 Results

5.5.1 Playback 1: songs of differentially aggressive males

I measured a total of six response variables that described the male reactions to the playback experiments (Table 5.5.1). The focal male blackbird responded to the playback by moving toward the speaker and searching around the speaker. In addition, other behavioural responses included tail moving, flying, and calling. Results from the PCA showed that PC1 explained 69.5% of the variation in all response variables. PC1 was strongly influenced by response duration (73.4%) and time spent within 5 m (60.8%). PC2 explained 20.2% of the variation in all response variables, so I included only PC1 in further analysis.

Table 5.5.1. Mean (±SD) values of response variables to the playback were calculated separately for treatments where songs from aggressive and non- aggressive males were presented. Overall, 120 playback treatments were done on 20 male blackbirds.

Response variable	No. of trials	Aggressive males	Non-aggressive males	Control
Response duration (s)	40	181.1 ± 11.6	191.1 ± 9.0	9.62 ± 0.3
Min distance (m)	40	5.0 ± 0.8	3.9 ± 0.6	11.47 ± 0.7
Min.dis latency (s)	40	92.1 ± 11.0	96.2 ± 10.1	134 ± 13.5
Within 5 m (s)	40	123.0 ± 14.9	112.8 ± 11.5	9.2 ± 3.6
No. of flights	40	3.6 ± 0.5	3.8 ± 0.5	0.95 ± 0.2
No. of calls	40	3.0 ± 1.4	4.4 ± 1.5	1.07 ± 0.5
PC1	40	69.4 ± 17.4	69.3 ± 12.6	-138.63 ± 4.7

Results from GLMM analyses showed that the significant predictors of male response were the nest distance to the road, playback treatment, the number of nest visits by focal males, and road/playback treatment interaction. Following our predictions, male blackbirds responded strongly to blackbird songs compared with the control song type (tūi) (Table 5.5.3). There was significant interactions between treatment and road /nest visit (Table 5.5.3). In addition, there were no differences in responses of male blackbirds to songs from aggressive and non-aggressive males (Table 5.5.3).

Table 5.5.2. Percentage of variance and principal component factor loadings of response variables in four principal components to playbacks of blackbird and tūi songs. Measures that contributed most to each PCA factor are highlighted in bold.

	PC1	PC2	PC3	PC4
Percentage of variance	69.5	20.2	10	2
Response variable				
Response duration (s)	**73.4**	20.8	**64.6**	1.5
Min distance (m)	-3.2	-1.1	1.7	12.3
Min.dis latency (s)	-30.1	**95.0**	3.6	1.2
Within 5 m (s)	**60.8**	22.1	**-76.2**	0.6
No. of flights	1.4	0.0	0.3	0.6
No. of calls	0.0	1.1	0.8	**-99.2**

Table 5.5.3. GLMM results of the influence of predictor variables on PC1. A significance level of $p \leq 0.05$ is shown by an asterisk (*).

	Estimate	SE	z	*p*
Intercept	-18.55	13.34	-1.39	0.18
Treatment : C_vs_Tr	124.69	11.00	11.34	≤ 0.001*
Treatment : NonAg_vs_Ag	-17.92	9.56	-1.88	0.06
Nest visit	42.31	16.44	2.57	0.02*
Male aggressiveness score	10.77	18.23	0.59	0.56
Road	-1.23	0.60	-2.07	0.05*
Treatment C_vs_Tr * Male aggressiveness score	4.15	15.05	0.28	0.78
Treatment NonAg_vs_Ag * Male aggressiveness	24.91	13.03	1.91	0.06
Treatment C_vs_Tr * Nest visit	38.13	13.75	2.77	0.01*
TreatmentNonAg_vs_Ag * Nest visit	21.39	11.78	1.82	0.07
Treatment C_vs_Tr * Road	-1.41	0.52	-2.69	0.01*

I found a strong effect of the males' nest distance from the road in the model (z = -2.7, *p* = 0.05*, Table 5.3.3). Males with nests closest to the road had the highest PC1 scores (Figure 5.5.1.A). Furthermore, in the GLMM, the number of nest visits influenced the responses of male blackbirds to the song (z= 2.57, p = 0.02*, Table 5.5.3). Males who visited their nest more during the chick raising had the highest PC1 scores (Table 5.5.3; Figure 5.5.1.B).

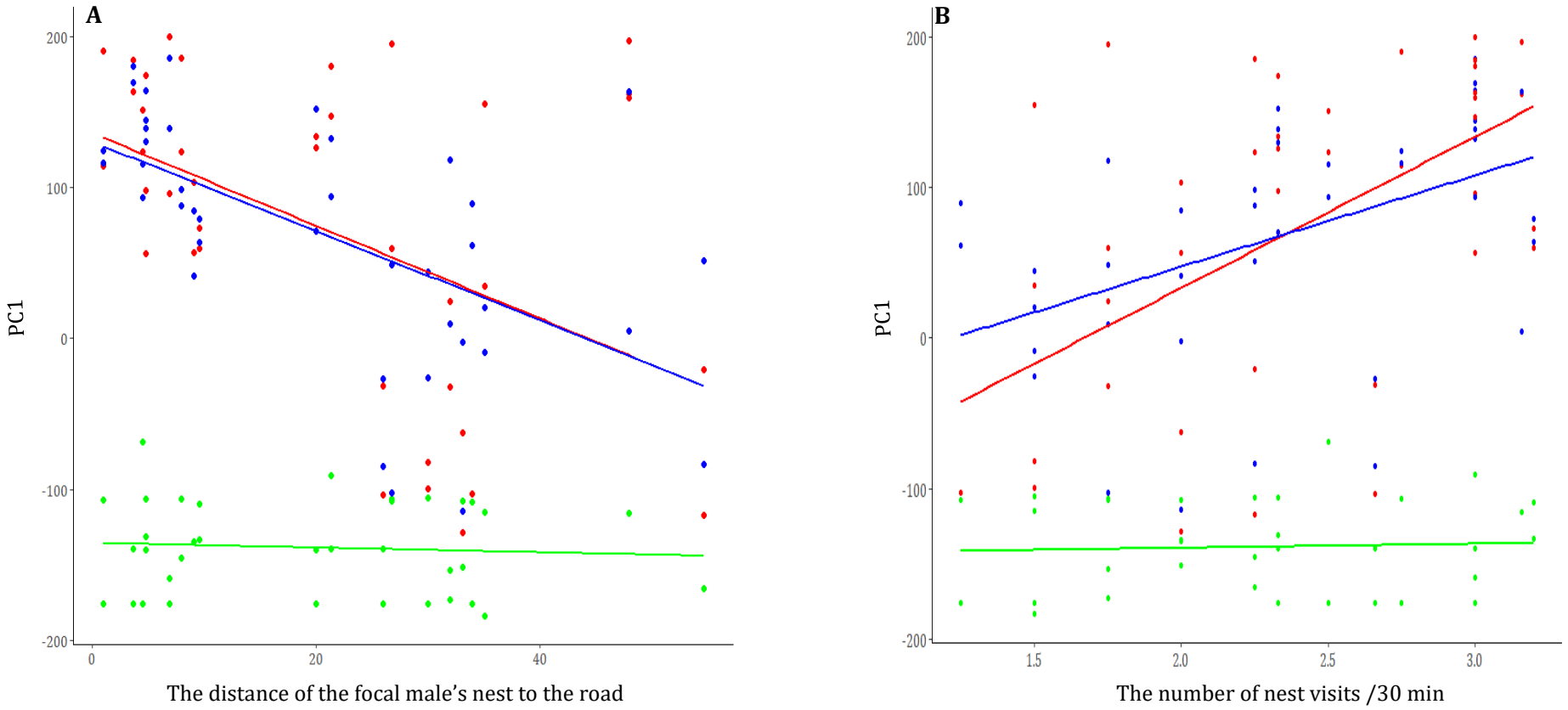

Figure 5.5.1. Correlations between PC1 and male response /nest visit. A) Correlation between PC1 and the distance of focal male's nest from the road. Red line = aggressive males; blue = non-aggressive males; green = tūi. Spearman's rank correlations for red line: r = -0.4, *p* = 0.007*, N = 40 playbacks; blue line: r = -0.6, *p* ≤ 0.001*, N = 40 playbacks; green line: r = -0.1, *p* = 0.7, N = 40 playbacks. B) Corrolation between PC1 and the number of nest visits by focal male. Spearman's rank correlations for the overall response to the songs from aggressive males (red line): r = 0.5, *p* ≤ 0.001*, N = 20 playbacks; non-aggressive males (blue line): r = 0.5, *p* ≤ 0.001*, N = 20 playbacks, tūi (green line): r = 0.0, *p* = 0.8, N= 20 playbacks.

