Antipredator cautiousness and colouration in the Eurasian blackbird *Turdus merula* and song thrush *Turdus philomelos*

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Abstract

Predation is an important driver of the evolution of animal colour and behaviour. More colourful animals are theorised to be under higher risk of predation due to being more conspicuous. However, empirical data suggests conspicuous colouration is often unrelated, or even negatively related, to predation risk. One explanation for this counterintuitive pattern is that conspicuously coloured individuals reduce their risk of predation by behaving cautiously (the compensation hypothesis). Studies of birds typically find the more conspicuously coloured sex (usually males) to be more cautious, supporting the compensation hypothesis. However, an alternative hypothesis is that female birds are less cautious than males because they have higher caloric requirements associated with reproduction. Obtaining calories usually comes at the expense of cautiousness, so female birds may need to be less cautious than males to meet their caloric requirements (the caloric requirements hypothesis).

The primary aim of my thesis is to test the compensation and caloric requirements hypotheses in the Eurasian blackbird *Turdus merula* and song thrush *Turdus philomelos*. I did this by measuring the bill and feather colouration of these birds using colour photography and spectrometry (respectively) and testing for a relationship between colouration intensity and cautiousness during both the breeding and non-breeding seasons. My main metrics of cautiousness were vigilance while foraging and escape behaviour when approached.

I found strong evidence for the caloric requirements hypothesis. Female blackbirds were less vigilant in the breeding than the non-breeding season, and female blackbirds with redder bill colouration were generally less cautious. My evidence for the compensation hypothesis was mixed. Song thrushes were more cautious than blackbirds, despite being less conspicuous. Female blackbirds tended to be less cautious than males, which could support either hypothesis. Blackbirds with more intense colouration were sometimes more cautious, which could support the compensation hypothesis, but this was not consistent across metrics of cautiousness. Overall, my results more strongly support the caloric requirements hypothesis than the compensation hypothesis, but individual antipredator behaviour is complex and may be influenced by both. My results also suggest the caloric requirements hypothesis is a potential mechanism for the evolution of sexual dichromatism in birds.

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Chapter 1 Introduction

1.1 Energetic trade-offs in antipredator behaviour

Foraging animals often face a trade-off between obtaining food and being vigilant to detect potential threats, such as predators (Fritz et al., 2002; Hart & Freed, 2005; Lima & Dill, 1990; McQueen et al., 2017; Post & Götmark, 2006a; Powolny et al., 2014; Reboreda & Fernandez, 1997). Increased vigilance may either reduce the time animals have available for foraging, or the efficiency of that foraging due to the increase in pauses (Fritz et al., 2002; Lima & Dill, 1990). Therefore, individuals which spend more time vigilant are likely to obtain less food, and thus have less energy to support their growth, maintenance, and reproduction (Lima & Dill, 1990; Reboreda & Fernandez, 1997). It has been demonstrated that being vigilant reduces food intake rate in mallard ducks *Anas platyrhynchos* (Fritz et al., 2002) and bite rate in elk *Cervus canadensis* and American bison *Bison bison* (Fortin et al., 2004).

There are also trade-offs between the intensity of an animal's response to the presence of a predator (real or perceived) and its likelihood of being predated. More intense (i.e., cautious) responses probably reduce predation risk, but increase energy expenditure (Lima & Dill, 1990; Martín et al., 2008; McQueen et al., 2017; Rodriguez-Prieto et al., 2009). More cautious responses include fleeing more often, fleeing longer distances, and taking more extreme action (e.g., flying rather than running, fleeing to cover rather than remaining in the open) in response to perceived threats (Lima & Dill, 1990; Martín et al., 2008; McQueen et al., 2017; Rodriguez-Prieto et al., 2009). More cautious individuals may also forage in the open for shorter lengths of time before retreating to safety or take longer to return to foraging after fleeing a perceived threat, thereby reducing their available foraging time (Ibáñez et al., 2014; McQueen et al., 2017; Silva et al., 2008). Therefore, while antipredator behaviours may reduce an animal's risk of predation, they are often costly in terms of reduced energy (food) intake and increased energy expenditure. Animals may also trade-off different elements of antipredator cautiousness against one another to conserve energy, such as individuals which flee potential predators at greater distances doing so in a less energy intensive way, such as running instead of flying (Martín et al., 2008). Given that antipredator behaviour can be costly, animals are expected to adjust their levels of cautiousness according to their surroundings, particularly their perceived risk of predation, to avoid the costs of being cautious unnecessarily (Lima & Dill, 1990).

1.2 Colouration and predation risk

It is theorised that being colourful is costly for animals (Amundsen, 2000; McQueen et al., 2017, 2019; Møller et al., 2011, Swierk et al., 2020). One of the major explanations given for this is that more colourful animals are under higher risk of predation because they are easier for predators to detect (Cain et al., 2019; Møller et al., 2011; Hart & Freed, 2005). Numerous studies demonstrate increased predation (or attacks on models) of more conspicuous individuals. This includes higher predation of more conspicuous species than less conspicuous ones (Huhta et al., 2003; Promislow et al., 1992, 1994; Smolinský et al., 2022; Vignieri et al., 2010), of males than females when they are the more conspicuous sex (Golovin et al., 2019), and of more conspicuous individuals compared to duller individuals of the same species and sex (Godin & McDonough, 2003; Stuart-Fox et al., 2003; Swierk et al., 2020). While these results make intuitive sense, they are not universal. Other studies, particularly of birds, have found no difference in predation pressure between individuals or models of varying conspicuousness (Cain et al., 2019; Post & Götmark, 2006b; Whiting, 2002). Some studies have even found that less conspicuous individuals are attacked or predated more (Götmark, 1992a, 1995; Post & Götmark, 2006a, 2006b; Promislow et al., 1992, 1994). A recent meta-analysis found that models of individuals with visually conspicuous signals were not significantly more likely to be attacked than less conspicuous models, and that these signals were as likely to decrease as increase predation risk (White et al., 2022). Furthermore, it is common in birds to find that the sex ratio is biased towards males, despite males usually being either more or similarly conspicuous to females (Diniz, 2011; Donald, 2007; Pascual et al., 2014a; Post & Götmark, 2006a) and equal sex ratios in offspring (Donald, 2007).

1.3 The compensation hypothesis

It is possible that more conspicuous individuals are not always predated more because they modify their behaviour in ways that reduce their predation risk (Cabido et al., 2009; da Silva Pinto et al., 2021; Hart & Freed, 2005; Hensley et al., 2015; Journey et al., 2013; Martín & López, 1999; McQueen et al., 2017; Swierk et al., 2020). This is the basis of the recently coined ‘compensation hypothesis’; more conspicuous individuals perceive themselves as being under higher risk of predation due to their colouration and are more cautious in an attempt to compensate for this (Pascual et al., 2014a, 2014b). Compensation may involve higher intensity escape attempts when captured by a predator (Pascual et al., 2014b), increased vigilance (Hart & Freed, 2005; McQueen et al., 2017; Pascual et al., 2014a; Pascual & Senar, 2013), or increased responsiveness to the threat of a predator (Cabido et al., 2009; Journey et al., 2013; Martín & López, 1999; McQueen et al., 2017). An experimental study of captive hermit crabs *Pagurus bernhardus* provides direct evidence for the compensation hypothesis (Briffa & Twyman, 2011). Crabs took longer to emerge from their shells after being startled when their shell colouration did not match that of their background (i.e., they were more conspicuous). There is also evidence for the compensation hypothesis from non-experimental studies, which have found that more conspicuous species (Journey et al., 2013; Møller et al., 2019; Silva et al., 2008; but see Hensley et al., 2015), sexes (Balph, 1977; Diniz, 2011; Hart & Freed, 2005; Martín & López, 1999; McQueen et al., 2017; Møller et al., 2019; Pascual et al., 2014a), and individuals (Cabido et al., 2009; Martín & López, 1999; McQueen et al., 2017; Pascual et al., 2014a, 2014b) are more cautious than less conspicuous ones. If most conspicuously coloured individuals behaviourally compensate for their conspicuousness in some way, this may increase their energy expenditure and reduce their foraging time and efficiency (see Section 1.1). The costs of compensation may contribute to the overall cost of being conspicuously coloured, alongside the costs of producing and maintaining this colouration and a potential increase in predation risk (Amundsen, 2000; Cabido et al., 2009; McQueen et al., 2017, 2019; Møller et al., 2011, Swierk et al., 2020).

1.4 The unprofitable prey hypothesis and compensation

In some cases, compensatory antipredator behaviour may be so effective that more conspicuous individuals receive less predation pressure than duller individuals (Cabido et al., 2009; Pascual et al, 2014a). If more conspicuous individuals are consistently more difficult for predators to catch (or more capable of escaping once captured) than less conspicuous individuals, predators may begin to avoid them (Post & Götmark, 2006b). In this case, their conspicuous colouration may begin to act as a warning signal to predators that they are a poor choice of prey. This is one potential mechanism for the Unprofitable Prey Hypothesis (UPH), which proposes that in some cases, conspicuous colouration may indicate to predators that an individual should not be attacked because they are ‘unprofitable’ prey (Baker & Parker, 1979). Prey may be unprofitable because they have low nutritional value, are difficult to eat or digest, or (as is particularly relevant to the compensation hypothesis) are difficult to catch (Baker & Parker, 1979). The UPH can be considered a subset of ‘broad sense aposematism’, recently defined by Hedley and Caro (2021) as any signal (including conspicuous colouration) which indicates to a predator that an individual should be avoided for any reason. This is an expansion of the classic definition of aposematism; conspicuous colouration which specifically warns a predator that an individual is toxic or otherwise inedible (Baker & Parker, 1979; Hedley & Caro, 2021).

The link between compensation and the UPH is beginning to be explored in birds (Cain et al., 2019; Pascual et al., 2014a). Birds are a particularly interesting study taxon because there are often male-biased sex ratios and female-biased predation, even in species where the males are more conspicuous (Diniz, 2011; Donald, 2007; Götmark, 1992a, 1995; Pascual et al., 2014a; Post & Götmark, 2006a, 2006b; Promislow et al., 1992, 1994). Therefore, if male birds compensate for their increased conspicuousness by being more cautious, and predators learn to target females instead, this intersection between the compensation and unprofitable prey hypotheses may provide an explanation for the female-biased predation and male-biased sex ratios. Further study of the compensation hypothesis may consequently shed light on this important aspect of bird population dynamics. However, it is important to note that there are other differences in the ecology of male and female animals which may influence their predation risk.

1.5 The caloric requirements hypothesis

Another possible explanation for the female-biased predation observed in birds relates to differing reproductive investment between males and females. Eggs are a more costly gamete to produce than sperm, and female birds often contribute more to parental care than males, even in species with biparental care (Askenmo et al., 1992; Diniz, 2011; Martin & Badyaev, 1996; Post & Götmark, 2006a; Powolny et al., 2014). Female birds are thus likely to have higher energetic requirements than males in the breeding season, meaning they may need to spend more time foraging (Diniz, 2011; Fogg et al., 2013; Post & Götmark, 2006a, 2006b). Similarly, female birds which are incubating eggs and brooding nestlings can only spend limited time away from the nest, so they may need to forage more intensely than normal during these periods (Fogg et al., 2013; Post & Götmark, 2006b). Female birds do generally have higher foraging rates than males in the breeding season, particularly during the egg-laying and incubation stage (Askenmo et al., 1992; Diniz, 2011; Fogg et al., 2013; Post & Götmark, 2006a, 2006b). Female birds have also been found to be less cautious than males in the breeding season (Diniz, 2011; Reboreda & Fernandez, 1997), possibly because they are spending more time foraging. Most studies which compared the cautiousness of male and female birds did so in sexually dichromatic species and attributed the differences they found to compensation rather than considering caloric requirement differences (Balph, 1977; Diniz, 2011; Hart & Freed, 2005; McQueen et al., 2017; Pascual et al., 2014a). However, there is some indication that female birds are more cautious than males even when the sexes do not differ in colouration (Powolny et al., 2014; Reboreda & Fernandez, 1997), which cannot be explained by the compensation hypothesis.

The idea that female birds are less cautious than males during the breeding season due to needing to forage more often or intensely to meet their higher caloric requirements was given the name ‘the foraging effort hypothesis’ by Diniz (2011). Increased foraging at the expense of cautiousness may also explain why predation risk for female birds appears to be the highest in the breeding season, particularly during nesting and incubation (Diniz, 2011; Post & Götmark, 2006a, 2006b). However, I propose that the foraging effort hypothesis may apply more broadly, to metrics of cautiousness other than vigilance while foraging, and even to differences in caloric requirements at the individual, as well as the sex level (see Section 1.7.1). Therefore, for the remainder of this thesis, I refer to the foraging effort hypothesis as ‘the caloric requirements hypothesis’. I define the caloric requirements hypothesis as a reduction in cautiousness in one animal (sex or individual) relative to another animal due to it having higher caloric requirements which limit the time and energy it can expend on being cautious.

It is important to note that male animals may also have higher caloric requirements in the breeding than the non-breeding season due to the energetic demands of production and maintenance of conspicuous colouration, courtship, territory defence, gonad development and sperm production, and involvement in parental care (Askenmo et al., 1992; Bryant, 1997; McQueen et al., 2021b; Schartz & Zimmerman, 1971; Vezina & Salvante, 2010). Males could even have higher caloric requirements than females while breeding, and therefore be less cautious and forage more. While this theory is not supported, at least in birds, by the results of most previous studies (Balph, 1977; Diniz, 2011; Hart & Freed, 2005; McQueen et al., 2017; Pascual et al., 2014a; Powolny et al., 2014), it should still be considered when seeking to test the caloric requirements hypothesis. The compensation and caloric requirements hypotheses are also not mutually exclusive, and both may be involved in shaping the evolution of intersexual and interindividual differences in cautiousness and colouration.

1.6 Why are birds sexually dichromatic?

1.6.1 What is sexual dichromatism?

In many animal species, males and females differ in traits such as size, possession of weapons, and colouration, which is known as sexual dimorphism (Amundsen, 2000). Male animals usually express these dimorphic traits, or ‘ornaments’, more strongly than females in sexually dimorphic species (Amundsen, 2000). Sexual dimorphism where male and female animals differ in colouration is known as sexual dichromatism. Sexual dichromatism is common in the natural world, especially in birds, where males are often more conspicuously coloured than females (Dale et al., 2015; Price & Birch, 1996).

1.6.2 Sexual selection

The classic theory explaining the existence of sexually dimorphic ornamentation in nature, including sexual dichromatism, is sexual selection (Amundsen, 2000; Darwin, 1871; Fargevieille et al., 2023). Sexual selection is based on the idea that because female animals invest more in each offspring than males, they should be choosier in selecting a mate (Amundsen, 2000; Johnstone et al., 1996). Females are assumed to invest more in each offspring than males because eggs are a larger and more energetically costly gamete to produce than sperm, and because they often contribute more to parental care (Askenmo et al., 1992; Dale et al., 2015; Powolny et al., 2014). Therefore, the reproductive success of females is theorised to be limited by the number of offspring they can produce and raise, while the reproductive success of males is limited only by the number of females they can mate with (Amundsen, 2000; Johnstone et al., 1996). Females should thus select the highest quality male possible to mate with, as this is predicted to increase the quality of their offspring (Johnstone et al., 1996; Kokko & Johnstone, 2002; West-Eberhard, 1978, 1983). Sexually dimorphic ornaments are thought to be costly for males to produce and maintain, so they may signal individual quality if only higher quality individuals are able to bear these costs and still express, or express to a greater extent, these traits (Amundsen, 2000; Cabido et al., 2009; McQueen et al., 2017, 2019; Møller et al., 2011, Swierk et al., 2020; West-Eberhard, 1978). Therefore, female animals may assess male quality through the presence and level of expression of sexually dimorphic ornaments (da Silva Pinto et al., 2021; Swierk et al., 2020; West-Eberhard, 1978, 1983). Female preference for more ornamented males is thought to have driven the evolution of these traits in nature and explain why males are usually the more ornamented sex (Amundsen, 2000; Dale et al., 2015; Darwin 1871). It is important to note that sexual selection may also be indirect, such as more ornamented males obtaining more matings because they are more successful in male-male competition or acquire better territories which are preferred by females (West-Eberhard, 1983). Under classic sexual selection theory, female animals should not be ornamented because they do not need to compete for mates, so ornamentation would be costly for them with no reproductive benefits (Amundsen, 2000; Darwin 1871).