Table 5.5.4. Mean (±SE) values of response variables to the playbacks were calculated separately for treatments where different types of songs were presented. Overall, 200 playback treatments were done on ten male blackbirds.

Response variable	First control N= 51	Second control N = 49	Europe dawn song N = 20	Neighbour dawn song N = 20	Neighbour daytime song N = 20	Stranger dawn song N = 20	Stranger daytime song N = 20
Response duration (s)	0.5 ± 0.2	31.9 ± 7.7	103.6 ± 13.5	139.1 ± 9.5	118.4 ± 12.07	1414.9 ± 8.9	149.0 ± 9.1
Min distance (m)	15.6 ± 1.0	10.7 ± 1.0	4.8 ± 1.2	2.1 ± 0.2	4.0 ± 1.0	3.4 ± 0.8	3.0 ± 0.5
Min.dis latency (s)	139.1 ± 7.7	121.9 ± 9.6	85.9 ± 12.5	56.9 ± 9.9	62.5 ± 11.3	52.0 ±0. 9	58.2 ± 9.8
Within 5 m	6.2 ± 3.1	55.9 ± 10.6	72.5 ± 15.5	114.4 ± 12.4	78.7 ± 14.8	115.5 ± 13.0	116.1 ± 12.0
Normal forage time (s)	6.9 ± 3.1	38.5 ± 10.7	129.0 ± 15.5	227.0 ± 12.4	160.8 ± 14.8	215.3 ± 13.0	213.3 ± 12.0
Normal forage distance (m)	13.6 ± 1.1	12.8 ± 1.5	18.2 ± 3.9	17.2 ± 2.7	13.1 ± 1.06	12.6 ± 2.5	11.8 ± 2.0
PC1	-7251.4 ± 4.0	-3926.6 ± 13.2	754.2 ± 21.2	3028.0 ± 28.4	1555.0 ± 22.7	2919.4 ± 21.3	2921.3 ± 16.1

5.5.2 Playback 2: song discrimination

Variation in response variables is presented in Table 5.5.4. Playback experiments were conducted on ten territories during the 2019 breeding season. PC1 was strongly related to the normal foraging time. PCA showed that PC1 explained 77.5% of the variation in all response variables (Table 5.5.5). Results from the first model assessed the response of males toward dawn songs from a neighbour, stranger and far stranger (Europe blackbirds). The GLMM analysis showed that the male response to the chaffinch song presented in the last part of the playback (control 2) was stronger than when presented in the first section of the playback (control 1) (Table 5.5.6). In contrast, the Tukey tests showed no difference in the blackbirds' responses between control treatments (Table 5.5.7). In addition, the overall response of male blackbirds was significantly different between dawn songs from blackbird and chaffinch songs (Table 5.5.6 and Table 5.5.7). Blackbird responses to the chaffinch songs were considerably weaker than blackbird's songs (Table 5.5.7).

Table 5.5.5. Percentage of variance and principal component factor loadings of response variables in four principal components to playbacks of blackbird and chaffinch songs. Measures that contributed most to each PCA factor are highlighted in bold.

	PC1	**PC2**	**PC3**	**PC4**
Percentage of variance	77.5	11.2	7	3
Response variable				
Response duration (S)	46.4	0.3	12.3	**87.7**
Min distance (m)	-4.0	4.2	-0.0	-1.7
Min.dis latency (s)	-31.0	56.9	**75.7**	6.0
Within 5 m	37.2	-61.0	63.6	-28.6
Normal forging time (s)	**73.9**	55.0	-7.0	-38.2
Normal foraging distance (m)	-0.1	2.5	-4.5	0.6

Table 5.5.6. GLM results from the influence of predictor variables on PC1 from the response of blackbirds to the dawn songs from the neighbour, stranger, and European blackbirds. A significance level of $p \leq 0.05$ is shown by an asterisk (*).

Fixed variable	Estimate	SE	z	*p*
Intercept	-138.0	20.4	-6.8	≤ 0.001*
Playback: control2	52.4	22.8	2.3	0.02*
Playback: Europe	175.7	24.3	7.2	≤ 0.001*
Playback: neighbour	289.4	24.3	11.9	≤ 0.001*
Playback: stranger	283.9	24.3	11.7	≤ 0.001*

Table 5.5.7. Tukey test results showed the significance of comparisons between playback treatments of dawn songs and the chaffinch song. A significance level of $p \leq 0.05$ is shown by an asterisk (*).

Playback treatments	Mean difference	Lower bound	Upper bound	*p*
Control2-Control1	64.5	-3.0	132.0	0.06
Neighbour-Europe	113.7	32.4	194.9	≤ 0.001*
Stranger-Europe	105.3	27.0	189.5	0.003*
Stranger-Neighbour	-5.4	-86.7	75.8	0.9

Additionally, there was no significant variation in response of male blackbirds to the dawn songs from the neighbour and stranger blackbirds from New Zealand (Table 5.5.6, Table 5.5.7). Male blackbirds respond equally and strongly to the dawn songs from neighbours and strangers (Figure 5.5.2). However, the response to the dawn songs from European blackbirds was significantly lower than the dawn songs from New Zealand blackbirds (Figure 5.5.2, Table 5.5.6 and Table 5.5.7).

Both the GLMM and post-hoc analyses of the playbacks from daytime songs showed significant differences in the response of male blackbirds to the control treatments and blackbird treatments. In addition, blackbirds responded significantly stronger to the daytime songs of stranger blackbirds compared to the daytime songs of neighbours (Table 5.5.9 and Figure 5.5.3). Although the post-hoc tests showed no difference between

the response of males to the control treatments (control 1 and control 2), results from GLMM analysis presented a significant variation between the two control treatments (Table. 5.5.8 and Table 5.5.9).