1.6.3 Why are female animals ornamented?

Counter to the predictions of classic sexual selection theory, many female animals are ornamented. Prior to the 1990s, the prevailing theory was that female ornamentation was completely non-functional (Amundsen, 2000; Fargevieille et al., 2023). This was based on the idea of a ‘correlated response’, where sexual selection for ornamentation in males drove some expression in females due to shared genes between the sexes (Amundsen, 2000; Darwin, 1871). Sexual selection was assumed not to be acting on females, except for in species with ‘sex role reversals’ (Darwin, 1871). In sex role reversed species, such as the red-wattled jacana *Jacana jacana* and red-necked phalarope *Phalaropus lobatus*, males perform all or most of the parental care and females compete for choosy males (Emlen & Wrege, 2004; Schamel et al., 2004).

However, it has more recently been proposed that female animals can benefit from ornamentation in similar ways to males. Male animals may indeed prefer females which are more ornamented if this signals their quality or future investment in parental care, meaning that more ornamented females may be more likely to obtain a mate or mate with a higher quality male (Amundsen, 2000). Mutual sexual selection is predicted to be especially likely in species where both sexes contribute significantly to parental care, as both may be able to increase their reproductive success by selecting a higher quality mate, such as one who will be a better parent to their shared young (Johnstone et al., 1996; Kokko & Johnstone, 2002). Even if females remain the choosier sex, it is likely that both sexes are actively involved in mate choice in many species, which could drive the evolution of female ornamentation (Amundsen, 2000; Johnstone et al., 1996; Kokko & Johnstone, 2002; Matysioková et al., 2017). Indeed, there is evidence from birds that more ornamented females are preferred by males (Amundsen, 2000; Amundsen et al., 1997; Griggio et al., 2005; Torres & Velando, 2005), demonstrating that sexual selection can act on females in species which are not sex role reversed.

Female animals may also obtain other social benefits from ornamentation. This ties into the ideas of West-Eberhard, who proposed that sexual selection was one component of a broader theory: social selection (West-Eberhard, 1978, 1983). While sexual selection is social competition for mates, social selection is social competition for any resource which affects reproductive success, including, but not limited to, mates (West-Eberhard, 1983). Social selection theory is certainly applicable to the evolution of ornamentation in both sexes, but may be more relevant to females, explaining the evolution of female ornaments when females do not appear to be competing for mates (West-Eberhard, 1983). More ornamented females may be more likely to win in situations where there is female-female competition for resources, such as food or higher quality territories, as well as mates (Amundsen, 2000; Dale et al., 2015; Dunn et al., 2015; West-Eberhard, 1983). Social selection theory has been supported in birds, with studies finding more ornamented females tend to be more dominant (Beltrão et al., 2021; Crowhurst et al., 2012).

1.6.4 Why are female animals less ornamented than males?

If female animals often benefit from ornamentation in similar ways to males, the more pertinent question may be why many female animals are unornamented, or much less so than males of the same species (Cain et al., 2019). Darwin and Wallace both proposed explanations for this, although they did not consider the potential benefits of ornamentation for females (Amundsen, 2000). Darwin's explanation was classic sexual selection theory (Darwin, 1871). Ornaments are costly to produce and maintain, and females obtain no benefits from ornamentation due to not being under sexual selection, so they are usually unornamented or less ornamented than males (Amundsen, 2000; Darwin, 1871; Soler & Moreno, 2012). Wallace was sceptical of sexual selection, and instead suggested that females were unornamented because ornaments make animals more conspicuous to predators, so they increase predation risk and are selected against by natural selection (Amundsen, 2000; Soler & Moreno, 2012; Wallace, 1889, 1891). The explanations of Darwin and Wallace have been synthesised, and combined with social selection theory, into a single explanation for sexually dimorphic ornamentation. The basis of this theory is that conspicuous ornamentation is selected against by natural selection in both sexes, while social selection for ornamentation is usually stronger in males than females (Dunn et al., 2015; Fargevieille et al., 2023; Soler & Moreno, 2012). Therefore, in species where there is not strong social selection on females, the balance between social and natural selection should favour greater ornamentation in males than females (and therefore sexual dimorphism), particularly when predation risk is high (Dale et al., 2015; Dunn et al., 2015; Fargevieille et al., 2023; West-Eberhard, 1983).

1.6.5 Why are socially monogamous songbirds dichromatic?

Despite the logic of the combined social and natural selection theory, it does not fully explain the patterns of sexual dimorphism (particularly dichromatism) observed in birds. Sexual dichromatism is present in at least 60% of passerines (Price & Birch, 1996), including many socially monogamous species in which both sexes are territorial and contribute to parental care (Amundsen, 2000; Kokko & Johnstone, 2002; Macedo et al., 2008). In such species, there is little difference between the sexes in the number of offspring which can be raised in a season, unless extra-pair paternity is common (Johnstone et al., 1996; Macedo et al., 2008). Such a situation should favour mutual ornamentation, with both sexes involved in mate choice and intrasexual competition (Johnstone et al., 1996; Kokko & Johnstone, 2002). There is also evidence that females are often predated more, or no less, than males in socially monogamous songbirds, even when they are less conspicuously coloured (Götmark, 1992a, 1995; Post &

Götmark, 2006a, 2006b; Promislow et al., 1992, 1994). This raises the question of why female birds are often less conspicuously coloured than males in socially monogamous species, if females are just as likely to benefit from this colouration through social selection and no more likely to be predated because of it.

The ‘nest predation hypothesis’ is the theory that female birds, including socially monogamous songbirds, are often less conspicuously coloured than males because this reduces predation risk at the nest (Martin & Badyaev, 1996; Matysioková et al., 2017; Wallace, 1889, 1891), even if female birds are not predated less than males overall. It is common for only female birds to build the nest, incubate the eggs, and brood nestlings, including in species where both sexes contribute to parental care by feeding the nestlings and fledglings (Martin & Badyaev, 1996; Post & Götmark, 2006a). In this case, female birds spend more time at the nest than males, so it may be beneficial for them to be more inconspicuously coloured to reduce the likelihood of nest detection by predators (Cain et al., 2019; Diniz, 2011; Martin & Badyaev, 1996; Matysioková et al., 2017; Post & Götmark, 2006a; Wallace, 1889, 1891). Female birds themselves are very vulnerable to predation while incubating and brooding, as are their eggs and nestlings, so being camouflaged at the nest may be beneficial to females in terms of both their own and offspring survival (Cain et al., 2019; Diniz, 2011; Wallace, 1889, 1891). However, most studies which have attempted to test the nest predation hypothesis find weak or no evidence in support of it (Dunn et al., 2015; Fargevieille et al., 2023; Haskell, 1996; Matysioková et al., 2017; Soler & Moreno, 2012; but see Martin & Badyaev, 1996). There is a general finding that female birds which contribute more to parental care, relative to males, are less conspicuous (Dale et al., 2015; Dunn et al., 2015; Fargevieille et al., 2023; but see Matysioková et al., 2017), but this is not necessarily due to nest predation.

In species where female birds contribute more to parental care than males, they are likely to have higher caloric requirements during the breeding season (see Section 1.5). This may increase their risk of predation due to the trade-offs between cautiousness and foraging, and cautiousness and energy expenditure (see Section 1.1). Conspicuous colouration is also theoretically predicted to increase predation risk (see Section 1.2), and requires energy to produce and maintain (Griffith et al., 2006; Koch & Hill, 2018; Hill, 2000; Møller et al., 2000; Roulin, 2016; Weaver et al., 2018). Female birds may thus be unable to bear the energetic and predation costs of both reproduction and conspicuous colouration. Female birds may also be unable to behaviourally compensate for having conspicuous colouration while still meeting their reproductive caloric requirements. Therefore, being conspicuously coloured may be more costly for female birds than males because they are unable, or less able, to compensate for the increased predation risk associated with this colouration. In this way, either the caloric requirements hypothesis alone, or a combination of the compensation and caloric requirements hypotheses could make conspicuous colouration more costly for female birds than males and be a mechanism for the evolution of sexual dichromatism. These mechanisms are consistent with the finding that male and female birds differ more in colouration when females contribute more to parental care, and presumably have higher reproductive caloric requirements (Dale et al., 2015; Dunn et al., 2015; Fargevieille et al., 2023; but see Matysioková et al., 2017). Female socially monogamous songbirds still tend to invest more in reproduction than males, despite mutual parental care (Diniz, 2011; Martin & Badyaev, 1996; Post & Götmark, 2006a; Powolny et al., 2014). Therefore, these mechanisms are probably applicable to the evolution of dichromatism in socially monogamous songbirds, although there may be many other factors involved.

1.7 Interindividual variation in colouration

1.7.1 Individual colouration and the compensation and caloric requirements hypotheses

Animals do not only vary in colouration intensity at the species or sex level, but at the individual level within a species and sex. Similarly to species or sexes with more conspicuous colouration, more conspicuously coloured individuals are thought to be under higher risk of predation, assuming the differences in individual colouration are large enough for predators to perceive (da Silva Pinto et al., 2021; McQueen et al., 2017; Pascual et al., 2014a; Ibáñez et al., 2014). Therefore, under the compensation hypothesis, more conspicuously coloured individuals are expected to perceive themselves as being under higher risk of predation, and be more cautious than less conspicuously coloured individuals of the same species and sex (see Section 1.3). Several studies have found that more conspicuously coloured male animals are more cautious (da Silva Pinto et al., 2021; McQueen et al., 2017; Pascual et al., 2014a, 2014b; Ibáñez et al., 2014). Only Ibáñez et al. (2014) tested whether colouration intensity was related to cautiousness in female animals, finding no relationship between the two in female Spanish terrapins *Mauremys leprosa* (although more intensely coloured males were more cautious). Therefore, it appears that the relationship between individual colouration and cautiousness may differ between sexes, and more studies testing for a relationship between female colouration intensity and cautiousness are required to understand these differences.

It is also possible that more colourful individuals will have higher caloric requirements and need to spend more time foraging than less colourful ones to maintain their colouration, in line with the caloric requirements hypothesis (see Section 1.5). If this was the case, more colourful individuals would be predicted to be less cautious than more colourful ones, contrary to the predictions of the compensation hypothesis and the findings of previous studies (da Silva Pinto et al., 2021; McQueen et al., 2017; Pascual et al., 2014a, 2014b; Ibáñez et al., 2014). There is currently no evidence that the caloric requirements hypothesis applies to individual colouration. However, the number of studies testing for a relationship between individual colouration intensity and cautiousness is small, particularly for female animals.

1.7.2 Evolution of interindividual colour variation

Ornaments such as conspicuous colouration are thought to have evolved because they are favoured by social selection (see Section 1.6). Specifically, more ornamented individuals are thought to be preferred by mates or more successful in intrasexual competition because they are perceived as being higher quality by conspecifics. Ornamentation may be an honest signal of individual quality if it is costly to produce (da Silva Pinto et al., 2021; Kokko & Johnstone, 2002; Swierk et al., 2020; West-Eberhard, 1978) or reliably associated with a desirable trait such as dominance or foraging ability (Baeta et al., 2008; Griffith et al., 2006; McQueen et al., 2017; Préault et al., 2005; West-Eberhard, 1978). Conspicuous colouration is thought to be costly because it may increase predation risk, require energy to produce and maintain, increase involvement in aggressive interactions, and need to be compensated for with increased cautiousness (Cabido et al., 2009; Møller et al., 2000; McQueen et al., 2017; Swierk et al., 2020). Therefore, more conspicuously coloured individuals are expected to be those which are able to bear these costs due to being higher quality. However, evidence for a relationship between colouration intensity and individual quality is mixed (Amundsen, 2000; Koch & Hill, 2018; Møller et al., 2000; Roulin, 2016; Weaver et al., 2018) and may be related to the mechanism by which the colouration is produced. In birds, most colouration is produced by carotenoids, melanins, or feather nanostructures (Delhey et al., 2010; Delhey & Peters, 2017). I will focus on carotenoid-based and melanin-based colouration in this thesis, as these are the types of colouration present in my study species.

1.7.3 Carotenoid-based colouration

Carotenoids are a family of pigments commonly used to produce yellow, orange, or red colouration in animals, including the bill and feather colouration of many bird species (Weaver et al., 2018). Birds cannot synthesise carotenoids themselves and must obtain them from their diets to produce this colouration (Koch & Hill, 2018; Møller et al., 2000; Weaver et al., 2018). Carotenoids are also thought to be involved in a range of other physiological processes in birds, including boosting immune function and acting as antioxidants (Griffith et al., 2006; Koch & Hill, 2018; Møller et al., 2000). There is generally thought to be a trade-off between allocation of carotenoids to colouration and these other processes (Koch & Hill, 2018). Therefore, individuals with more intense colouration are thought to be those which are healthier or better quality, or at least those which have more access to carotenoids (Griffith et al., 2006; Koch & Hill, 2018; Weaver et al., 2018). It has been suggested that individuals with more intense carotenoid-based colouration are more efficient foragers, or occupy territories with more access to carotenoids, which may make them more desirable mates (Baeta et al., 2008; Griffith et al., 2006; Préault et al., 2005; Senar et al., 2003). This role of carotenoids as a signal of individual or territory quality is thought to explain why individuals with more intense carotenoid-based colouration are often more successful in intrasexual competition and at obtaining mates (Møller et al., 2000). However, the relationship between carotenoid colouration and individual health and quality appears to be complex. Studies have found highly variable relationships between carotenoid colouration intensity and various metrics of quality, such as immune function and body condition (Griffith et al., 2006; Koch & Hill, 2018; Møller et al., 2000; Weaver et al., 2018). Carotenoid-based colouration can be sexually dichromatic in birds, with males tending to express carotenoid-based signals more strongly than females (Dehley & Peters, 2017).

1.7.4 Melanin-based colouration

Melanins are the most common type of pigment found in birds and are synthesised in their bodies rather than extracted from food (Griffith et al., 2006; Negro et al., 2018). The two major types of melanin found in birds are eumelanin (which produces brown to black colouration), and pheomelanin (which produces lighter brown to yellowish colouration) (Galván & Wakamatsu, 2016; Negro et al., 2018). Similarly to carotenoids, melanins are involved in a range of physiological processes in birds, so there may be trade-offs between melanin allocation to these processes and colouration (Griffith et al., 2006). In particular, pheomelanin production may be costly because it requires cysteine, which is also used to synthesise the antioxidant glutathione (Negro et al., 2018). However, excess cysteine is toxic, so pheomelanin production may help to remove it instead of being costly (Galván et al., 2012). Melanin concentrations are also linked to a number of other traits in birds, including higher dominance and aggression, lower sensitivity to stress, and stronger immune systems (Ducrest et al., 2008; Jawor & Breitwisch, 2003; Grffith et al., 1999; Roulin, 2016; Quesada & Senar, 2007). In fact, levels of melanin-based colouration are theorised to be related to personality in animals, with darker individuals tending to be more aggressive and dominant, and less cautious and neophobic (Ducrest et al., 2008). Therefore, individuals with darker melanin-based colouration may be preferred as mates if this signals overall individual quality or is a proxy for another desirable trait (Ducrest et al., 2008; Grffith et al., 1999; Roulin, 2016). However, individuals with darker melanin-based colouration may also be less attentive mates and parents and be less preferred mates for this reason (Grffith et al., 1999; Jawor & Breitwisch, 2003). Interestingly, melanin-based colouration is a more common, but less extreme, driver of sexual dichromatism in birds than carotenoid-based colouration, with males usually being darker than females due to a higher quantity or proportion of eumelanin (Badyaev & Hill, 2000; Delhey, 2018; Delhey & Peters, 2017; Negro et al., 2018).

1.8 The study species

1.8.1 General information

The study species selected were the Eurasian blackbird *Turdus merula* (hereafter 'blackbird') and song thrush *Turdus philomelos* (hereafter 'song thrush'). These species are medium sized songbirds (blackbirds; ~70-150g, song thrushes; ~60-110g) (Congdon, 2010; Higgins et al., 2006). Blackbirds and song thrushes were introduced to Aotearoa New Zealand in the 1800s from England and have since become common, particularly in urban and suburban habitats (Congdon, 2010; Higgins et al., 2006). Both species forage mainly on the ground for invertebrates such as earthworms, slugs, and snails (Higgins et al., 2006; Post & Götmark, 2006a). Blackbirds tend to forage more vigorously than song thrushes, disturbing large quantities of soil and leaf litter (Higgins et al., 2006). Blackbirds and song thrushes will also consume berries and fruit, although these are a smaller part of their diet than invertebrates (Higgins et al., 2006). Blackbirds may also eat skinks and are known to steal food from song thrushes (Higgins et al., 2006).

Blackbirds are sexually dichromatic, and able to be sexed by sight (Delhey & Peters, 2008; Faivre et al., 2001; Higgins et al., 2006; Post & Götmark, 2006a). Males have black plumage, and bills which range from yellow to dark orange (Bright & Waas, 2002; Delhey et al., 2010; Faivre et al., 2001, 2003; Figure 1.1; Higgins et al., 2006; Préault et al., 2005). Female blackbirds have brown plumage and are generally described as having brown to light yellow bills (Bright & Waas, 2002; Delhey et al., 2010; Faivre et al., 2001, 2003; Figure 1.1; Higgins et al., 2006), although some females have orange bills (Higgins et al., 2006; pers. obs.). The bill colouration of blackbirds is carotenoid-based (Baeta et al., 2008; Delhey et al., 2010; Faivre et al., 2001, 2003; Negro et al., 2018), while their feather colouration is melanin-based (Delhey et al., 2010). The bill colouration of male blackbirds probably signals their quality in some way (Bright & Waas, 2002; Bright et al., 2004; Faivre et al., 2001; Préault et al., 2005). It has not been tested whether female bill colouration or feather colouration in either sex is associated with individual quality. Male blackbirds are generally considered to be more conspicuously coloured than females (Faivre et al., 2003; Ibáñez-Álamo & Soler, 2017; Post & Götmark, 2006a), although it is possible that males were not more conspicuous than females in their ancestral forest habitat (Tomiałojć & Bursell, 2006).

Figure 1.1. Photographs of the study species; male blackbird (left), female blackbird (middle), and song thrush (right). Photographs retrieved from https://nzbirdsonline.org.nz/, credit (left to right) Neil Fitzgerald, Neil Fitzgerald, Ormond Torr

Song thrushes are not sexually dichromatic and cannot be sexed by sight, although males are slightly larger than females on average in both blackbirds and song thrushes (Congdon, 2010; Higgins et al., 2006). Song thrushes are characterised by warm brown plumage on their heads, backs, and wings, and creamy-white plumage dotted with brown or black chevrons on their undersides (Figure 1.1; Higgins et al., 2006). Song thrush bills are generally grey to black, with some yellow colouration around the cutting edges of the mandibles and base of the lower mandible (Higgins et al., 2006). Song thrushes are usually less conspicuous than blackbirds when both species are foraging on the ground (Higgins et al., 2006; pers. obs.). The feather colouration of song thrushes is presumably melanin-based. The yellow colouration of song thrush bills may be carotenoid-based, while the rest of their bill colouration is probably melanin-based.

1.8.2 Breeding biology

Blackbirds of both sexes are territorial for most of the year (males March/April – December, females May/June - December) in Aotearoa (Gurr, 1954; Higgins et al., 2006), although only males sing territorial songs (Creighton, 2000a; Gurr, 1954; Higgins et al., 2006). Male and female blackbirds settle on overlapping, but distinct, territories prior to the breeding season, although unpaired individuals may move during the breeding season to form a pair (Creighton, 2000a, 2001a). While blackbirds of both sexes are territorial, males appear to be more involved in defending the nest from predators (Ibáñez-Álamo & Soler, 2017) and are somewhat more aggressive (Creighton, 2000a, 2001a; Gurr, 1954). Blackbird eggs are laid from June to February in Aotearoa, although primarily from late August to December (Higgins et al., 2006). Clutches consist of around 1-5 eggs, and up to six clutches may be laid in a single breeding season, although only 2-3 can be raised successfully (Higgins et al., 2006). Only the female blackbird builds the nest and incubates the eggs, while the sexes contribute fairly equally to feeding the nestlings and fledglings (Creighton, 2000; Halupka & Wysocki, 2004; Higgins et al., 2006; Ibáñez-Álamo & Soler, 2017; Post & Götmark, 2006a). Male blackbirds sometimes brood the nestlings, but this is primarily done by the female (Higgins et al., 2006). Male blackbirds rarely feed females on the nest (Higgins et al., 2006). Blackbird eggs hatch after around 12-15 days of incubation (Higgins et al., 2006). The nestlings fledge around 11-15 days after hatching and continue to be fed by the adults for up to a few weeks (Higgins et al., 2006). Blackbird fledglings are usually fed by both parents, but sometimes only the male will feed them while the female begins another clutch (Higgins et al., 2006). Blackbirds are socially monogamous, with limited evidence (based on a small sample size) for extrapair paternity being common (14% of chicks; Creighton, 2000a). Extra-pair paternity may mostly be the result of forced copulations, as female blackbirds have rarely been observed to seek out or willingly accept copulations from males other than their mates (Creighton, 2000a; Halupka &

Wysocki, 2004). Mate guarding by male blackbirds is common while their mate is fertile (Creighton 2001b; Halupka & Wysocki, 2004), while female blackbirds do not mate guard (Creighton, 2000b). Polygamy occurs occasionally, especially where the territory of a male blackbird overlaps with those of multiple females (Creighton, 2000a; Halupka & Wysocki, 2004).

Song thrushes are territorial from around April – January in Aotearoa, although they probably leave their territory often to forage (Higgins et al., 2006). The territory is defended by both sexes, although it is unknown whether they contribute equally to this (Higgins et al., 2006). Only male song thrushes sing territorial songs (Higgins et al., 2006). Unlike blackbirds, the sexes appear to establish a territory together as a pair (Congdon, 2010). The majority of song thrush eggs are laid from late August to December in Aotearoa, although occasionally as early as May (Congdon, 2010; Higgins et al., 2006). Around 1-6 eggs are laid in a clutch, usually 3-4 (Congdon, 2010; Higgins et al., 2006). Up to three broods may be reared in a season, and up to five clutches may be laid if some fail (Congdon, 2010; Higgins et al., 2006). The eggs hatch after around 12-15 days and fledge after another 12-15 days (Congdon, 2010; Higgins et al., 2006). These fledglings are then fed by their parents for several weeks until they become independent (Higgins et al., 2006). Usually only female song thrushes build the nest, incubate the eggs, and brood the nestlings, while both sexes feed the nestlings and fledglings (Congdon, 2010; Higgins et al., 2006). However, males sometimes assist with nest building and may feed females while they are incubating (Congdon, 2010; Higgins et al., 2006). There is little information on the level of extrapair paternity in song thrushes available, although they are considered socially monogamous (Congdon, 2010).

1.8.3 Predators and antipredator behaviour

In their native ranges, predation of adult blackbirds and song thrushes by raptors such as the Eurasian sparrowhawk *Accipiter nisus* is common (Lawrence, 1985; Post & Götmark, 2006a; Solonen, 1997). However, the only avian predator known to be present at the urban study site in Aotearoa is the small owl *Ninox novaeseelandiae*, or Ruru. Ruru are known predators of blackbirds and song thrushes, but as they are usually nocturnal or crepuscular, they are unlikely to be a threat to blackbirds and song thrushes foraging during the day (Busbridge & Stewart, 2018; Higgins, 1999). Therefore, blackbirds and song thrushes foraging during the day at the study site are probably most at risk from mammalian predators (Higgins et al., 2006), which are also a threat in their native ranges (White et al., 2014). Domestic cats *Felis catus* are a substantial predator of birds in urban areas in Aotearoa (van Heezik et al., 2010), and are probably the most common diurnal predator of blackbirds and song thrushes at the study site. Some predation of blackbirds and song thrushes by rats *Rattus* spp. and brushtail possums *Trichosurus vulpecula* is also likely, particularly at night or while on the nest (Congdon, 2010; Higgins et al., 2006). Rats, cats, and brushtail possums are all present at the study site, and rats and cats were active during the day (pers. obs.). It is important to note that blackbirds and song thrushes evolved alongside diurnal avian predators, so their diurnal antipredator behaviours may still be responsive to the perceived threat of aerial predation (Lima & Dill, 1990), even if this is unlikely at the study site.

During the breeding season, adult blackbirds and song thrushes may also respond to the presence of potential nest and fledgling predators. In their native range these include a range of birds and mammals (Götmark, 1992b; Grégoire et al., 2003; Weidinger, 2009). In urban Aotearoa, the most likely avian nest predators are the introduced Common myna *Acridotheres tristis*, Common starling *Sturnus vulgaris*, and Australian magpie *Gymnorhina tibicen*, which were all present at the study site (pers. obs.) and are known to destroy nests and predate eggs and chicks (Higgins et al., 2006; Morgan et al., 2006; Tindall et al., 2007). Probable mammalian predators of nests also present at the study site (pers. obs.) include cats, rats, brushtail possums, and house mice *Mus musculus* (Congdon, 2010; Higgins et al., 2006; Morgan et al., 2006; van Heezik et al., 2008). Mustelids are also likely predators of both young and adult song thrushes and blackbirds in Aotearoa (Higgins et al., 2006), but are uncommon in urban areas (Miller, 2020) and were not observed at the study site during data collection.

Song thrushes and blackbirds have similar antipredator behaviours. While foraging on the ground, both species raise their heads and scan to detect potential predators (Lawrence, 1985; pers. obs.). Blackbirds produce both warning and alarm calls, which may be followed by an 'alarm rattle' if the bird is surprised or a potential predator is very near (Higgins et al., 2006). Blackbirds and song thrushes produce distress calls when caught and handled (Inglis et al., 1982; pers. obs.). Song thrushes also produce a variety of warning or alarm calls, though usually quieter than those of blackbirds (Higgins et al., 2006). In response to an approaching predator, blackbirds and song thrushes will usually either run away across the ground or fly into a tree or other source of cover (Martín et al., 2008; pers. obs.; Rodriguez-Prieto et al., 2009). Freezing or crouching in an attempt to avoid detection does not appear to be a common antipredator strategy in either species (Martín et al., 2008; pers. obs.).

1.8.4 Rationale for selection

Blackbirds and song thrushes were considered ideal for testing the compensation and caloric requirements hypotheses. Blackbirds and song thrushes allow the compensation hypothesis to be tested at the species level, as they are closely related species with similar ecology which differ in conspicuousness. Blackbirds were also ideal for testing the compensation hypothesis at the sex and individual levels, as they are sexually dichromatic and there is individual variation in bill and feather colouration in both sexes. Furthermore, blackbirds possess both melanin-based and carotenoid-based colouration which differs between sexes and individuals, allowing the compensation hypothesis to be tested for both types of colouration.

Female blackbirds also invest more in reproduction than males, as usually only they build the nest, lay and incubate the eggs, and brood the nestlings. Therefore, the caloric requirements of female blackbirds are likely to be higher than those of males during the breeding season, which allows the caloric requirements hypothesis to be tested. Female blackbirds have already been shown to forage more than males in the breeding season, which may be reflective of a difference in caloric requirements (Post & Götmark, 2006a). There is also some evidence that sparrowhawks predate female blackbirds more than males in Europe and that the sex ratio is male-biased (Post & Götmark, 2006a). Female-biased predation of blackbirds could be explained by females being less cautious than males, either because of their higher reproductive caloric requirements or their reduced need for compensatory cautiousness due to being less conspicuous.

Blackbirds are also a good example of a songbird species where the existence of sexual dichromatism is puzzling. Blackbirds are socially monogamous, so the numbers of potential offspring per season are probably similar between males and females (aside from extrapair paternity). There is also no evidence that female blackbirds are selecting males based on their colouration, or that females seek out extrapair copulations. Conversely, male and female blackbirds are both territorial and aggressive towards individuals of the same sex. Therefore, social and sexual competition are expected to be similar between sexes in blackbirds, which should favour the evolution of monomorphic ornamentation. It is thus unclear why male and female blackbirds differ in bill and feather colouration. It is possible that caloric requirement differences, or a combination of compensation and caloric requirement differences, are contributing to reduced female conspicuousness in blackbirds, which will be explored in this thesis.

1.9 Rationale, aims, and hypotheses

The major aim of my thesis is to explore the relationship between colouration and cautiousness across individuals, sexes, species, and seasons, with a particular focus on testing the compensation and caloric requirements hypotheses. These hypotheses are both quite new in the field of animal behaviour and have only been tested explicitly by a small number of studies. Furthermore, these two hypotheses are not mutually exclusive and may interact to influence cautiousness behaviour and the evolution of bird colouration. Despite this, until now, they have never both been tested for in the same study. Most previous studies have also focussed on a single type of colour variation (between species, between sexes, or between individuals of the same sex and species), and none have considered all three of these together. Furthermore, there are no prior studies which test for a relationship between cautiousness and colouration intensity in female birds, even though their colouration can be as variable as that of males (Delhey & Peters, 2008). There are also no previous studies which test for a relationship between cautiousness and both carotenoid-based and melanin-based colouration intensity in the same species. My thesis will contribute to addressing these knowledge gaps.

Firstly, my thesis will test the compensation hypothesis in three ways; (1) comparing the cautiousness of a more conspicuous species (blackbird) to that of a related less conspicuous species (song thrush), (2) comparing the cautiousness of male blackbirds (more conspicuous) to that of females (less conspicuous), and (3) comparing the cautiousness of more conspicuous individual birds (blackbirds of both sexes) to that of less conspicuous individuals of the same sex. Individual conspicuousness was measured as both bill and feather colouration intensity, which are carotenoid-based and melanin-based signals respectively. The compensation hypothesis predicts that the more colourful individuals will be more cautious in all of these comparisons.

Next, my thesis will test the caloric requirements hypothesis by comparing the cautiousness of all these birds between the breeding and non-breeding seasons, with a particular focus on the comparison between male and female blackbirds. The caloric requirements hypothesis predicts that female blackbirds will be less cautious in the breeding season than the non-breeding season, and less cautious than male blackbirds in the breeding season. Male blackbirds may also be less cautious in the breeding than the non-breeding season, but the seasonal difference is predicted to be smaller than that of females. As song thrushes cannot be sexed by sight, I will be unable to detect sex differences in behaviour across seasons. However, I still predict some reduction in cautiousness in the breeding season under the caloric requirements hypothesis due to some observed individuals being female or increased caloric requirements in both sexes. The caloric requirements hypothesis also predicts that more intensely coloured individual birds will be less cautious.

Unlike most previous studies, I hope that I will be able to test the predictions of the compensation and caloric requirements hypotheses separately. In particular, the predictions of the caloric requirements and compensation hypotheses differ when comparing male and female blackbirds across seasons in such a way that I should be able to conclude whether compensation for differences in conspicuousness or differences in caloric requirements (or neither, or both) is the most likely explanation for the results I obtain (Figure 1.2). I will then discuss the potential implications of my results for the evolution of colour in birds, particularly the evolution of sexual dichromatism in socially monogamous songbirds such as the blackbird.