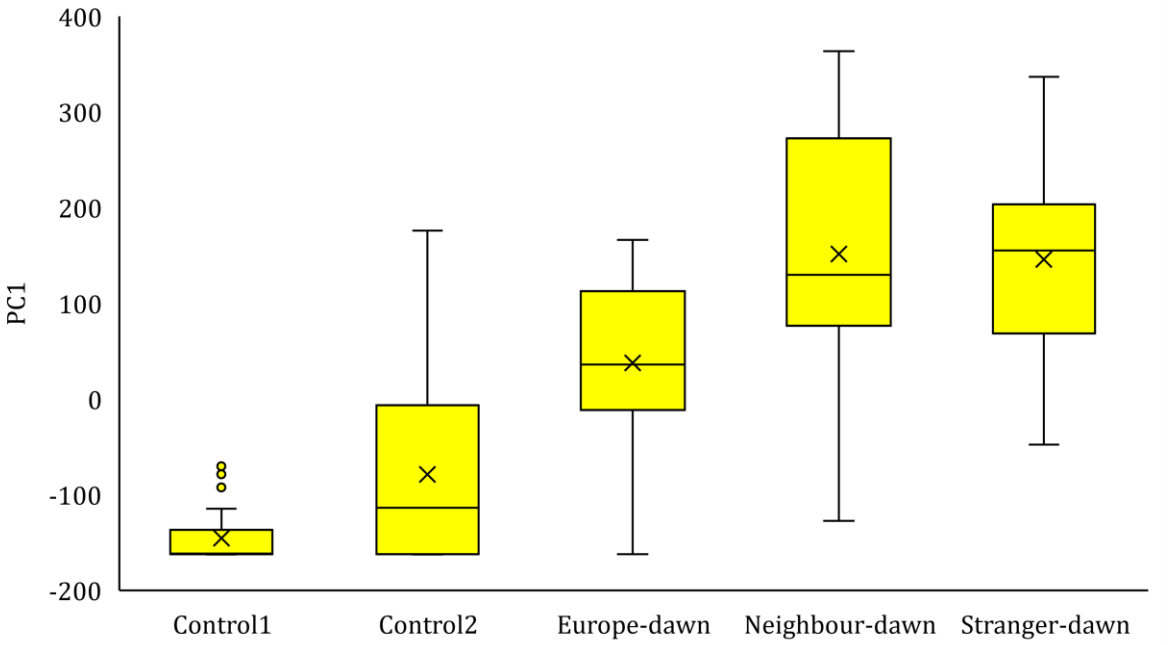

Figure 5.5.2. Box and whisker plots of PC1 (overall response) of male blackbirds to different types of playback treatments. Number of treatments: control1 = 32; control2 = 28; dawn song from European blackbirds = 20; dawn songs from neighbours = 20; and dawn songs from the strangers = 20.

Table 5.5.8. Results from the GLMM for PC1 (overall response to dawn song playback) in blackbirds. A significance level of $p \leq 0.05$ is shown by an asterisk (*).

Fixed variable	Estimate	SE	t	*p*
Intercept	-141.5	17.7	-8.0	≤ 0.001*
Playback: control2	58.8	22.1	2.7	0.01
Playback: neighbour	219.2	22.3	9.9	≤ 0.001*
Playback: stranger	287.5	22.3	12.9	≤ 0.001*

Table 5.5.9. Tukey test of comparisons between playback treatments of daytime songs from blackbirds and chaffinch songs. A significance level of $p \leq 0.05$ is shown by an asterisk (*).

Playback treatments	Mean difference	Lower bound	Upper bound	*p*
Control1-control2	58.1	-1.9	118.2	0.06
Stranger-Neighbour	68.3	6.8	129.79	0.02*

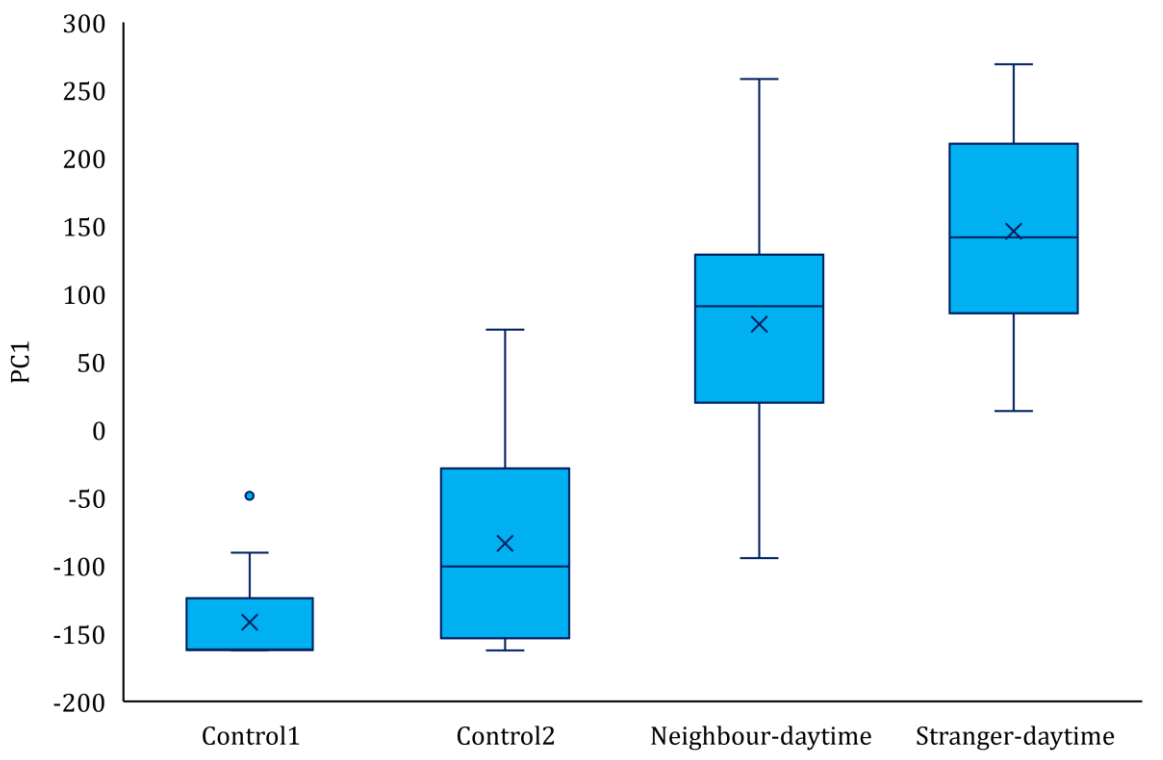

Figure 5.5.3. Box and whisker plots of PC1 (overall response) in male blackbirds to different types of daytime songs from neighbour and stranger blackbirds and chaffinches (control1 and control2). Number of treatments: control1 = 20; control2 = 20; neighbour daytime song = 20; and stranger daytime song = 20.

5.6 Discussion

5.6.1 Songs of differentially aggressive males

Territorial blackbird males can use songs to communicate and transfer information about their short-term intentions in aggressive situations (Dabelsteen and Pedersen, 1990b). A study of male blackbirds showed that aggressive males increase the twitter frequency in response to playback (Ripmeester et al., 2007). Although I found that the low frequency, maximum frequency, and bandwidth of songs in aggressive males were higher than non-aggressive ones, I did not find variation in the response of males toward the songs from aggressive and non-aggressive males. There were also no significant differences in the response of aggressive and non-aggressive males to the playback songs. Contrary to my expectations, aggressiveness as a personality trait did not appear to play a role in either the song as a signal of the sender or the response of the receiver. I hypothesised that blackbird song characteristics contain information regarding the behavioural traits of individuals. However, further study is needed to understand which song characteristics might vary between individuals with different behavioural traits. I also speculated that the strength of behavioural trait (aggressiveness) might vary during the breeding season in blackbirds. For example, blackbirds earlier in breeding season or before mating might be more aggressive toward any other male intruding on his territory. Studies on great tits, *Parus major*, explain that fast explorer individuals increase their singing activities and have a higher song rate before egg-laying at dawn (Naguib et al., 2010, 2016). While other studies show faster explorers sing at a lower song rate but with longer songs before egg-laying (Amy et al., 2010) and generally show a stronger vocal response (Snijders et al., 2015).

Interestingly, males that had nests closer to the road reacted more strongly to the playbacks. Many studies have shown negative impacts of roads on species, such as habitat loss, collisions with vehicles, noise and light pollution, and population fragmentation (Lowry et al., 2013; Maron and Kennedy, 2007). Studies have also found benefits such as warm road surfaces, low predation pressure, streetlights (prolonging diurnal activity, singing-post, and insects as prey), and higher food availability – benefits that make road-sides an attractive environment to some birds (McMullen et al., 2014; Morelli et al., 2014). In addition, research has shown the modification of behaviours in many bird species in cities, e.g., earlier breeding in swifts and swallows (Marzluff, 2001), nesting behaviour in

dark-eyed juncos, *Junco hyemalis* (Bressler et al., 2020), higher-pitched songs in urban blackbirds (Nemeth and Brumm, 2009), and higher aggressiveness in noisy miners, *M. melanocephala*, and Australian magpies, *Gymnorhina tibicen* (Parsons et al., 2006). Moreover, bird abundance and density increase, and bird diversity is low in cities (Husby and Husby, 2014). I also found that nest success was higher near the road (chapter 2), and I found a positive correlation between road and male response to the playback. Although I cannot predict the positive or negative direction of road on blackbirds, road might have a big effect on the response of males. I speculated that aggressive males might dominate the territories near the road because of the possibility of, e.g., lower predation or higher density of blackbird territories near roads. However, more evidence is needed to investigate these possibilities.

Aggression may be related to mate choice and pairing (Ophir et al., 2005), parental provisioning (Barnett et al., 2012), and breeding output (Szász et al., 2014). Individuals with different levels of aggression may use different reproductive strategies, which leads to variation in life-history trade-offs within a population. The majority of studies demonstrate a negative link between aggression and male provisioning; for example, in western bluebirds, *Sialia Mexicana* (Duckworth 2006) and house wrens, *Troglodytes aedon* (Barnett et al., 2012). However, unlike other studies, male blackbirds that used more aggressive responses towards all playbacks had a significantly higher number of nest visits, a measure of parental investment. I speculate that there may be a relationship between aggression and parental care which is related to this investment. Aggressive responses to playbacks may indicate a male's overall aggressiveness to threats, including nest defence.

5.6.2 Song discrimination

This study offered the first evidence in blackbirds for this level of neighbour–stranger distinction, which is comparable to similar studies in other passerines. Debesteen (1984) showed that the response of blackbirds differed towards songs from different times of day; however, there no studies related to the response of blackbirds to daytime and dawn songs of neighbours and strangers. My results revealed that male blackbirds responded strongly to the dawn songs from both neighbours and strangers, which was unexpected. However, males appear to identify songs from European blackbirds, as the response to the European blackbird songs was much weaker than the response to local birds (Figure

5.5.4). Although the blackbird response did not differ between dawn songs from neighbour and stranger, the response of blackbirds to daytime songs between neighbour and stranger showed clear evidence that individual males could discriminate between conspecific neighbours and strangers based on acoustic cues.

I applied a control treatment before or after blackbird playback songs to make sure blackbirds did not respond to other species and can recognise the blackbird song. Interestingly blackbirds were often vigilant towards the control treatment if played after the blackbird playback (section four). However, the response to this song was much weaker than the response to the blackbird song. This result showed blackbirds could distinguish between a blackbird and other species' songs. When the male responded aggressively toward the blackbird's song, he tended to act more aggressively to the other species around his territory for a period of time. Furthermore, in my method, the gap duration between blackbird and control song was short; therefore, the duration should be considered in future analyses.

I predicted the blackbirds would have different levels of recognition of blackbird songs. Interestingly, blackbirds responded to European blackbird's songs, but contrary to my prediction, this response was much weaker than towards local blackbirds. This suggests they do not interpret blackbird songs from Europe to be as threatening as blackbird songs from New Zealand.

The dawn songs in many songbirds are more complicated, elaborate, variable and more intense than the songs used during the day. There also seems to be a more aggressive response towards the dawn song (Nelson and Croner, 1991; Staicer et al., 2019). The dawn songs in field sparrows, *Spizella pusilla*, and chipping sparrow, *Spizella passerine*, are structurally more complex than daytime songs, which serve different functions (Liu and Kroodsma, 2007; Nelson and Croner, 1991). Blackbird song is one of the most advanced and complex model systems that motivate an aggressive response: e.g., fight among male blackbirds (Dabelsteen, 1984a, 1984c; Ripmeester et al., 2007). I assumed that territorial males would assess the complexity of the song then employ different strategies to respond to the songs. Generally, song complexity is higher in dawn songs, which may also reflect a stronger motivational state of males. Hence males equally and strongly responded to dawn songs from both neighbour and stranger, showing that the dawn song can provoke the strongest response.

The noticeable difference in response to the daytime songs between neighbours and strangers appears to support the dear enemy effect. Such acoustic discrimination has now been documented in a wide range of bird species: alder flycatcher, *Empidonax alnorum* (Lovell and Lein, 2004), shearwater, *Puffinus l. lherminieri* (Mackin, 2005), corncrake, *Crex crex* (Budka and Osiejuk, 2013) and yellow-bellied tit, *Parus venustulus* (Wei et al., 2011). In blackbirds, the strength of the dear enemy effect may be conditional on the type of song and depending on the types of songs (daytime and dawn song) from the neighbour and stranger. Therefore, male blackbirds appear to discriminate between dawn and day songs, perhaps based on complexity and source, and respond appropriately.

In conclusion, this research provides new knowledge on the response of blackbirds to different song types and contexts. Although the first playback song experiment did not detect any effects of aggressiveness in senders and receivers of the song signals, variation in response to the playback revealed the other important aspects of songs in blackbirds. It showed that the distance of territories from the road could impact the behavioural traits of individuals. In addition, the aggressive response of male blackbirds was correlated with parental care behaviour. Furthermore, the response of blackbirds to the dawn and daytime songs from neighbours and strangers explained the potential importance of song complexity (dawn song) and song type (daytime- dawn songs) that stimulated different levels of male responses. Further, daytime song discrimination has demonstrated the dear enemy hypothesis in blackbirds. However, more research is required to investigate which components of songs such as motif or twitter durations and frequencies vary in different songs of blackbirds. More playback experiments would also reveal more details about the factors that influence the degree of aggressive response of the male blackbird to the song.

5.7 References

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Chapter 6:

Conclusions

Fledged chicks and male blackbird

6.1 . Overview

The central aim of my thesis was to investigate variation in behavioural traits of a free-living model species, the common blackbird, by comparing the effect of a range of ultimate and proximate factors. I investigated the concept of personality and individuality and the consequences of behavioural trait patterns on breeding investment and success. This conclusions chapter provides an overview of the key findings from my research in relation to the eight questions I proposed in Chapter 1.

Are there significant differences between the sexes, and across different age classes of blackbirds, in shared behavioural traits?

Contrary to what I had predicted, I did not find significant differences between males and females in any of the behavioural traits I measured that are exhibited by both sexes. These shared behavioural traits included activity, boldness, parental investment, vigilance, aggression, exploration, anti-predator behaviour and neophobia. Equality in the expression of the variety of behavioural traits between males and females is also reported in other monogamous species with biparental care, for example, in zebra finches,

Taeniopygia guttata (Brust et al., 2013; Schuett and Dall, 2009). Nonetheless, Blackbird species do exhibit sexual dimorphism and variation in some specific traits such as singing in males, nest building, egg-laying and incubating in females (Biddle et al., 2015; Dabelsteen and Pedersen, 1990; Hall-Craggs, 1962; Karakaya and Arikan, 2015; Kucherenko and Ivanovskaya, 2020; Mendes et al., 2011). Blackbirds are a socially monogamous species where both males and females are involved in parental care and in jointly defending a territory year-round (Chamberlain et al., 1999; Fernández-Juricic and Tellería, 2000; Groom, 1993). The similarity in the range of behavioural traits I investigate is therefore not surprising, as males and females deal with similar challenges like human disturbance, food limitations, intraspecific interactions and threats posed by predators. Although males and females have different plumage patterns and colouration, they are approximately the same size and weight, so they require similar amounts of food. Therefore, I concluded that the similarity in the behavioural traits of male and female blackbirds that I observed in my study is related to the sahred environmental social challenges faced by the sexes. I did find an effect of age on behaviour; I found that juveniles of both sexes spent significantly less time under cover of vegetation compared to adult males and females. Juvenile birds don't have fixed territories and the conspecific owners of territories push these younger birds to marginal habitat, often away from the limited vegetation available for nesting activities. It is also possible that juveniles may have less experience of possible threats and hazards; hence they may forage in open areas more than adults and likely face considerable higher risks of mortality. Unfortunately, I was constrained to only being able to identify two age classes of blackbirds: first-year versus older individuals. That may have limited my ability to detect some behavioural differences that are related to the experience of older birds.