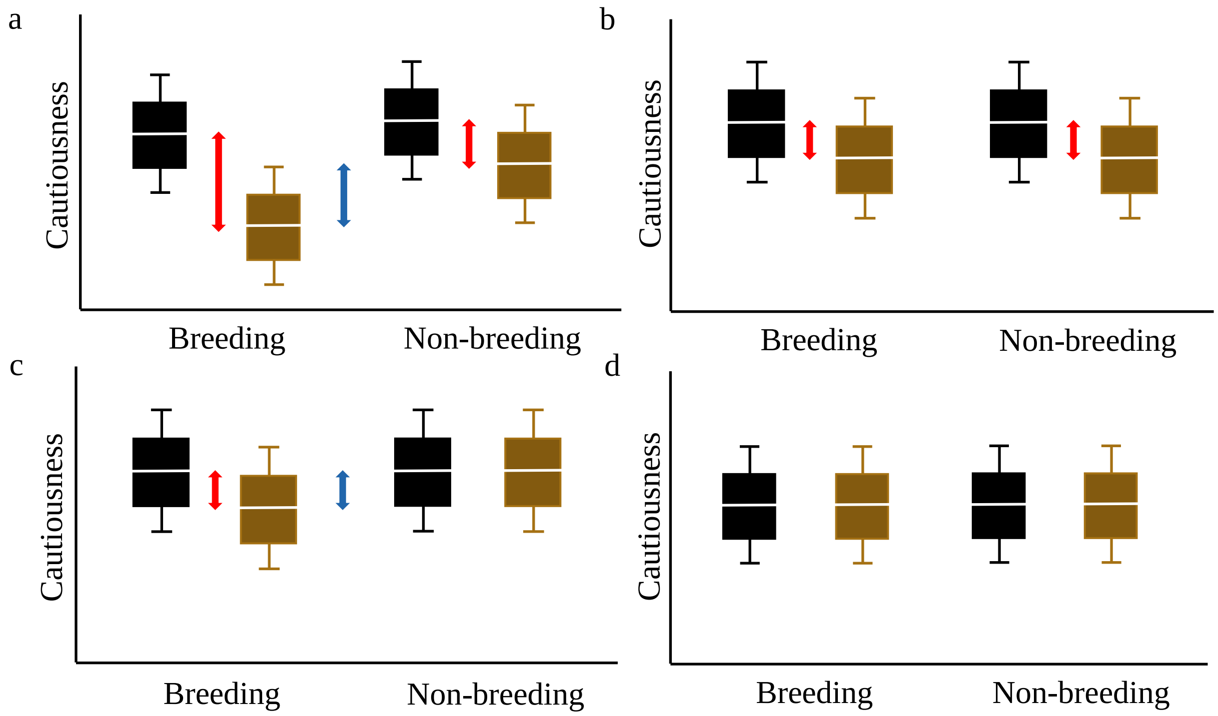

Figure 1.2. Potential patterns in cautiousness across sexes and seasons in the Eurasian blackbird *Turdus merula* under various scenarios. The brown box plots represent females, and the black box plots represent males. The red arrows represent predicted differences between females and males in the same season, and the blue arrows represent predicted differences between females across seasons. a) Males are more cautious than females, and the difference is larger during the breeding season, supporting both the caloric requirements and compensation hypotheses. b) Males are more cautious than females but there is no difference due to season, supporting the compensation but not the caloric requirements hypothesis. c) Males are more cautious than females during the breeding season, but there is no difference during the non-breeding season, which supports the caloric requirements but not the compensation hypothesis. d) There is no sex difference in either season, which does not support either the caloric requirements or the compensation hypothesis.

While not the main focus of this thesis, my study design also enabled me to test for relationships between a number of other variables. These were (1) bill and feather colouration intensity, (2) bill colouration intensity and body condition, (3) feather colouration intensity and body condition, (4) cautiousness and body condition, and (5) cautiousness and age. The results of these comparisons will be discussed briefly in the discussion and provide further insights into the many drivers of individual cautiousness and colouration intensity in birds. I also included a number of other variables in my models to control for their potential effects, which I will address briefly in the discussion.

Chapter 2 Methodology

2.1 Study site

All research was conducted in the Auckland Domain/Pukekawa, which is a large (~76 hectare; Wilcox, 2004) public park located in the urban suburb of Grafton in Auckland, Aotearoa, near the city centre. The study area consists of a mixture of grassy areas with scattered trees, paths, gardens, streams and associated riparian areas, and mature native forest (Figure 2.1; Wilcox, 2004). It has a large population of blackbirds and song thrushes and fairly low human traffic in the areas where the birds are most abundant. The majority of observations were of birds foraging in the open in grassy areas or around the gardens, although some were observed in clearings near to the mature forest.

Figure 2.1. Map of the study site. The shaded area represents the region of the Auckland Domain/Pukekawa in which the data were collected. Map retrieved from Google (n.d.).

2.2 Permissions and ethics

All capture and handling of birds was carried out under the supervision of personnel holding Department of Conservation New Zealand National Bird Banding Scheme (NZNBBS) Level 3 Banding Certifications. Animal ethics for this project was approved by the University of Auckland Animal Ethics Committee (Approval Number AEC22064). Permission to conduct the study in Pukekawa was granted by Auckland Council on 16/02/2022. A Department of Conservation (DOC) permit was not required for this study as blackbirds and song thrushes are non-native.

2.3 Bird capture, banding, and measurements

We caught a total of 41 blackbirds (14 females and 27 males) and eight song thrushes via mist netting from March - May 2022 (non-breeding season). An additional one female and three male blackbirds were caught in August 2022 (start of the breeding season) to increase numbers before the breeding season. Each bird captured was fitted with a numbered metal band and unique combination of colour bands. Birds were then weighed using a Pesola, and their minimum and maximum tarsus lengths recorded using calipers. The weight and tarsus measurements of most birds (37/49) were performed by the same, trained person to minimise variation. Birds were aged as either juveniles (in their first year of life) or adults (older than a year) based on bill and plumage colouration (Higgins et al., 2006; Khokhlova, 2009).

At least 3-5 feathers were collected from the dorsal region of each bird for later feather colour measurement. Colour photographs were also taken of the birds using a Samsung Galaxy A7 phone, with the same settings each time (Aperture F1.9, Focal Length 3.60mm, Auto White Balance, no flash). Photographs were taken on a black velvet background to reduce glare and reflections. Gray and White Balance Targets from the ColourChecker Passport Photo 2 (X-Rite

Pantone, Grand Rapids, MI, USA) were included in all photos of birds caught in the non-breeding season to allow image calibration during the colour analyses. Unfortunately, this was unavailable for the August trip, meaning bill colour could not be recorded for those birds (n = 4). They were also excluded from the body condition and feather colour analyses due to the small sample size.

2.4 Vigilance data

I collected data on the vigilance of the blackbirds and song thrushes between 9:30am and 5:00pm during two periods: non-breeding (late April – 1 August 2022), and breeding (late October 2022 – early January 2023). While August is within the breeding season of blackbirds and song thrushes in Aotearoa (Higgins et al., 2006), observations ceased before I detected any signs of breeding (e.g., mating attempts or individuals collecting nesting material).

To begin an observation, I would approach a focal bird to within a distance where its behaviour was easily observable using binoculars, and observe for at least one minute, or until it begun foraging with head lowered in my presence. Observations were at least three minutes, although many were longer (up to ten minutes). If a bird moved out of my sight before the three-minute mark, the observation was paused. If it did not return within a further three minutes the observation was considered incomplete and not included in the analyses. However, if the bird returned the observation was resumed and the pause accounted for in the analyses.

I dictated all observations into a voice recording app on my phone, noting whenever the bird raised or lowered its head, started or stopped preening, flew across the ground and landed while remaining in sight the entire time, or clearly interacted with another blackbird or song thrush (which usually involved chasing or being chased). In the breeding season observations, I also recorded each time a focal individual fed a fledgling. A ‘head up’ was defined as the bird raising its head above the horizontal line of its body with its gaze directed away from the ground, while also not obviously processing or searching for food (as in Diniz, 2011; Powolny et al., 2014). Similarly, a 'head down' was defined as any time spent foraging, including searching for food, pecking, and eating. Walking and running were not coded separately because they were usually paired with another behaviour e.g., walking with head down while searching for food, running to chase a conspecific. To avoid observing the same individual multiple times in the same day, I only observed one unbanded individual of each species and sex within an approximately 70 metre radius each day. This radius was chosen because breeding blackbirds have territories around 65-80 metres across in Aotearoa (Bull, 1958; Gurr, 1954; Williams, 2006). I also varied the time of day each location was visited. Banded individuals were observed a maximum of five times per observation period to avoid commonly resighted individuals having a disproportionate influence on the overall data. During the breeding season, blackbird fledglings could be reliably identified by their plumage and behaviour and were not observed. This was more difficult with song thrushes, but individuals which were obviously fledglings (yellow gape and down feathers, begging or being fed by a parent) were also not observed.

For each observation, I also recorded the following:

(1) Species: whether the focal bird was a blackbird or song thrush.

(2) Banded: whether the focal bird was banded, and its band combination.

(3) Sex: whether the focal bird was male or female (if a blackbird), unknown if a song thrush.

(4) Season: which season/observation period the observation was from.

(5) Date: the date of the observation. This was converted to Julian date (i.e., days since the start of the year).

(6) Time: the time the observation began, recorded as minutes since midnight.

(7) Location: the general area of Pukekawa the observation was collected in. There were five locations in total, which differed in habitat.

(8) Cover: the type of habitat the bird was in. This was scored as either open (completely exposed and not obscured from view in any direction) or cover (partially obscured by something during the observation, including long grass, dense leaf litter, trees and bushes). Birds mostly or completely obscured from sight were not observed. If a bird moved between different levels of cover this was noted and the type of cover it was in for the majority of the observation was used in the analyses.

(9) Distance: the distance between the focal bird and full cover. Full cover was defined as anything into which the bird could move and be completely obscured from sight. Distances were measured to the nearest metre using a 30-metre measuring tape, except for distances under five metres, which were estimated by eye. Distances over 30 metres were standardised to 35 metres, and distances under a metre to 0.5 metres.

(10) Weather: categorised as sunny (sun and no/few clouds visible), cloudy sun (sun and many clouds visible), overcast (no sun and many clouds visible), or clear (no sun and no/few clouds visible; this often occurred late in the day on previously sunny days).

(11) Conspecifics: the numbers of *Turdus* spp. (blackbirds and song thrushes) present in the general area, judged to be visible to the focal bird (i.e., not obviously obscured from its sight) and present during the majority of the observation period. These numbers were used to

calculate the number of *Turdus* spp. present during the observation that were the same species as the focal bird and the number that were the other species.

(12) Temperature: the air temperature at the end of the observation, measured to the nearest 0.5°C. The thermometer was placed in the shade whenever possible to avoid inflated readings.

The recordings were coded using BORIS version 7.13 (Friard & Gamba, 2016). From the raw data, I calculated the length of the focal period (‘runtime’), total counts, total durations, mean durations, and inter-event intervals for each of the ‘head up’, ‘preen’, ‘conspecific’, and ‘fly’ behaviours, and total number and inter-event interval for ‘fledgling feeds’ in the breeding season. The number of times the observation was paused, the total duration of these pauses, and the proportion of time paused were also calculated.

In total, I collected 187 focal vigilance observations (75 male blackbirds, 66 female blackbirds, and 46 song thrushes) in the non-breeding season, and 102 observations (47 male blackbirds, 39 female blackbirds, and 16 song thrushes) in the breeding season. The numbers of observations of each sex and species in each season which were terminated before three minutes were also recorded. For observations with pauses, the average interval between head raises was corrected using the following equation:

$$\frac{\big((Total\ number\ of\ head\ raises - 1)\ \times average\ head\ raise\ interval\big) - \big((total\ number\ of\ pauses - 1) \times average\ pause\ duration\big)}{Total\ number\ of\ head\ raises\ - 1}$$

Proportion of time with head down, head up rate (raises per minute), average head up duration (seconds), and average interval between head raises (seconds) were used to represent vigilance in the statistical analyses. These are common measures of vigilance (e.g., Hart & Freed, 2005; Pascual et al., 2014a, 2014b, Pascual & Senar, 2013; Powolny et al., 2014). Proportion of time with head down, rather than up, was chosen as it was considered a better indication of time spent foraging. While birds may raise their heads in response to a variety of factors, particularly conspecifics (Askenmo et al., 1992; Krebs, 1980; McQueen et al., 2017), head down proportion as defined in this thesis should truly represent the time spent foraging.

2.5 Escape behaviour data

I collected data on the escape behaviour of birds when approached by a potential threat; flight initiation distance, distance moved after fleeing, and type of movement. Flight initiation distance (hereafter 'FID') was defined as how far away a bird was from an approaching threat (in this case myself) when it first took obvious evasive action (as in Martín et al., 2008; Rodriguez-Prieto et al., 2009). Distance moved after fleeing was defined following Martín et al., (2008) and type of movement (evasive action) was either hop/run or fly. To collect these data, I would walk directly at a focal bird until it fled, maintaining eye contact and wearing neutral coloured clothing. After the bird departed, I recorded FID and distance moved using a 30-metre measuring tape. FID was recorded to the nearest 0.1 metre, while distance moved was recorded to the nearest metre due to the difficulties associated with tracking a bird as it moved away rapidly. FID was only recorded when the bird's movement was clearly caused by my approach, which was usually obvious by watching its eyeline to ensure it had seen me when it began to move. If it was unclear whether my approach caused the movement the observation was discarded and reattempted later. Distances moved were standardised to 0.5 metres if less than a metre, and 35 metres if over 30 metres. FID, distance moved, and type of movement are all used as metrics of cautiousness in this thesis (as in Martín et al., 2008).

The escape behaviour data were collected during non-breeding (mid-May – 2 August 2022) and breeding (late October 2022 - mid January 2023) periods, from 9:30am - 5pm. Non-breeding season observations ceased before any signs of breeding were detected. FID observations were either collected directly after a focal observation of the same bird, or as a standalone observation. If the observation was stand alone, I waited at least one minute or until the bird was engaged in foraging before approaching. I collected the same additional information (with the same definitions) as for a focal vigilance observation (see Section 2.4). As with the vigilance data, I did not approach the same individual more than once in a day and approached individuals a maximum of five times per season. The FID data were also dictated into the voice recorder app and coded using BORIS. In total, I collected 100 FID measurements (39 male blackbirds, 32 female blackbirds, and 29 song thrushes) in the non-breeding season and 103 (47 male blackbirds, 41 female blackbirds, and 15 song thrushes) in the breeding season.

I also recorded the number of steps I was able to take before the bird took evasive action to use in estimating starting distance (as in Rodriguez-Prieto et al., 2009). Starting distance is the distance between the focal bird and an approaching threat (usually a human observer) at the beginning of their approach, and is usually correlated with FID (Blumstein, 2003; Hensley et al., 2015; Martín et al., 2008; Rodriguez-Prieto et al., 2009). First, I estimated my step length by walking 10 steps purposefully on grassy substrate and measuring the distance walked. This was done 15 times and the lengths were averaged, giving a mean step length of 1.1028 metres. This was multiplied by the number of steps to give an estimate of the distance walked before the bird took flight, then added to the bird's FID to give an estimate of starting distance.

2.6 Body condition calculations

Scaled Mass Index (SMI; Peig & Green, 2009) was used as the metric of body condition. This metric has been shown to perform better than its alternatives when using the relationship between body mass and a measure of body size to estimate body condition in living organisms

(Peig & Green, 2010). As tarsus maximum had the stronger correlation with mass on a log-log scale (0.56 as opposed to 0.42), it was selected as the measure of length over tarsus minimum (Peig & Green, 2009). Scaled Mass Index was then calculated using the formula $\hat{M}_i = M_i[\frac{L_0}{L_i}]^{bSMA}$, where $\hat{M}_i$ is the predicted body mass of individual i based on a standardised measure of body length (in this case maximum tarsus length), M_i is the body mass of individual i, L_0 is the mean body length value for the population being studied, L_i is the body length measurement for individual i, and $bSMA$ is the scaling exponent (Peig & Green, 2009). $bSMA$ was calculated as the slope of a Standardised Major Axis (SMA) regression between log(body mass) and log(maximum tarsus length) (Peig & Green, 2009), using the smatr R package (Warton et al., 2012). Separate values of $bSMA$ were calculated for male blackbirds, female blackbirds, and song thrushes. The SMI of each individual was then subtracted from its actual body mass, giving a metric of body condition (how much the bird actually weighed relative to how much it would be expected to weigh). Individuals with higher values of this metric were assumed to be in better condition, as they were heavier for their size relative to other individuals.