How do sex-specific traits vary in blackbirds?

The sex-specific traits that I included in my analyses were aggressiveness in males and nesting behaviour in females. I found that nesting behaviour in female blackbirds reflected females anticipating the clutch size she was about to produce. Female blackbirds built stronger and thicker nests when expecting more eggs per clutch. Several studies report similar findings, e.g., in tree swallows *(Tachycineta bicolor*; Rendell and Robertson, 1993), northern flickers (*Colaptes auratus*; Wiebe and Swift, 2001) and Eurasian magpies (*Pica pica;* Soler et al., 2001). In addition, my results showed that

variation in nest dimensions aligned with nest use - nests become stretched with use but retain their overall shape–indicating flexibility. Overall, my findings indicated evidence of elaborate nesting building and site selection behaviour in female blackbirds.

As I predicted, the aggressive behaviour displayed by male blackbirds in response to playbacks of intraspecific songs showed that blackbirds had the ability to discriminate songs from different sources: neighbour, stranger (southern hemisphere) and distant stranger (northern hemisphere). The strength of aggressiveness in territorial males was associated with the song complexity (dawn song) and song type (dawn song versus daytime song). The aggressive responses of blackbirds toward daytime songs were consistent with the dear enemy hypothesis. These results support the prediction that male blackbirds may be able to evaluate the degree of the potential threat of an intruder based on the intruder's vocal signal. It is important for territorial birds to differentiate between neighbour and stranger intrusions, i.e., to minimise costly aggressive responses to a low-risk neighbour, while showing a strong response to the greater threat of an unfamiliar conspecific (Bee and Gerhardt, 2001; Hardouin et al., 2006; McArthur et al., 1981). I also predicted that the responses of males would be more aggressive with increasingly aggressive male song playbacks. This was not supported by my results. The lack of correlation here may be due to the variation in song responses of males and a weak association between the songs males sing and the aggressive behaviours they display. For example, song characteristics, posture and rate of singing may synergistically indicate aggression, something song playback alone cannot simulate. Hence, it is also possible that the songs chosen for the playback experiments did not adequately reflect the aggressiveness of male blackbirds.

What external factors influence the variation of behavioural traits in blackbirds?

I found that variability of behavioural traits was associated with weather parameters. Behavioural traits also significantly vary over the years. Weather parameters are likely a strong proxy for food availability given the reliance of blackbirds on access to soil invertebrates such as earthworms (Grubb, 1978; Schlicht and Kempenaers, 2020). I didn't measure food abundance or availability directly, but I observed the foraging activities of blackbirds during the day; activities relating to their metabolism and energy requirements. Earthworms and fruits were the main food items consumed by blackbirds at my field site. And given weather influences soil moisture, it follows that the availability

of earthworms will vary with rainfall and temperature. Foraging behaviour of blackbird generally increased with increasing temperatures and rainfall at my field site. For example, during the three years of my study, I found more time was spent in foraging activities in the year with the lowest amount of annual rainfall and the highest yearly temperature (2019). I suggested that in drier and warmer years, individuals might need to search for longer periods of time as food is scarcer and they have to move longer distances. In 2019, birds spent more time in the open, away from vegetation (low shyness) searching for food. During the driest year, I also observed the highest aggression rate, potentially associated with greater movement and higher chances of encountering intraspecific competitors or higher competition. On a smaller timescale, increasing daily temperature was linked to increasing blackbird activity, aggression, and vigilance traits. This effect is likely due to increasing breeding activities with seasonal changes e.g., winter, spring to summer and other energetic costs such as moult in later summer/ early autumn.

How do behavioural traits associated with foraging vary between breeding and non-breeding seasons?

Unsurprisingly, I found that blackbirds were more aggressive and vigilant (Chapter 3), and more likely to take risks during the breeding season compared to the non-breeding season (Chapter 4). This type of seasonal variation in different behavioural traits can be related to photoperiodic control, non-photoperiodic control, and endogenous circannual rhythm (Kunc et al., 2005; Schmaljohann, 2018; Verhulst and Nilsson, 2008). In this study, I did not measure the endocrine levels of birds but the seasonal changes I detected in individuals, especially aggression, are likely to result from hormonal variations. In addition, during the breeding season, individuals are more likely to have to trade-off breeding and survival (Cooper (Jr.) et al., 2015; Kawecki and Stearns, 1993; Rodriguez-Prieto et al., 2009). As with all birds, blackbird breeding activities require additional energy and are associated with higher levels of risk (Møller, 2014). In particular, nesting activities result in individuals being exposed to predators and therefore, higher levels of vigilance are likely to be expressed.

How consistent are individual blackbirds across a repertoire of behavioural traits?

Behavioural repeatability is important for characterising inter-individual behavioural differences and understanding the variation of behavioural traits (Archard and Braithwaite, 2010; Bell et al., 2009). Contrary to my expectations, the behaviours that I measured had low to medium repeatability. High repeatability of some behavioural traits has been recorded in kittiwakes (*Rissa tridactyla*, foraging trips), (Harris et al., 2020), blue tits (*Cyanistes caeruleus,* movement and neophobia), (Kluen and Brommer, 2013), and great tits (*Parus major,* aggressiveness), (Araya-Ajoy and Dingemanse, 2017). However, studies have found that individuals from some taxa show high flexibility in their behaviour, for example, movements in migratory strategy in thin-billed prions sea birds (Quillfeldt et al., 2010) and shyness in field crickets (*Gryllus campestris*) (Fisher et al., 2015). Behavioural flexibility is important because the interaction between 'individual' and 'environment' allows individuals to respond quickly to rapidly changes biotic and abiotic factors (Vines et al., 2016). Relevant variable factors include food availability, the degree of hunger, weather, intraspecific interactions, human disturbance, and predator pressure. Overall, I speculated that flexibility in behaviours allows blackbirds to broadly adapt to human modifications of natural habitats in urban areas, leading to successful intra-specific temporal niche partitioning.

Do different behavioural traits correlate within individuals in a form a behavioural syndrome?

The behavioural syndrome concept refers to suites of behaviours that co-vary across the contexts or situations (Dingemanse et al., 2012, 2012; Garamszegi and Herczeg, 2012). I found that 'shyer' blackbirds had higher activity levels while in open areas. Shyer blackbirds move more rapidly in open areas to forage quickly and achieve their requirements (food) in a shorter time. Other studies have found that the level of activity in individuals is linked to feeding rate, predator risk, metabolic expenditures and population/community dynamics (Roche et al., 2016; Sih et al., 2004). Additionally, the level of activity is a trade-off between foraging and risk avoidance (Li et al., 2015; Reboreda and Fernandez, 1997). Hence in my study shyer individuals may reduce the possibility of encountering dangers and human disturbance by foraging quickly in open habitats when compared with bolder individuals. I also found risk-taking blackbirds were more vigilant (Chapter 4). Similar to my result, studies on woodchucks (*Marmota monax*) and red squirrels (*Sciurus vulgaris*) show a negative correlation between flight initiation and vigilance. It has also been observed that living in human-occupied areas may result

in behavioural modifications (Møller et al., 2015; delBarco-Trillo, 2018). Individuals might be expected to be more vigilant to decrease the threshold of flight initiation distance in urban areas. Such adaptations to human disturbance help individuals minimise energy expenditure and avoid unnecessary escapes by increasing vigilance and risk-taking behavioural traits (Lippmann; Uchida et al., 2019). Finally, I found that males who responded more aggressively toward intraspecific songs had a higher rate of nest visits (first playback, Chapter 5). It has been revealed that individual aggressiveness can be associated with increased parental provisioning and breeding success and with mate choice (Barnett et al., 2012; Ophir et al., 2005; Szász et al., 2019). In my study, I did find that higher levels of aggressiveness in males were associated with greater male parental investment.

How does variation in behaviour correlate with breeding success?

Behavioural scientists have shown links between the flexibility of behavioural traits and life-history traits of individuals within a population (Sepp et al., 2018). My study discovered association between behavioural traits and breeding investment (eggs per season), breeding stage (age of chicks and number of chicks) and breeding success. I found that risk-taking blackbirds had more eggs per season, an activity that requires more resources and hence foraging time and more risky encounters. Risk-takers might build nests in areas with high detectability by predators and higher human disturbance. Breeding in high-risk environments is likely to be associated with higher mortality and, therefore, individuals 'value' current breeding opportunities more than future opportunities. In theory, this can result in risk-takers increasing egg production (parental investment) in the current season at the cost of maintaining good body condition (somatic effort) and investing in future offspring. Intriguingly, in my study, risk-takers did have higher breeding investments than risk-averse individuals, but further research is needed.

My experiments exposing birds to novel objects allowed me to explore risk-taking behaviour by breeding birds. The responses of paired blackbirds to the novel object and predator model were strongly associated with the age and number of nestlings (Chapter 4). The strength of nest defence by pairs is expected to increase with offspring number, quality and vulnerability, parental experience, and nest accessibility and conspicuousness (Fernández and Llambías, 2013; Magrath et al., 2010; Montgomerie and

Weatherhead, 1988; Onnebrink and Curio, 1991). Pairs with a greater number of chicks (investment) should have the strongest response toward the predator and novel objects. In addition, responses should be highest for younger chicks that were more vulnerable and benefitted from protection; the harm-to-offspring hypothesis (Fernández and Llambías, 2013). My results confirmed the harm-to-offspring hypothesis, with greater responses to novel objects and predator models when chicks were at early stages of development. In my study, shyer blackbirds had higher reproductive success (Chapter 3), which contradicts the POLS hypothesis (Pace-Of-Life Syndrome). Exactly why this was the case is unknown. It is possible that shyer blackbirds were more proficient foragers or had nests that were less detectable to predators. Shyer blackbirds may spend more time in vegetation and would be less easily detected by predators.

What makes blackbirds so well adapted to urban environments?

Urbanisation of natural landscapes has been increasing exponentially around the world over the last few centuries. On the one hand, cities are potentially dangerous environments with novel anthropocentric situations (Marín-Gómez and MacGregor-Fors, 2021; Shochat et al., 2010; Slabbekoorn and Ripmeester, 2008). On the other hand, urban might have some benefits for urban animals, such as warmer temperatures, nocturnal illuminated areas, availability of anthropogenic food (Evans et al., 2010; Morelli et al., 2014). Interestingly, my findings showed evidence of successful adaptations of blackbirds to the urban environment. Tolerance of human activities was observed, and the variation of the behavioural traits of the birds at my study site wasn't strongly influenced by human disturbances. Blackbirds are one of the most abundant birds in urban areas and are particularly successful in that they can be found across several habitat types, indicating flexibility (van Heezik & Adams, 2016). Blackbirds are probably least vulnerable to residential densification and landscaping and gardening trends as their densities remain the same across different residential types and undeveloped patches. They have traits that are associated with urban-adapted species, i.e. omnivorous ground feeding, sedentary and very widespread (Croci et al. 2008). This result suggests that blackbirds successfully habituate, and even benefit from, the presence of humans and the changes humans make to the environment. For example, I found that nest success was higher in nests close to the road. Several possibilities could explain this result. Predator risk may generally be low in territories near the road because of passing humans and road activity (day and night). Road noise

might also mask chick calls from predator detection; hence roads may provide a safer nest location. Moreover, I also found that blackbirds that had their territories closer to the road responded more aggressively toward conspecific songs (first playback song, Chapter 5). Roadsides may have some benefits such warm road surfaces, low predation pressure, prolonging diurnal activity, singing post, insects as prey, and food availability (McMullen et al., 2014; Morelli et al., 2014). It is possible that blackbirds are actively competing for these more successful roadside nesting locations. In addition, if these locations are better nesting areas, then they may contain higher densities of breeding birds, hence individuals may have to engage in more conspecific interactions to protect their territories.

6.2 Future research opportunities and directions with blackbirds

1. More detailed research is needed on parameters that influence survival, breeding success, and behavioural variation of blackbirds across gradients environmental variation, e.g., predator-free (reserved areas), suburban and urban areas. Such research could explore the links between environmental parameters (habitat characteristics, food availability, predator, human modification) and foraging and breeding success and survival of blackbirds. This work would reveal possible explanations for the correlations between behavioural traits and their consequences on survival and breeding success.
2. A specific area of recommended research is the expansion of the investigation into the influence of different factors on blackbird nest characteristics such as female experience, predation pressure, nest placement, latitude, temperature, and structural properties of nests. This is a relatively unexplored aspect of blackbird nesting behaviour but directly relates to adaptability to changing environmental conditions.
3. Future studies need to consider the age of individuals to investigate how age and experience influence behavioural variation during the lifespan of individuals.
4. Further experimental studies of blackbird behaviour could measure availability, abundance and quality of food and microclimate variation across the different seasons.

5. Measuring more details of song characteristics related to the variation of the song across the breeding season can help us understand how song characteristics reflect behavioural traits of the sender of vocal signals.
6. Future studies regarding the habituation of a range of urban bird species and the impact of different urban parameters on these species can help us understand how wildlife cope in urban ecosystems.

6.3 Concluding remarks

Looking back on my research on blackbirds and my academic life, I realise that individuals, either birds or humans, have unique journeys. My own specific journey began in a small city in Iran where I was born. As I remember, my unique personality traits were consistently repeatable - explorative and risk-taking behaviour. My bold childhood exploratory behaviour began at age four, when I left home to explore the city and countryside. While my family was looking for me, I had walked far away from my home, and I thoroughly enjoyed my adventure. My love and passion for nature meant I knew what I wanted to do in the future as a zoologist. I studied Zoology as a bachelor's degree, and I did a master's degree at Ferdowsi University, Iran, in 2009. I found a unique and brilliant topic for my master thesis, selecting the topic of bird song, a topic that began a new season of my life. I was searching for recording equipment, as there was no scientific expertise in bird song research in my country. Finally, I fashioned my own recording equipment with the help of a shotgun microphone which I then set up on a heavy metal plate connected to a video camera, and finally started song recording.

During my MSc, I was in contact with Professor Donald Kroodsma and Greg Budney from Cornell University. They sent the book “The Singing Life of Birds” to me in Iran, but it never arrived. When I finished my master’s study, I started looking for a PhD position in bird research. Kroodsma and Budney helped me discover my dream of exploring nature by suggesting I contact my current supervisor Professor Dianne Brunton. I now had an excellent opportunity to undertake a PhD with her fantastic team. Moving to New Zealand led to another new season of my life - love, support, teamwork, and independence. I finally met Greg Budney in 2016 when I had the opportunity to complete the Cornell Field-based Sound Recording held in California, an important part of my PhD development. Greg presented me with the book that I didn't get in 2011. I have experienced love with my

husband, and we have built our life together in New Zealand. I found an international family, people who always support, smile and are there for each other. We have celebrated our happiness, achievements and supported each other through many difficulties.

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7 Appendices

7.1 Risk-taking (FID)

Table 7.1.1 Procedure of backward step removal of fixed factors for selecting the best GLMM model of flight initiation distance. A significance level of $p \leq 0.05$ is shown by an asterisk (*).