2.7 Bill colouration measurements

2.7.1 Selection of colour measurement methodology

Variation among blackbirds was the focus of the bill colour analyses due to the low sample size of song thrushes (n = 8). I selected colour photography as the method of measuring bill colouration in this thesis. This method is different to that of previous studies of blackbird bill colouration, which generally used a Yolk Colour Fan (Baeta et al., 2008; Faivre et al., 2001, 2003; Préault et al., 2005) and/or a spectrometer (Bright et al., 2004; Faivre et al., 2001). While spectrometry can be more accurate, it is a more invasive method than colour photography for measuring animal colouration. Spectrometry requires either a sample to be collected from the animal or it to be handled for long enough for the spectrometer to be held next to it to collect the required readings (Stevens et al., 2009; Troscianko & Stevens, 2015). Achieving this can be difficult, particularly when the animal is moving or the area to be measured is small or uneven, such as a bird's bill (Stevens et al., 2009). In contrast, photographs are non-invasive, quick, simple, capture the entire area of interest, and have been shown to provide comparable results to spectrometry when calibrated correctly (Stevens et al., 2009; Troscianko & Stevens, 2015; Yang et al., 2021).

One disadvantage of using colour photography was that it did not allow ultraviolet (UV) colouration to be measured. There is some evidence that the bills of male blackbirds reflect in the UV spectrum, particularly the UVA (309-350nm) waveband (Bright et al., 2004). There is also some evidence that female blackbirds may prefer males with UV colouration over those without, although there is no evidence that it affects male-male interactions (Bright & Waas, 2002). However, most other studies of blackbird bill colouration do not account for the presence of significant UV reflectance (e.g., Baeta et al., 2008; Delhey et al., 2010; Faivre et al., 2003; Préault et al., 2005). To further explore whether UV reflectance was present in my study population, I photographed blackbirds of both sexes using a modified digital camera capable of taking photographs in the UV spectrum (Canon EOS RP with quartz conversion, with a Canon EF 50mm f/1.8 II lens, Kolari Vision KV-FL1 Multispectral IR UV Flash, and Kolari Vision UV bandpass filter). The photographs did not show strong reflection in the UV spectrum, so I focussed on measuring colouration in the visible spectrum. As the bill colouration of blackbirds is mainly produced by carotenoids (Baeta et al., 2008; Delhey et al., 2010; Faivre et al., 2001, 2003), which primarily reflect in the visible spectrum (Britton, 2008), the digital photography should have captured the majority of variation in bill colouration.

2.7.2 Image selection and linearisation

I selected images for analysis which included the entirety of the bird's bill and the Gray and White Balance Targets, and had minimal glare or obvious variation in lighting across them. The photos were in JPEG rather than RAW format, meaning the relationship between the radiance of light reaching the phone's camera sensor and the pixel values of the images produced was probably nonlinear (Troscianko, 2019a). As a result, the differences in pixel values within the photos are unlikely to correspond well to differences in reflectance percentage (Troscianko, 2019a). To address this, I calibrated the camera by manually determining the relationship between pixel values and reflectance (Troscianko, 2019a) using the Multispectral Image Calibration and Analysis toolbox (micaToolbox) version 2.2.2 (Troscianko & Stevens, 2015), run as a plugin in ImageJ version 1.53t (Schneider et al., 2012). Calibration included using the camera (Samsung Galaxy A7) to take photographs of the full X-Rite ColourChecker Passport in evenly lit full shade on grass in Pukekawa. The brightest possible photograph which was not overexposed was selected and loaded into the Model Linearisation Function of the micaToolbox, which is prepopulated with standard reflectances from the X-Rite ColourChecker Passport. Reflectance values are similar across ColourChecker Passports (BabelColor, 2022; Myers, 2010; Troscianko, 2019a). The areas on the photograph of the ColourChecker corresponding to each of the grey standards were selected in turn, and several linearisation models were produced. The best-fitting of these was the JT Linearisation, which had an R^2 fit of over 0.999 for red, blue, and green (which indicates the model is highly suitable; Troscianko, 2019a). This model was selected and used in further analyses.

2.7.3 Measurement of bill colour reflectance

The selected photos were converted into multispectral images using the micaToolbox and JT linearisation model (see above). The standard reflectances used were 'white' and 'N5 grey' from the developer's ColourChecker Passport, which correspond to the Gray and White

Balance Targets present in the images. Multiple standards are not required for generating multispectral images when the camera has been linearised (Troscianko (2019b), so only the Gray Balance Target was used. One male blackbird was excluded from the colour analyses as the Gray Balance Target was partially obscured in all photographs.

The mean reflectance of ten small circular regions on each mandible of each individual bird were measured from the multispectral images. Regions from the start of the nostril to the end of the bill (but not the nostril itself) were selected at random. This was done using a custom Circle Tool macro with a radius of two pixels in ImageJ. Reflectance was measured from circles rather than points to take advantage of the 'regions of interest' feature, which allowed the mean reflectances and standard deviations of each circular area to be recorded. From these, I calculated the mean reflectance, standard error of that mean, maximum reflectance, minimum reflectance, and range in reflectance for red, blue, and green for each mandible of each bird. A Principal Component Analysis (PCA) was then run on the mean, minimum, maximum, and range in red reflectance values, and the standard error of the mean red reflectance value, for both mandibles (see Figure 6.1; Table 6.1; Table 6.2). The first principal component was considered to represent a bill redness score, as higher values were associated with lower values of virtually all these variables (and thus birds with less red bills). The sign was reversed on this score so that higher values were associated with birds with redder bills.

2.8 Feather colouration measurements

Feather colouration was measured using an Ocean Optics (Ocean Optics Inc., Dunedin, FL, USA) USB 2000+ spectrometer, lit by an Ocean Optics PX-2 Pulsed Xenon Light Source and attached to a fibre-optic reflection probe. This was held at 45° from each feather and illuminated a circular area of ~1mm diameter. The colour spectra were extracted using

SpectraSuite Windows Vista version 6.2. The settings used were 5 scans to average, 10 boxcar, and 300 milliseconds integration time. An Ocean Optics flat white standard was used as the light standard and black velvet fabric was used as the dark standard. Feathers were laid out for measurement on the black velvet, overlaid 2-3 deep to better mimic how they would sit on a bird. This method increases the similarity between colour measurements taken from feathers and the measurements which would be obtained from a live bird in the field (Quesada & Senar, 2006a). Five measurements of the tips of 3-5 back feathers were made per individual, with the probe lifted between measures to reduce sampling error and better represent the overall colour of the bird (Quesada & Senar, 2006a). This resulted in spectral measurements from 300-700nm (visual spectrum).

The spectra were imported into R using the 'pavo' package (Maia et al., 2019). Negative values were corrected by adding the closest integer (17) to the lowest value in the dataset to all the reflectance measurements at all wavelengths for all birds. Neither of the more standard methods of replacing all values with zero or adding the value of the lowest negative reading for a particular bird to that bird's entire spectrum were suitable. The former would have resulted in many birds having spectra with mostly zero values and the latter would have resulted in birds with more negative spectra ending up with higher reflectance values. As the goal was to compare colour between individuals, rather than obtain absolute reflectances, this transformation was more suitable. The spectra were then smoothed with a span of 0.05 using the 'procspec' function of the pavo package. This reduced noise and smoothed the curves while maintaining their shape. The measurements taken in the breeding season were not included in the dataset, and neither was the male blackbird which lacked a corresponding bill colouration measurement. The summary function in 'pavo' was used to extract hue, chroma, and (mean) brightness for each individual, which are commonly used variables in the study of bird colouration through spectrometry (Renoult et al., 2017).

To condense these three variables, I ran a PCA. The first principal component (88.6% of the variation in the data; see Figure 6.2; Table 6.3; Table 6.4) was designated a ‘feather colour score’. While hue, chroma, and brightness are often analysed separately in colouration studies (Renoult et al., 2018), this high proportion of variation explained indicates they are highly correlated in my study birds, supporting the use of the first principal component to represent them all. This component corresponded to high brightness, high hue, and low chroma. The sign was reversed so that birds with higher feather colour scores had darker coloured feathers (lower brightness), as well as higher chroma and lower hues.

2.9 Statistical analyses

2.9.1 General

All statistical analyses were performed in R version 4.2.1 (R Core Team, 2022). First, Sex and Species were combined into a single ‘Sex’ variable with the levels Male (blackbird), Female (blackbird), and Thrush. All observations with NA values were excluded from the analyses (complete case analysis; Ibrahim et al., 2005). This was chosen over alternatives as NA values were believed to occur randomly, it did not involve modifying the data in any way, and usually only a very small number (<10) of observations were removed from each model. Linear mixed models (LMMs) with Gaussian response distributions were used in all analyses unless otherwise specified, using the lmer function of the ‘lmerTest’ package (Kuznetsova et al., 2017). The models were plotted to check for normality and homogeneity of variance in their residuals. Response variables were only transformed if these plots revealed the model assumptions were severely violated, and this could be improved by a simple transformation, as LMMs have been shown to be very robust to violations of their assumptions (Schielzeth et al., 2020). Models began with all variables of potential interest and were reduced through manual backwards stepwise removal of predictor variables based on AIC score, using the drop1()

function in R. In the event of a tie in AIC, the term with the higher p-value based on the ‘anova’ function was removed first. This process continued until all terms retained in the model had a p-value of 0.10 or lower. The only exception was when terms were non-significant in the model but retained because they were of explicit interest for the research question (e.g., sex/species, season). Correlations between numeric predictor variables were plotted using the ‘corrplot’ R package (Wei & Simko, 2021), which confirmed none had correlations greater than 0.8 (which can bias model results; Schielzeth et al., 2020).

The ‘emmeans’ (Lenth, 2022) and ‘multcomp’ (Hothorn et al., 2008) packages were used for post-hoc analyses of the model results. Model outputs were converted into tables using the ‘stargazer’ (Hlavac, 2022) and ‘sjPlot’ (Lüdecke, 2022) packages. Raincloud plots were produced using the ‘ggdist’ (Kay, 2022) and ‘ggforce’ (Pedersen, 2022) packages, and the ‘gghalves’ package (Tiedemann, 2022) from the erocoar GitHub repository. The plot_model function from the ‘effects’ package (Fox & Weisberg, 2019) was used to plot model results. Colours for the graphs were selected based on colourblindness visibility, mainly from the RColourBrewer package (Neuwirth, 2022).

2.9.2 Vigilance data

To reduce the number of models, I ran a PCA combining the four vigilance variables (proportion of time with head down, head up rate, average head up duration, and average interval between head raises). From this, the first principal component (representing 55.9% of the variation in the dataset; see Figure 6.3; Table 6.5; Table 6.6) was extracted for analysis. This principal component is used as a ‘vigilance score’ in this thesis, as higher values were associated with longer average head up durations, greater head up rates, lower proportions of time spent foraging, and smaller intervals between head ups.

This vigilance score was used as the response variable in an LMM. The variables included in the starting model are displayed in Table 2.1 under ‘Vigilance (full)’. Sex represents sex/species, runtime represents the total length of the observation, distance represents distance to cover, pause represents the number of pauses in the observation, pauseprop represents the proportion of the total observation which was paused, otherspecies represents the number of individuals of the other species of *Turdus* spp. to the focal bird present during the observation, samespecies represents the number of individuals of the same species of *Turdus* spp. to the focal bird present during the observation, banded represents whether or not the individual was banded, and temp represents temperature. Bird ID and date of observation were included as random effects.

The interaction terms between sex and cover and sex and distance to cover were included in all cautiousness models (vigilance, FID, distance moved, and type of movement) as it has been suggested that male and female blackbirds, and blackbirds and thrushes, may use cover differently when foraging (Higgins et al., 2006). As time of day can affect foraging intensity (and therefore vigilance) in birds (Askenmo et al., 1992; Avery & Krebs, 1984; McNamara et al., 1994), which is likely to be partially related to temperature (Avery & Krebs, 1984), the interaction between temperature and time was included in the vigilance model. This was made a three-way interaction with season because the relationship between temperature, time, and vigilance might vary across seasons, considering temperatures were warmer overall in the breeding season. Whether the bird was banded was included as a variable in all cautiousness models to control for the possibility that the cautiousness of birds which had been previously caught differed from that of the population (e.g., because they were less cautious/neophobic), or that their escape behaviour was affected by prior experience with myself during capture.

Table 2.1. Variables included in starting models (prior to model selection) of the factors affecting cautiousness in Eurasian blackbirds and song thrushes. See the main text for definitions of terms. Asterixes represent interactions between variables.

Vigilance (full)	Runtime, weather, pause, pauseprop, location, otherspecies, samespecies, banded, sex*season, sex*cover, sex*distance, season*time*temp
FID (full)	Weather, location, otherspecies, samespecies, banded, vigilance yes, sex*season, sex*cover, sex*distance, season*time, season*temp, time*temp, sex*startdist, season*startdist
Distance moved (full)	Weather, location, otherspecies, samespecies, banded, vigilance yes, sex*cover, sex*distance, season*time, season*temp, time*temp, sex*startdist, season*startdist, FID*type, sex*season*FID
Type of movement (full)	Weather, location, otherspecies, samespecies, banded, vigilance yes, sex*cover, sex*distance, season*time, season*temp, time*temp, sex*startdist, season*startdist, FID, sex*season*FID
Vigilance (banded)	Time, temp, pause, runtime, cover, mass, datecap, sex*age*bill redness score, sex*age*feather darkness score, sex*season*bill redness score, sex*season*feather darkness score, sex*season*body condition, bill redness score*feather darkness score*body condition
FID (banded)	Distance, mass, datecap, sex*startdist, season*startdist, sex*body condition, season*body condition, season*bill redness score, season*feather darkness score, age*startdist, age*startdist, feather darkness score*bill redness score, sex*age*bill redness score, sex*age*feather darkness score.
Distance moved (banded)	Mass, datecap, cover, FID*startdist, season*feather darkness score, season*body condition, sex*body condition, feather darkness score*bill redness score, season*bill redness score, age*sex*type,

	age*sex*FID, age*sex*startdist, age*sex*bill redness score, age*sex* feather darkness score

While the results of the vigilance score analyses are the focus of this thesis, individual models for proportion of time with head down (Table 6.7), head up rate (Table 6.8), average interval between head raises (Table 6.9), and average head up duration (Table 6.10) were run with the same predictor variables, with head up interval and duration log-transformed due to indications of heterogeneity of residuals and non-normality. These models were run to determine whether there were very different patterns across measures. While there were some differences, these were not considered large enough to merit further discussion of these models. The proportions of complete observations (with runtimes over three minutes) were also analysed across sexes and seasons using a simple linear model (LM) with sex and season as the predictor variables.

2.9.3 FID data

I also used LMMs to test for relationships between sex and season in the FID and distance moved data. The variables included in the starting FID model are presented in Table 2.1 under ‘FID (full)’. Startdist represents starting distance, and vigilance yes indicates whether or not the FID observation followed a focal vigilance observation of the same bird. The three-way interaction term between season, temperature, and time was split into its component two-way interactions prior to model selection as these variables were considered unlikely to have such a complicated relationship with FID. The variables included in the starting models for distance moved and type of movement are also displayed in Table 2.1 under ‘distance moved (full)’ and ‘type of movement (full)’. Type of movement (hop or fly) was analysed as a binomial response variable using a Generalised Linear Mixed Model (GLMM) with a logit link function.