Explanatory variable	Estimate	SE	z	*p*
Model 1	**AIC= 1949.8**			
Intercept	-92.36	894.62	-0.10	0.92
Year	0.05	0.44	0.10	0.92
repeat.	-0.07	0.10	-0.66	0.51
Season: non-breeding	1.49	0.53	2.80	0.01*
Start distance	0.46	0.06	7.63	≤ 0.001*
Sex: juvenile	-0.85	1.01	-0.84	0.40
Sex: male	-1.12	0.82	-1.37	0.18
Model 2	**AIC = 1947.8**			
Intercept	0.52	1.29	0.41	0.68
Repeat	-0.06	0.07	-0.81	0.42
Season: non-breeding	1.51	0.48	3.18	≤ 0.001*
Start distance	0.46	0.06	7.91	≤ 0.001*
Sex: juvenile	-0.85	1.01	-0.84	0.40
Sex: male	-1.12	0.82	-1.37	0.18
Best Model	**AIC = 1946.5**			
Intercept	0.43	1.28	0.33	0.74
Season: non-breeding	1.50	0.48	3.16	≤ 0.001*
Start distance	0.45	0.06	7.90	≤ 0.001*
Sex: juvenile	-0.67	0.99	-0.68	0.50
Sex: male	-1.17	0.82	-1.42	0.16

Model4	**AIC = 1944.5**			
Intercept	-0.19	1.16	-0.17	0.86
Season: non-breeding	1.40	0.47	3.08	0.002*
Sex: male	0.44	0.05	7.79	≤ 0.001*

7.2 Neophobia (response to a novel object)

Table 7.2.1 Procedure of backward step removal of fixed factors for selecting the best GLMM model of inspection time of blackbird in presence of a novel object A significance level of p ≤ 0.05 is shown by an asterisk (*).

Explanatory variable	**Estimate**	**SE**	**z**	***p***
Model 1	**AIC = 782.1**			
Intercept	0.71	0.75	0.94	0.35
Treatment: control	1.26	0.35	3.66	≤ 0.001*
Colour: blue	-2.65	0.60	-4.41	≤ 0.001*
Colour: pink	0.78	0.69	1.14	0.26
Colour: red	0.35	0.51	0.68	0.50
Repeat: repeat 1	2.59	0.54	4.77	≤ 0.001*
Age of chicks	-0.13	0.08	-1.74	0.08
Number of people	0.00	0.04	0.12	0.90
Number of chicks	0.01	0.23	0.04	0.97
Colour*repeat	-3.07	0.78	-3.92	≤ 0.001*
Model 2	**AIC = 780.1**			
Intercept	0.73	0.45	1.61	0.11
Treatment: control	1.27	0.35	3.67	≤ 0.001*
Colour: blue	-2.65	0.60	-4.42	≤ 0.001*
Colour: pink	0.78	0.69	1.13	0.26
Colour: red	0.34	0.51	0.68	0.50
repatObjnovel1	2.59	0.54	4.77	≤ 0.001*

Age of chicks	-0.13	0.08	-1.76	0.08
Number of people	0.00	0.04	0.12	0.91
Colour*repeat	-3.07	0.78	-3.92	≤ 0.001*
Best Model	**AIC = 778.1**			
Intercept	0.74	0.45	1.64	0.11
Treatment: control	1.27	0.35	3.67	≤ 0.001*
Colour: blue	-2.67	0.59	-4.49	≤ 0.001*
Colour: pink	0.78	0.69	1.14	0.26
Colour: red	0.35	0.50	0.70	0.48
Repeat: repeat 1	2.60	0.54	4.81	≤ 0.001*
Age of chicks	-0.13	0.08	-1.76	0.08
Colour*repeat	-3.08	0.77	-3.99	≤ 0.001*

Table 7.2.2 Procedure of backward step removal of fixed factors for selecting the best GLMM model of the number of movements around the novel object. A significance level of p ≤ 0.05 is shown by an asterisk (*).

Explanatory variable	Estimate	SE	z	p
Model 1	**AIC = 87.20**			
Intercept	-1.85	0.64	-2.87	≤ 0.001*
Treatment: control	0.96	0.17	5.84	≤ 0.001*
Colour: blue	-0.20	0.26	-0.76	0.45
Colour: pink	-0.50	0.26	-1.91	0.06
Colour: red	-0.31	0.24	-1.31	0.19
repatObjnovel1	-0.07	0.25	-0.28	0.78
Age of chicks	0.20	0.05	3.77	≤ 0.001*
Number of people	-0.02	0.02	-1.11	0.27
Number of chicks	0.40	0.20	1.96	0.05*
Colour*repeat	0.48	0.39	1.22	0.22
Model 2	**AIC = 873.85**			
Intercept	-1.71	0.62	-2.77	0.01*

Treatment: control	0.91	0.13	6.94	≤ 0.001*
Colour: blue	-0.20	0.22	-0.90	0.37
Colour: pink	-0.42	0.23	-1.80	0.07
Colour: red	-0.05	0.14	-0.34	0.73
Age of chicks	0.19	0.05	3.64	≤ 0.001*
Number of people	-0.02	0.02	-1.18	0.24
Number of chicks	0.39	0.19	2.00	0.05*
Model3	**AIC = 871.10**			
Intercept	-1.64	0.58	-2.83	≤ 0.001*
Treatment: control	0.80	0.10	8.12	≤ 0.001*
Age of chicks	0.18	0.05	3.79	≤ 0.001*
Number of people	-0.02	0.02	-1.20	0.23
chicks	0.38	0.19	2.07	0.04*
Best Model	**AIC = 870.60**			
Intercept	-1.69	0.58	-2.93	≤ 0.001*
Treatment: control	0.80	0.10	8.18	≤ 0.001*
Age of chicks	0.18	0.05	3.75	≤ 0.001*
Number of chicks	0.39	0.18	2.11	0.03*

Table 7.2.3 Procedure of backward step removal of fixed factors for selecting the best GLMM model of the nest visit in presence of the novel object. A significance level of p ≤ 0.05 is shown by an asterisk (*).

Explanatory variable	Estimate	SE	z	p
Model1	**AIC = 781.90**			
Intercept	0.75	0.28	2.68	0.01*
Treatment: control	-0.13	0.14	-0.98	0.33
Colour: blue	0.19	0.27	0.69	0.49
Colour: pink	-0.05	0.27	-0.18	0.85
Colour: red	-0.40	0.23	-1.73	0.08
Repeat: repeat 1	-0.36	0.24	-1.49	0.14
Age of chicks	0.02	0.03	0.83	0.41

Number of people	-0.03	0.02	-1.90	0.06
Number of chicks	0.14	0.08	1.65	0.10
Colour*repeat	0.48	0.35	1.36	0.17
Model 2	**AIC = 780.30**			
Intercept	0.74	0.28	2.59	0.01*
Treatment: control	-0.24	0.12	-2.03	0.04*
Colour: blue	-0.07	0.21	-0.31	0.75
Colour: pink	0.06	0.26	0.23	0.82
Colour: red	-0.22	0.15	-1.40	0.16
Age of chicks	0.03	0.03	0.98	0.33
Number of people	-0.03	0.02	-2.10	0.04*
Number of chicks	0.14	0.08	1.62	0.11
Best Model	**AIC = 776.70**			
Intercept	0.67	0.28	2.35	0.02*
Treatment: control	-0.32	0.09	-3.78	≤ 0.001*
Age of chicks	0.04	0.03	1.34	0.18
Number of people	-0.03	0.02	-2.22	0.03*
Number of chicks	0.14	0.08	1.69	0.09

7.3 Antipredator behavioural trait

Table 7.3.1. Procedure of backward step removal of fixed factors for selecting the best GLMM model of the number of attacks (antipredator response). A significance level of p ≤ 0.05 is shown by an asterisk (*).