2.9.4 Colouration and condition data

First, to determine whether any of these variables were related to one another, an LM was run with bill redness score as the response variable and all possible (up to three-way) interactions between sex/species, age (juvenile or adult), and body condition as the predictor variables. A similar LM was then run with feather darkness score as the response variable, and all possible up to three-way interactions between sex/species, age, bill redness score, and body condition as the predictor variables.

Using a subset of the dataset that included only observations of banded blackbirds for vigilance (n = 100), FID (n = 52), and distance moved (n = 51), I examined the relationships between these behaviours and colouration, age, and body condition using LMMs. The number of observations of banded song thrushes was very small (n = 7), so these were excluded from the analyses. To prevent overparameterisation, only the variables which were significant in the full models (including all the birds) were included in the starting models alongside the colour, age, and condition variables and various interactions. The variables included in the starting models are shown in Table 2.1 under 'vigilance (banded)', 'FID (banded)', and 'distance moved (banded)'. Mass represents the weight of the bird (in grams) and datecap represents the date it was captured (in Julian format). Interaction terms were chosen because they were either significant in the model of the full dataset, of particular interest to my research question, or significant in one of the variable relatedness LMs.

Chapter 3 Results

3.1 Vigilance

3.1.1 Vigilance score

Overall, I found large species differences in vigilance behaviour. Song thrushes had significantly higher vigilance scores than blackbirds of both sexes ($p < 0.001$), which was the case for all sex-season comparisons except between song thrushes in the breeding season and blackbirds of both sexes in the non-breeding season (Figure 3.1; Table 3.1; Table 6.11). Female blackbirds were significantly more vigilant in the non-breeding season than the breeding season ($p = 0.028$; Table 6.11). There was also a trend towards female blackbirds in the breeding season being more vigilant than males in the non-breeding season ($p = 0.089$; Table 6.11). All other comparisons were non-significant ($p > 0.10$; Table 6.11). Blackbirds and song thrushes in open habitat had vigilance scores which were significantly higher than those in cover ($p < 0.001$; Table 3.1). Vigilance scores also increased with each additional time the observation was paused ($p < 0.001$; Table 3.1). There was a further trend towards vigilance score increasing with an increase in temperature, although this was weak ($p = 0.065$; Table 3.1). Finally, though time of day and total observation length were significantly or weakly significantly related to vigilance score ($p = 0.028$ and $p = 0.056$, respectively), their contributions were very small (estimates ~ 0.00; Table 3.1).

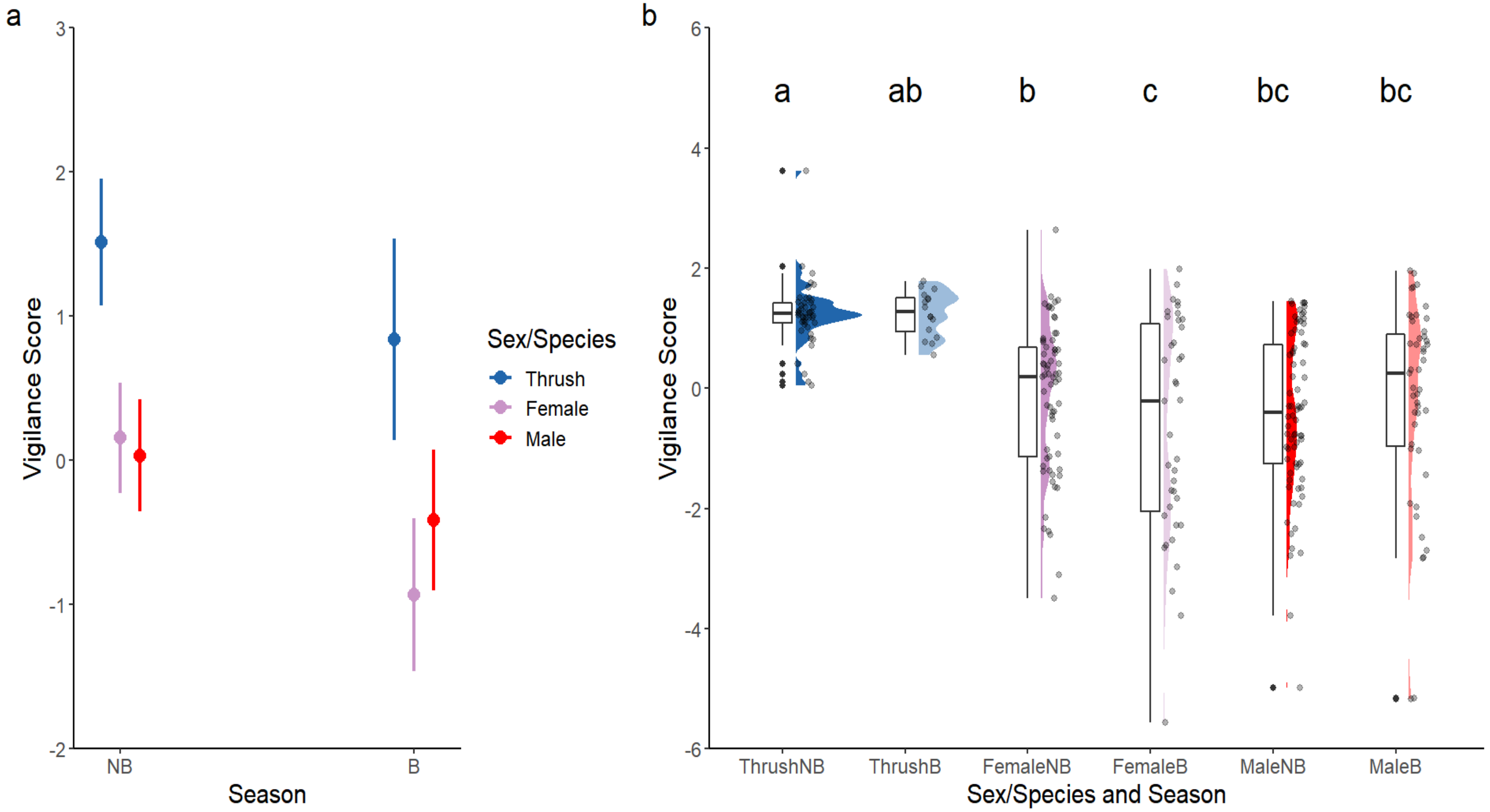

Figure 3.1. Relationships between the vigilance of foraging Eurasian blackbirds and song thrushes, their sex/species, and the season. Vigilance is a vigilance score obtained from a Principal Component Analysis (PCA), with higher values representing greater vigilance (see Section 2.9.2 for details). Sex/species was either thrush (song thrush), female (female blackbird), or male (male blackbird), while season was either B (breeding) or NB (non-breeding). a) Predicted vigilance scores based on the sex/species of the bird and the season, controlling for other variables in the model. b) Raincloud and box plots of the vigilance scores of the study birds for each combination of sex/species and season. The boxplots represent median values (middle lines), interquartile ranges (boxes), ranges (whiskers), and outliers (bold points) in the data. The letters above the graph indicate which groups had significantly different means ($p < 0.05$) based on post-hoc analyses of a linear mixed model, see Table 6.11 for values.

Table 3.1. Results of a Linear Mixed Model (LMM) testing for relationships between factors and the vigilance of foraging Eurasian blackbirds and song thrushes. Vigilance is a vigilance score (PC1) obtained from a Principal Component Analysis (PCA), with higher values representing greater vigilance. Variance attributed to the random effects of individual ID and date of observation is also presented. Factors include sex/species (male blackbird, female blackbird, or song thrush), season (breeding/B or non-breeding/NB), cover (open or cover), runtime (the length of the observation, in seconds), pause (the number of times the observation was paused), temp (air temperature, in °C), and time (the time the observation began, in minutes since midnight). Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	PC1 ~ Sex*Season + Cover + Runtime + Pause + Temp + Time + (1|ID) + (1|Date)					
Predictors	*Estimates*	*CI*	*std. Error*	*df*	*Statistic*	*p*
(Intercept)	1.28	-0.32 – 2.89	0.82	191.17	1.57	0.117
Sex	-	-	-	-	26.69	**<0.001 *****
Sex [Female - Thrush]	-1.36	-1.83 – -0.89	0.24	258.64	-5.67	**<0.001 *****
Sex [Male - Thrush]	-1.48	-1.95 – -1.01	0.24	212.91	-6.23	**<0.001 *****
Season	-	-	-	-	5.68	**0.020 ***
Season [B - NB]	-0.68	-1.55 – 0.20	0.44	164.83	-1.52	0.130
Cover	-	-	-	-	19.45	**<0.001 *****
Cover [Cover - Open]	-0.96	-1.38 – -0.53	0.22	274.90	-4.41	**<0.001 *****
Runtime	-0.00	-0.00 – 0.00	0.00	266.85	-1.92	**0.056 .**
Pause	0.46	0.27 – 0.66	0.10	274.78	4.63	**<0.001 *****
Temp	0.06	-0.00 – 0.13	0.03	83.22	1.87	**0.065 .**
Time	-0.00	-0.00 – -0.00	0.00	272.63	-2.21	**0.028 ***
Sex × Season	-	-	-	-	1.90	0.152
Sex [Female] × Season [B]	-0.41	-1.26 – 0.44	0.43	265.58	-0.95	0.343
Sex [Male] × Season [B]	0.23	-0.61 – 1.07	0.43	265.52	0.54	0.590

Random Effects	
Residual effect	1.26
ID effect	0.11
Date effect	0.18
Observations	287
Marginal R^2 / Conditional R^2	0.311 / 0.438
Terms dropped (in order): Weather, Location, Sex:Distance, Season:Time:Temp, SameSpecies, OtherSpecies, PauseProp, Sex:Cover, Season:Time, Distance, Season:Temp, Temp:Time, Banded	

3.1.2 Proportions of complete observations

The proportion of complete observations (longer than three minutes) was affected by both sex and season, with season being the more influential factor (Figure 3.2; Table 3.2; Table 6.12). The proportion of observations complete in the non-breeding season (0.698) was higher than in the breeding season (0.614) ($p = 0.011$; Table 3.2). There were also some significant differences across combinations of sex and season. The proportion of observations of female blackbirds completed in the breeding season (0.591) was significantly ($p < 0.05$) lower than that of song thrushes (0.719) and blackbirds of both sexes (males = 0.694, females = 0.688) in the non-breeding season (Table 6.12). The proportion of complete observations of male blackbirds in the breeding season (0.627) was lower than that of male blackbirds ($p = 0.028$) and song thrushes ($p = 0.046$) in the non-breeding season (Table 6.12). Finally, the proportion of complete observations of song thrushes in the breeding season (0.640) was lower than that of song thrushes in the non-breeding season ($p = 0.028$; Table 6.12). However, there were no significant differences in the percentages of complete observations across sexes/species overall (Table 6.12).

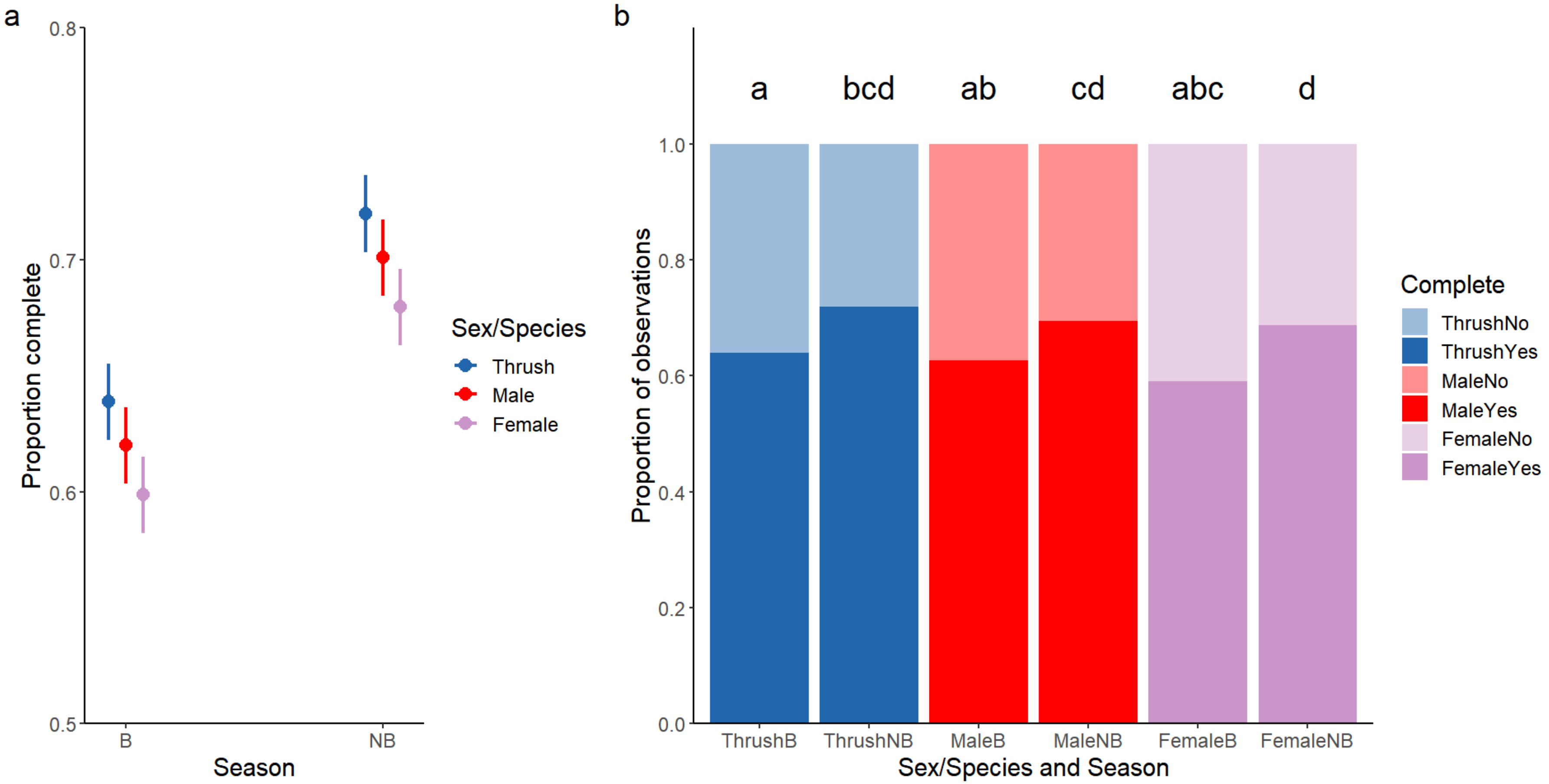

Figure 3.2. Proportions of complete (longer than three minutes) and incomplete (terminated before three minutes) observations of foraging Eurasian blackbirds and song thrushes. Sex/species was either male (male blackbird), female (female blackbird), or thrush (song thrush), while season was either B (breeding) or NB (non-breeding). a) Predicted proportions of complete observations based on sex/species and season. b) Proportions of complete and incomplete observations for each combination of sex/species and season. Incomplete observations are indicated with lighter colours, and complete observations with darker colours. The letters above the graph indicate which groups had significantly different means ($p < 0.05$) based on post-hoc analyses of a linear model, see Table 6.12 for values.

Table 3.2. Results of a linear model testing for relationships between the proportion of complete observations (longer than three minutes) of foraging Eurasian blackbirds and song thrushes, their sex/species, and the season. Sex/species was either male (male blackbird), female (female blackbird), or thrush (song thrush), while season was either B (breeding) or NB (non-breeding). Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	Proportion ~ Sex + Season					
Predictors	*Estimates*	*CI*	*std. Error*	*df*	*Statistic*	*p*
(Intercept)	0.60	0.56 – 0.63	0.01	2.00	71.31	**<0.001 *****
Sex	-	-	-	-	7.64	0.116
Sex [Female - Thrush]	-0.04	-0.08 – 0.00	0.01	2.00	-3.91	**0.060 .**
Sex [Male - Thrush]	-0.02	-0.06 – 0.03	0.01	2.00	-1.83	0.209
Season	-	-	-	-	93.16	**0.011 ***
Season [NB - B]	0.08	0.04 – 0.12	0.01	2.00	9.65	**0.011 ***
Observations	6					
R^2 / R^2 adjusted	0.982 / 0.955					

3.2 Escape behaviour

3.2.1 FID

There were no significant differences in FID between sexes/species (Table 6.13) and the sex-season interaction was non-significant (Figure 3.3; Table 3.3). However, there were significant interactions between both sex/species and starting distance ($p = 0.032$; Figure 3.3c; Table 3.3) and season and starting distance ($p < 0.001$; Figure 3.3d; Table 3.3). Birds initiated flight sooner in the non-breeding season than the breeding season ($p < 0.001$; Table 3.3). Overall, blackbirds and song thrushes began to flee when I was an average of 6.76 metres further away from them in the non-breeding season than the breeding season. In terms of the interaction with starting distance; for each one metre increase in starting distance a bird's FID would be expected to be 0.26 metres longer ($p < 0.001$) in the breeding season than the non-breeding season (Table 3.3). There appears to be little relationship between FID and starting distance in blackbirds of both sexes (Figure 3.3c), with no detectable difference in the slope of this relationship based on sex ($p = 0.621$). However, FID increased with starting distance in song thrushes, indicating they began to flee earlier when approached from a greater distance (Figure 3.3c). For each one metre increase in starting distance, a bird's FID was expected to be 0.21 metres ($p = 0.038$) and 0.25 metres ($p = 0.009$) longer if it was a song thrush than a male or female blackbird, respectively (Table 3.3). There was also a significant relationship with distance to cover; for each one metre closer to cover, a bird begun fleeing 0.06 metres earlier ($p = 0.049$; Table 3.3).

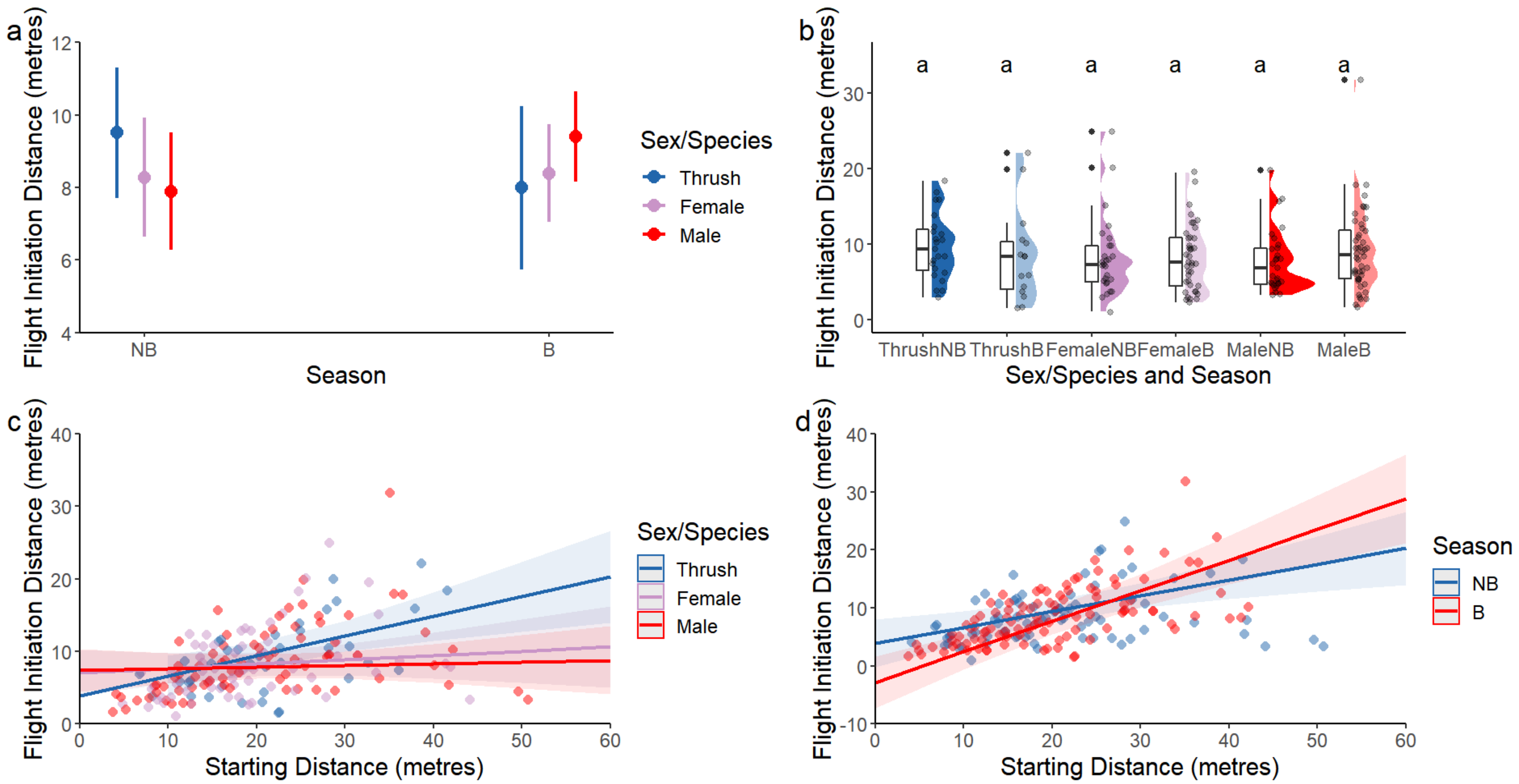

Figure 3.3. Predicted Flight Initiation Distances (FIDs) of Eurasian blackbirds and song thrushes. All figures except b) represent predicted relationships after controlling for other factors in the model, while b) represents the raw data. FID represents the distance between a blackbird or song thrush and an approaching human at which the bird first took evasive action such as running or flying away and starting distance represents the distance between the bird and the human at the beginning of their approach. Sex/species was either male (male blackbird), female (female blackbird), or thrush (song thrush), while season was either B (breeding) or NB (non-breeding). a) Predicted FIDs based on the sex/species of the bird and the season. The lines represent 95% confidence intervals around the means indicated by the points. b) Raincloud and box plots of FIDs for each combination of sex/species and season. The boxplots represent median values (middle lines), interquartile ranges (boxes), ranges (whiskers), and outliers (bold points) in the data. The letters above the graph indicate which groups had significantly different means ($p < 0.05$) based on post-hoc analyses of a linear mixed model, see Table 6.13 for values. c) Predicted FIDs based on the sex/species of the bird and the starting distance. The ribbons represent 95% confidence intervals around the mean values illustrated by the trendlines. d) Predicted FIDs based on the season and starting distance. The ribbons represent 95% confidence intervals around the mean values illustrated by the trendlines (although note that FIDs below 0 are impossible in reality).

Table 3.3. Results of a Linear Mixed Model (LMM) testing relationships between factors and the Flight Initiation Distances (FIDs, in metres) of Eurasian blackbirds and song thrushes, alongside variance attributed to the random effects of individual ID and date of observation. FID represents the distance between a blackbird or song thrush and an approaching human at which the bird first took evasive action such as hopping or flying away. Factors include sex/species (male blackbird, female blackbird, or song thrush), season (breeding/B or non-breeding/NB), StartDist (starting distance; the distance between the bird and the human at the beginning of their approach), and distance (to cover, in metres). Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	FID ~ Sex*Season + Sex*StartDist + Season*StartDist + Distance + (1|ID) + (1|Date)					
Predictors	*Estimates*	*CI*	*std. Error*	*df*	*Statistic*	*p*
(Intercept)	4.74	0.39 – 9.08	2.20	163.80	2.15	**0.033 ***
Sex	-	-	-	-	2.52	**0.083 .**
Sex [Female - Thrush]	3.13	-1.87 – 8.13	2.53	160.46	1.24	0.218
Sex [Male - Thrush]	3.50	-1.29 – 8.29	2.43	169.99	1.44	0.151
Season	-	-	-	-	11.60	**<0.001 ******
Season [B - NB]	-6.76	-10.83 – -2.70	2.06	170.83	-3.28	**0.001 ****
StartDist	0.27	0.11 – 0.44	0.08	167.66	3.26	**0.001 ****
Distance	-0.06	-0.12 – -0.00	0.03	171.00	-1.98	**0.049 ***
Sex × Season	-	-	-	-	1.54	0.218
Sex [Female] × Season [B]	1.64	-1.91 – 5.19	1.80	163.35	0.91	0.362
Sex [Male] × Season [B]	3.03	-0.44 – 6.51	1.76	167.97	1.72	**0.087 .**
Sex × StartDist	-	-	-	-	3.53	**0.032 ***
Sex [Female] × StartDist	-0.21	-0.41 – -0.01	0.10	166.82	-2.09	**0.038 ***
Sex [Male] × StartDist	-0.25	-0.44 – -0.06	0.09	168.84	-2.64	**0.009 ****

Season × StartDist	-	-	-	-	14.79	**<0.001 *****
Season [B] × StartDist	0.26	0.12 – 0.39	0.07	141.91	3.85	**<0.001 *****
Random Effects						
Residual effect	12.98					
ID effect	5.06					
Date effect	0.00					
Observations	182					
Marginal R^2 / Conditional R^2	0.345 / NA					
Terms dropped (in order): Location, Weather, Sex:Cover, Season:Time, Season:Temp, SameSpecies, Sex:Distance, Banded, VigilanceYes, Cover, OtherSpecies, Temp:Time, Temp, Time						

3.2.2 Distance moved

Distances moved after FID were influenced by a number of factors and their interactions. Post-hoc analysis of the interaction between sex/species and season indicated that there were two significant comparisons (Figure 3.4a; Table 6.14). Male blackbirds in the non-breeding season moved an average of 4.45 metres ($p = 0.033$) and 4.26 metres ($p = 0.027$) further after fleeing than females in the non-breeding and breeding seasons, respectively (Table 6.14). There were also significant interactions between sex and FID ($p = 0.024$) and sex and type ($p < 0.001$), and a weak interaction ($p = 0.081$) between FID and starting distance (Table 3.4). While there was a weak negative relationship between distance moved and FID in male blackbirds and song thrushes, this was stronger and positive in female blackbirds (Figure 3.4d). On average, for each one metre increase in FID, a bird's distance moved would be expected to be 0.56 metres longer if it was a female blackbird than if it was a song thrush ($p = 0.013$; Table 3.4). The differences in slope between FID and distance moved were not significant for song thrushes and male blackbirds ($p = 0.591$) or male and female blackbirds ($p = 0.567$) (Table 3.4). The only significant portion of the interaction between sex and type was between male and female blackbirds, with female blackbirds flying 4.99 metres less than males on average ($p = 0.043$; Figure 3.4c; Table 6.15). In terms of the interaction between FID and starting distance (Figure 3.4b), each one metre increase in starting distance increases the slope of the relationship between FID and distance moved by 0.02 (Table 3.4). At the average value of starting distance in the dataset, each one metre increase in FID is predicted to decrease distance moved by 0.59 metres ($p = 0.060$; Table 3.4).

Several other factors significantly affected distance moved. One of these was sex/species ($p < 0.001$; Table 3.4), with female blackbirds moving shorter distances on average than male blackbirds and song thrushes by 3.79 metres ($p < 0.001$) and 2.47 metres ($p = 0.075$), respectively (Table 6.14). Blackbirds and song thrushes both moved greater distances when they flew compared to when they hopped (estimate = 8.62 metres, $p < 0.001$; Table 3.4). There was no significant difference in distance moved between song thrushes and male blackbirds ($p = 0.493$, Table 6.14). There was also no evidence that season affected distance moved ($p = 0.509$; Table 3.4). There was weak evidence that birds in cover moved shorter distances than birds in the open; on average 2.24 metres less ($p = 0.090$; Table 3.4). Finally, banded birds moved 1.66 metres ($p = 0.073$) less on average than unbanded birds (Table 3.4).

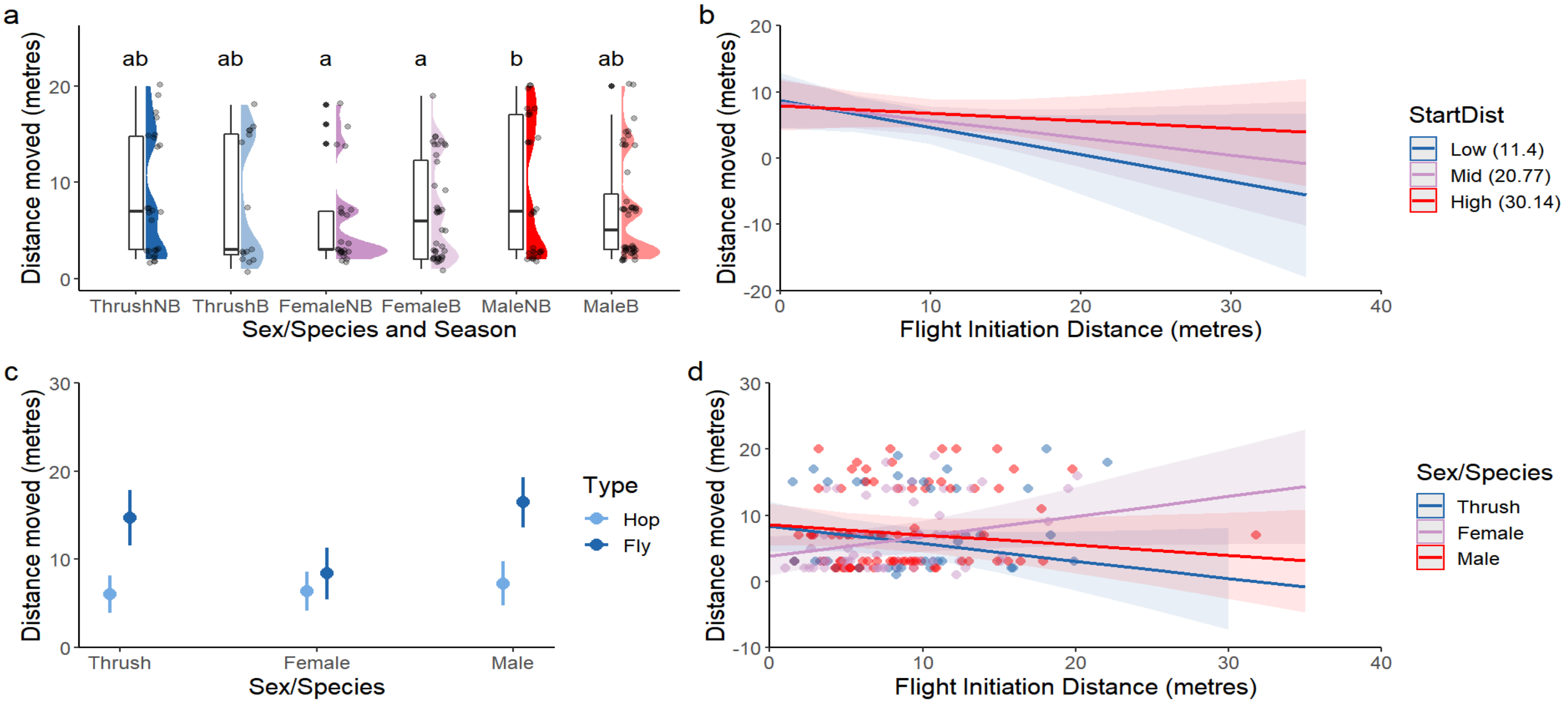

Figure 3.4. Predicted distances moved by Eurasian blackbirds and song thrushes after fleeing an approaching human. All figures except a) represent predicted relationships after controlling for other factors in the model, while a) represents the raw data. FID represents flight initiation distance (the distance between a blackbird or song thrush and the approaching human at which the bird first took evasive action such as hopping or flying away) and starting distance represents the distance between the bird and the approaching human at the start of their approach. Sex/species was either male (male blackbird), female (female blackbird), or thrush (song thrush), while season was either B (breeding) or NB (non-breeding). a) Raincloud and box plots of distances moved by the study birds for each combination of sex/species and season. The boxplots represent median values (middle lines), interquartile ranges (boxes), ranges (whiskers), and outliers (bold points) in the data. The letters above the graph indicate which groups had significantly different means ($p < 0.05$) based on post-hoc analyses of a linear mixed model, see Table 6.14 for values. b) Predicted distances moved based on the sex/species of the bird and its FID. The ribbons represent 95% confidence intervals around the mean values illustrated by the trendlines (although note that distances moved below 0 are impossible in reality). c) Predicted distances moved based on the sex/species of the bird and the type of movement chosen (hop or fly). The lines represent 95% confidence intervals around the means indicated by the points. d) Predicted distances moved based on a bird's starting distance (StartDist) and FID at the mean value of starting distance in the dataset (20.77 metres), and one standard deviation either side of this (11.4, 30.14). The ribbons represent 95% confidence intervals (although note that distances moved below 0 are impossible in reality).