Explanatory variable	Estimate	SE	z	p
Model 1	**AIC= 2792.2**			
Intercept	-7.78	0.00	-18131.38	≤ 0.001*
Treatment	-1.60	0.00	-3724.07	≤ 0.001*
Sex	0.30	0.00	727.78	≤ 0.001*
Number of people	0.00	0.00	-0.68	0.50
Age of chicks	0.09	0.00	208.85	≤ 0.001*

Number of chicks	0.06	0.00	144.83	≤ 0.001*
Model 2	**AIC = 2784.8**			
Intercept	-8.49	1.57	-5.40	≤ 0.001*
Treatment	-1.60	0.06	-28.40	≤ 0.001*
Sex	0.42	0.79	0.53	0.22
Age of chicks	0.09	0.01	7.72	≤ 0.001*
Number of chicks	0.06	0.05	1.24	0.60
Model 3	**AIC = 2784.3**			
Intercept	-8.33	1.57	-5.32	≤ 0.001*
Treatment	-1.60	0.06	-28.43	≤ 0.001*
Sex	0.42	0.79	0.53	0.60
Age of chicks	0.09	0.01	7.79	≤ 0.001*
Best Model	**AIC= 2781.6**			
Intercept	-8.08	1.46	-5.52	≤ 0.001*
Treatment	-1.60	0.06	-28.43	≤ 0.001*
Age of chicks	0.09	0.01	7.79	≤ 0.001*

Table 7.3.2. Procedure of backward step removal of fixed factors for selecting the best GLMM model of alarm call (antipredator response). A significance level of p ≤ 0.05 is shown by an asterisk (*).

Explanatory variable	**Estimate**	**SE**	**z**	**p**
Model 1	**AIC= 636.59**			
Intercept	0.44	0.63	0.70	0.48
Treatment	-0.51	0.19	-2.66	0.01*
Sex	0.09	0.19	0.47	0.64
Number of people	-0.02	0.01	-1.78	0.07
Age of chicks	0.06	0.05	1.33	0.18
Number of chicks	-0.41	0.17	-2.51	0.01*
Best Model	**AIC= 634.81**			
Intercept	**0.49**	**0.62**	**0.78**	**0.43**
Treatment	**-0.51**	**0.19**	**-2.66**	0.01*

Number of people	**-0.02**	**0.01**	**-1.78**	0.08
Age of chicks	**0.06**	**0.05**	**1.33**	0.18
Number of chicks	**-0.42**	**0.16**	**-2.52**	0.01*

Table 7.3.3 Procedure of backward step removal of fixed factors for selecting the best GLMM model for delay to visit nest as a post stress response. A significance level of p ≤ 0.05 is shown by an asterisk (*).

Explanatory variable	**Estimate**	**SE**	**z**	p
Model 1	**AIC = 3794.70**			
Intercept	35.60	4.69	7.60	≤ 0.001*
Treatment	-1.32	1.08	-1.23	0.22
Sex	2.25	1.19	1.89	0.07
Number of people	0.01	0.07	0.20	0.84
Age of chicks	-0.55	0.30	-1.86	0.06
Number of chicks	-4.75	1.34	-3.55	≤ 0.001*
Model 2	**AIC = 3792.4**			
Intercept	35.64	4.68	7.62	≤ 0.001*
Treatment	-1.34	1.07	-1.25	0.21
Sex	2.24	1.19	1.88	0.07
Age of chicks	-0.55	0.30	-1.87	0.06
Number of chicks	-4.71	1.33	-3.55	≤ 0.001*

Table 7.3.4 Procedure of backward step removal of fixed factors for selecting the best GLMM model for nest visit as a post stress response. A significance level of p ≤ 0.05 is shown by an asterisk (*).

Explanatory variable	**Estimate**	**SE**	**z**	p
Model 1	**AIC= 1652.4**			
Intercept	-0.26	0.26	-1.00	0.32
Treatment	0.13	0.06	2.01	0.04
Sex	0.03	0.08	0.38	0.70
Number of people	-0.01	0.00	-1.84	0.07
Age of chicks	0.03	0.02	1.62	0.11

Number of chicks	0.27	0.07	3.74	≤ 0.001*
Best Model	**AIC = 1650.6**			
intercept	-0.25	0.26	-0.95	0.34
Treatment	0.13	0.06	2.01	0.04
Number of people	-0.01	0.00	-1.84	0.07
Age of chicks	0.03	0.02	1.62	0.11
Number of chicks	0.27	0.07	3.73	≤ 0.001*

7.4 Playback 1: songs of differently aggressive males

Table 7.4.1 Procedure of backward step removal of fixed factors for selecting the best GLMM model for PC1 (overall response to song of differently aggressive males). A significance level of p ≤ 0.05 is shown by an asterisk (*).

Explanatory variable	**Estimate**	**SE**	**z**	**p**
Model 1: Treatment*Nest visit +Road + Male aggressiveness score			**AIC= 1307.28**	
Intercept	-18.19	13.19	-1.38	0.19
Treatment: C_vs_Tr	120.16	9.05	13.28	≤ 0.001*
Treatment: NonAg_vs_Ag	-6.85	7.84	-0.87	0.38
Nest visit	40.34	16.24	2.48	0.02*
Road	-1.39	0.59	-2.35	0.03*
Male aggressiveness score	11.45	18.02	0.64	0.53
Treatment C_vs_Tr * Nest visit	52.86	13.09	4.04	≤ 0.001*
Treatment NonAg_vs_Ag * Nest visit	21.33	11.35	1.88	0.06
Model 2: Treatment*Male aggressiveness score+ Nest visit +Road			**AIC= 1321.01**	
Intercept	-18.70	13.30	-1.41	0.18
Treatment: C_vs_Tr	136.49	11.23	12.15	≤ 0.001*
Treatment: NonAg_vs_Ag	-11.61	9.74	-1.19	0.24
Male aggressiveness score	11.24	18.17	0.62	0.55
Nest visit	41.63	16.39	2.54	0.02*
Road	-1.26	0.60	-2.10	0.05*

Treatment C_vs_Tr * Male aggressiveness score	5.79	16.74	0.35	0.73
Treatment NonAg_vs_Ag * Male aggressiveness score	27.43	14.51	1.89	0.06

Model 3: Treatment * Road + Nest visit + Male aggressiveness score			**AIC= 1324.51**	
Intercept	-18.55	13.42	-1.38	0.19
Treatment : C_vs_Tr	140.79	7.89	17.83	≤ 0.001*
Treatment : NonAg_vs_Ag	1.40	6.85	0.20	0.84
Road	-1.17	0.60	-1.95	0.06
Nest visit	43.27	16.55	2.62	0.02*
Male aggressiveness score	10.30	18.35	0.56	0.58
Treatment C_vs_Tr * Road	-1.96	0.51	-3.86	≤ 0.001*
Treatment NonAg_vs_Ag * Road_	-0.15	0.44	-0.34	0.74

Best Model: Treatment * Male aggressiveness score+ Treatment * Nest visit_+ Treatment * Road			**AIC= 1289.39**	
Intercept	-18.55	13.34	-1.39	0.18
Treatment : C_vs_Tr	124.69	11.00	11.34	≤ 0.001*
Treatment : NonAg_vs_Ag	-17.92	9.56	-1.88	0.06
Nest visit	42.31	16.44	2.57	0.02*
Male aggressiveness score	10.77	18.23	0.59	0.56
Road	-1.23	0.60	-2.07	0.05*
Treatment C_vs_Tr * Male aggressiveness score	4.15	15.05	0.28	0.78
Treatment NonAg_vs_Ag * Male aggressiveness	24.91	13.03	1.91	0.06
Treatment C_vs_Tr * Nest visit	38.13	13.75	2.77	0.01*
TreatmentNonAg_vs_Ag * Nest visit	21.39	11.78	1.82	0.07
Treatment C_vs_Tr * Road	-1.41	0.52	-2.69	0.01*
Treatment NonAg_vs_Ag * Road	0.11	0.45	0.24	0.81