Table 3.4. Results of a Linear Mixed Model (LMM) testing for relationships between factors and the distance moved after fleeing an approaching human (in metres) of Eurasian blackbirds and song thrushes, alongside variance attributed to the random effects of individual ID and date of observation. Factors include sex/species (male blackbird, female blackbird, or song thrush), season (breeding/B or non-breeding/NB), FID (Flight Initiation Distance; the distance between a blackbird or song thrush and the approaching human at which the bird first took evasive action such as hopping or flying away), type (the type of movement; hop or fly), StartDist (starting distance; the distance between the bird and the human at the start of their approach), cover (open or cover), and banded (yes or no). Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	Move ~ Sex*Season + Sex*FID + Sex*Type + FID*StartDist + Cover + Banded + (1|ID) + (1|Date)					
Predictors	*Estimates*	*CI*	*std. Error*	*df*	*Statistic*	*p*
(Intercept)	17.80	11.66 – 23.93	3.11	163.87	5.73	**<0.001 *****
Sex	-	-	-	-	8.69	**<0.001 *****
Sex [Female - Thrush]	-11.16	-17.40 – -4.93	3.16	159.99	-3.54	**<0.001 *****
Sex [Male - Thrush]	0.85	-5.10 – 6.80	3.01	160.51	0.28	0.778
Season	-	-	-	-	0.48	0.509
Season [B - NB]	-0.82	-4.05 – 2.41	1.62	63.58	-0.51	0.613
FID	-0.59	-1.20 – 0.03	0.31	159.79	-1.89	**0.060 .**
Type	-	-	-	-	55.81	**<0.001 *****
Type [Fly - Hop]	8.62	5.27 – 11.98	1.70	157.37	5.08	**<0.001 *****
StartDist	-0.04	-0.19 – 0.11	0.08	150.01	-0.53	0.599
Cover	-	-	-	-	2.90	**0.090 .**
Cover [Cover - Open]	-2.24	-4.84 – 0.36	1.31	159.83	-1.70	**0.090 .**
Banded	-	-	-	-	3.37	**0.073 .**
Banded [Yes - No]	-1.66	-3.48 – 0.16	0.90	45.62	-1.84	**0.073 .**

Sex × Season	-	-	-	-	0.30	0.738
Sex [Female] × Season [B]	1.02	-3.02 – 5.06	2.05	156.35	0.50	0.619
Sex [Male] × Season [B]	-0.31	-4.39 – 3.77	2.06	151.03	-0.15	0.880
Sex × FID	-	-	-	-	3.82	**0.024 ***
Sex [Female] × FID	0.56	0.12 – 1.01	0.22	157.56	2.51	**0.013 ***
Sex [Male] × FID	0.10	-0.28 – 0.49	0.19	163.61	0.54	0.591
Sex × Type	-	-	-	-	7.75	**<0.001 *****
Sex [Female] × Type [Fly]	-6.64	-10.95 – -2.33	2.18	163.19	-3.04	**0.003 ****
Sex [Male] × Type [Fly]	0.56	-3.87 – 4.98	2.24	159.51	0.25	0.803
FID × StartDist	0.02	-0.00 – 0.03	0.01	163.33	1.76	**0.081 .**
Random Effects						
Residual effect	20.34					
ID effect	2.23					
Date effect	0.23					
Observations	182					
Marginal R^2 / Conditional R^2	0.363 / 0.432					

Terms dropped (in order): Sex:Distance, Sex:Season:StartDist, Sex:StartDist, Sex:Cover, Location, Season:Sex:Type, Season:Sex:FID, Weather, StartDist:FID:Type, FID:Type, Time:Temp, Season:FID, SameSpecies, Distance, Season:Time, Time, VigilanceYes, OtherSpecies, Season:Type, StartDist:Type, Season:Temp, Temp, Season:StartDist

3.2.3 Type of movement

The type of movement used by blackbirds and song thrushes to flee appears to depend on an interaction between sex/species, season, and FID (Table 3.5). In particular, male blackbirds in the non-breeding season and female blackbirds in the breeding season appear to be much more likely to fly rather than hop when FID is high (Figure 3.5c). The interactions between sex/species and FID (p = 0.546) and season and FID (p = 0.986) were not significant on their own (Table 3.5). However, there was some evidence for a relationship between type of movement and the interaction between sex/species and season (p = 0.093; Table 3.5). This was largely driven by male blackbirds being unlikely to fly in the breeding season (Figure 3.5a). Post-hoc analyses revealed that the odds of a female blackbird flying in the breeding season were 6.68 greater than a male in the breeding season (p = 0.062; Table 6.16). The odds of a male blackbird flying in the non-breeding season were also 6.88 greater than those of a male in the breeding season, although this difference was non-significant (p = 0.112; Table 6.16).

There was also a weakly significant association between type of movement and the interaction between sex/species and distance to cover (p = 0.063; Figure 3.5b; Table 3.5). This was driven by the odds of a bird flying being 1.15 greater (p = 0.019) for each one metre increase in distance to cover if that bird was a male blackbird than if it was a thrush, with no significant differences between male and female blackbirds (p = 0.250) or female blackbirds and thrushes (p = 0.129) (Table 3.5). The individual factors of sex/species (p = 0.376), season (p = 0.287), FID (p = 0.984), and distance to cover (p = 0.316) were all non-significant in the model (Table 3.5; Table 6.16). Finally, there was a weakly significant relationship between location within Pukekawa and type of movement (p = 0.093; Table 3.5).

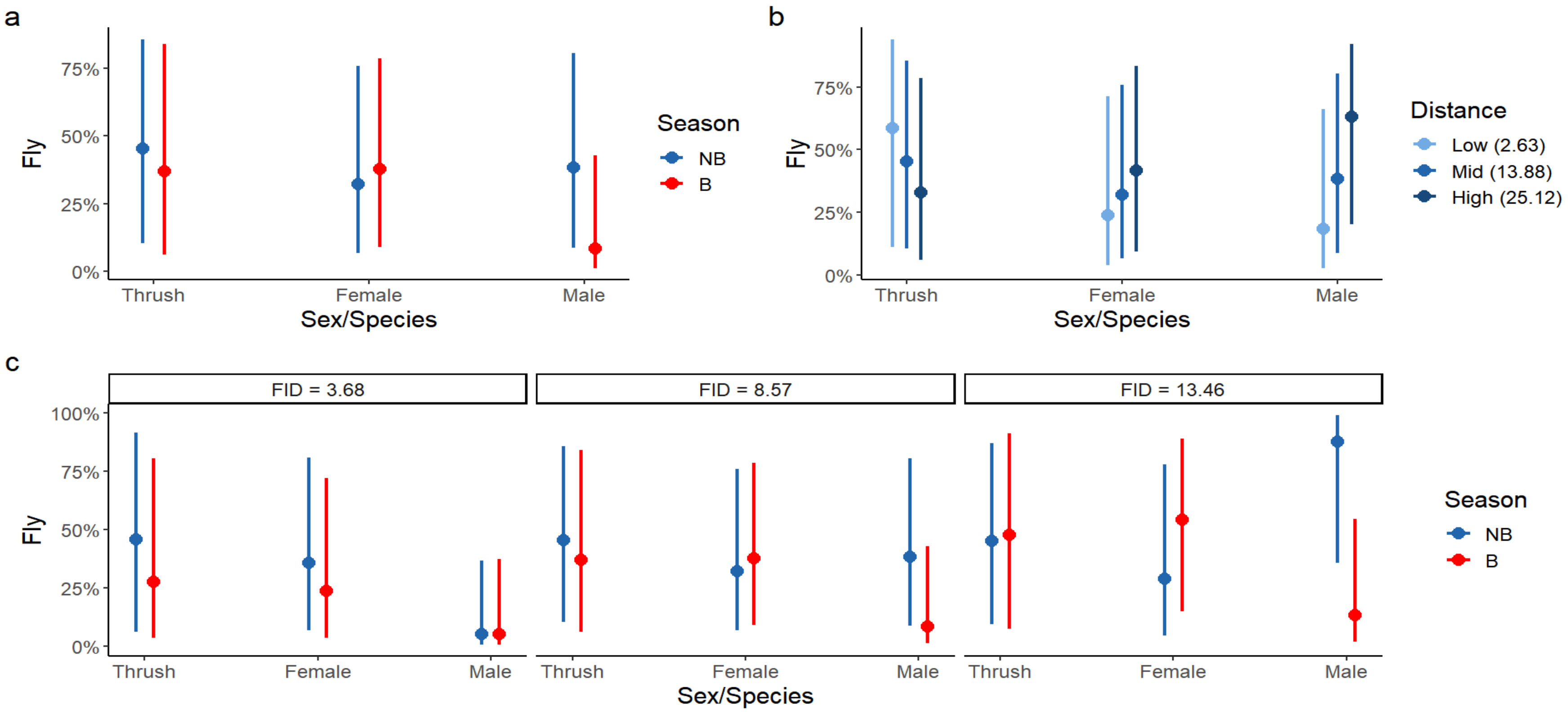

Figure 3.5. Predicted type of movement (fly or hop) chosen by Eurasian blackbirds and song thrushes fleeing an approaching human. Percentages represent the percentage of birds which chose to fly rather than hop. Figures represent predicted relationships after controlling for other factors in the model. Sex/species was either male (male blackbird), female (female blackbird), or thrush (song thrush), while season was either B (breeding) or NB (non-breeding). The lines represent 95% confidence intervals around the means indicated by the points. a) Predicted type of movement chosen based on a bird's sex/species and the season. b) Predicted type of movement chosen based on a bird's sex/species and distance to cover (in metres) at the mean distance to cover in the dataset (13.88 metres) and one standard deviation on either side of this (2.63, 25.12). c) Predicted type of movement chosen based on a bird's sex/species, its flight initiation distance (FID), and the season at the mean FID in the dataset (8.57 metres) and one standard deviation on either side of this (3.68, 13.46).

Table 3.5. Results of a Generalised Linear Mixed Model (GLMM) with a binomial distribution and logit link function testing for relationships between factors and the type of movement (fly or hop) selected by Eurasian blackbirds and song thrushes fleeing an approaching human, alongside variance attributed to the random effects of individual ID and date of observation. Factors include sex/species (male blackbird, female blackbird, or song thrush), season (breeding/B or non-breeding/NB), FID (Flight Initiation Distance; the distance between a blackbird or song thrush and the approaching human at which the bird first took evasive action such as hopping or flying away), distance (to cover, in metres), and location (Lovers A, Lovers B, Gardens, Gully, or Wintergardens). Overall statistics and p-values for terms involving categorical predictors were based on chi-squared tests performed by the Anova function of the 'car' package. Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	Type ~ Sex*Season*FID + Sex*Distance + Location + (1|ID) + (1|Date)				
Predictors	*Odds Ratios*	*CI*	*std. Error*	*Statistic*	*p*
(Intercept)	1.65	0.04 – 62.57	3.06	0.27	0.787
Sex	-	-	-	1.96	0.376
Sex [Female - Thrush]	0.23	0.01 – 9.96	0.44	-0.77	0.441
Sex [Male - Thrush]	0.00	0.00 – 0.18	0.00	-2.66	**0.008 ****
Season	-	-	-	1.14	0.287
Season [B - NB]	0.32	0.01 – 10.30	0.56	-0.65	0.518
FID	1.00	0.77 – 1.29	0.13	-0.02	0.984
Distance	0.95	0.87 – 1.05	0.05	-1.00	0.316
Location	-	-	-	7.95	**0.093 .**
Location [Gardens - Gully]	1.37	0.23 – 8.30	1.26	0.35	0.729
Location [Lovers A - Gully]	0.15	0.02 – 1.22	0.16	-1.78	**0.076 .**
Location [Lovers B - Gully]	0.60	0.10 – 3.71	0.56	-0.55	0.584
Location [Wintergardens - Gully]	0.78	0.06 – 9.51	0.99	-0.20	0.842
Sex × Season	-	-	-	4.76	**0.093 .**
Sex [Female] × Season [B]	0.94	0.01 – 66.82	2.04	-0.03	0.976

Sex [Male] × Season [B]	13.43	0.12 – 1548.63	32.54	1.07	0.284
Sex × FID	-	-	-	1.21	0.546
Sex [Female] × FID	0.97	0.71 – 1.33	0.16	-0.18	0.853
Sex [Male] × FID	1.65	1.09 – 2.52	0.36	2.34	**0.019 ***
Season × FID	-	-	-	0.00	0.986
Season [B] × FID	1.10	0.79 – 1.53	0.18	0.55	0.580
Sex × Distance	-	-	-	5.53	**0.063 .**
Sex [Female] × Distance	1.09	0.98 – 1.21	0.06	1.52	0.129
Sex [Male] × Distance	1.15	1.02 – 1.29	0.07	2.35	**0.019 ***
Sex × Season × FID	-	-	-	7.00	**0.030 ***
Sex [Female] × Season [B] × FID	1.08	0.71 – 1.64	0.23	0.36	0.716
Sex [Male] × Season [B] × FID	0.61	0.38 – 0.99	0.15	-2.00	**0.046 ***
Random Effects					
Residual effect	3.29				
ID effect	0.00				
Date effect	0.07				
Observations	182				
Marginal R^2 / Conditional R^2	0.400 / 0.413				
Terms dropped (in order): Weather, StartDist:FID, Season:Time, Temp:Time, VigilanceYes, SameSpecies, OtherSpecies, Sex:Season:StartDist, Sex:StartDist, Season:StartDist, Season:Temp, Temp, StartDist, Sex:Cover, Cover, Time, Banded					

3.3 Bill colour

3.3.1 Relationships with body condition and age

Bill redness score was unrelated to the three-way interaction between body condition, age, and sex/species (p = 0.535; Table 3.6) and the two-way interactions between age and body condition (p = 0.130; Table 3.6) and sex/species and body condition (p = 0.525; Figure 3.6b; Table 3.6). However, bill redness score was significantly related to the interaction between sex/species and age. Adult male blackbirds had the highest bill redness scores of any age and sex/species (Figure 3.6a), which were significantly higher than those of adult female blackbirds (p < 0.001; Table 6.17) and juvenile male blackbirds (p = 0.002; Table 6.17). There was high variation in the predicted values of bill redness scores for both juvenile and adult song thrushes (Figure 3.6a) due to only four of each being captured. Age (p = 0.112; Table 3.6) and body condition (p = 0.761; Table 3.6) did not have significant relationships with bill redness score, but there was a significant association with sex/species (p = 0.009; Table 3.6). Post-hoc analysis indicated that male blackbirds had significantly higher bill redness scores than females (p = 0.043), while there were no significant differences between blackbirds and song thrushes (Table 6.17).

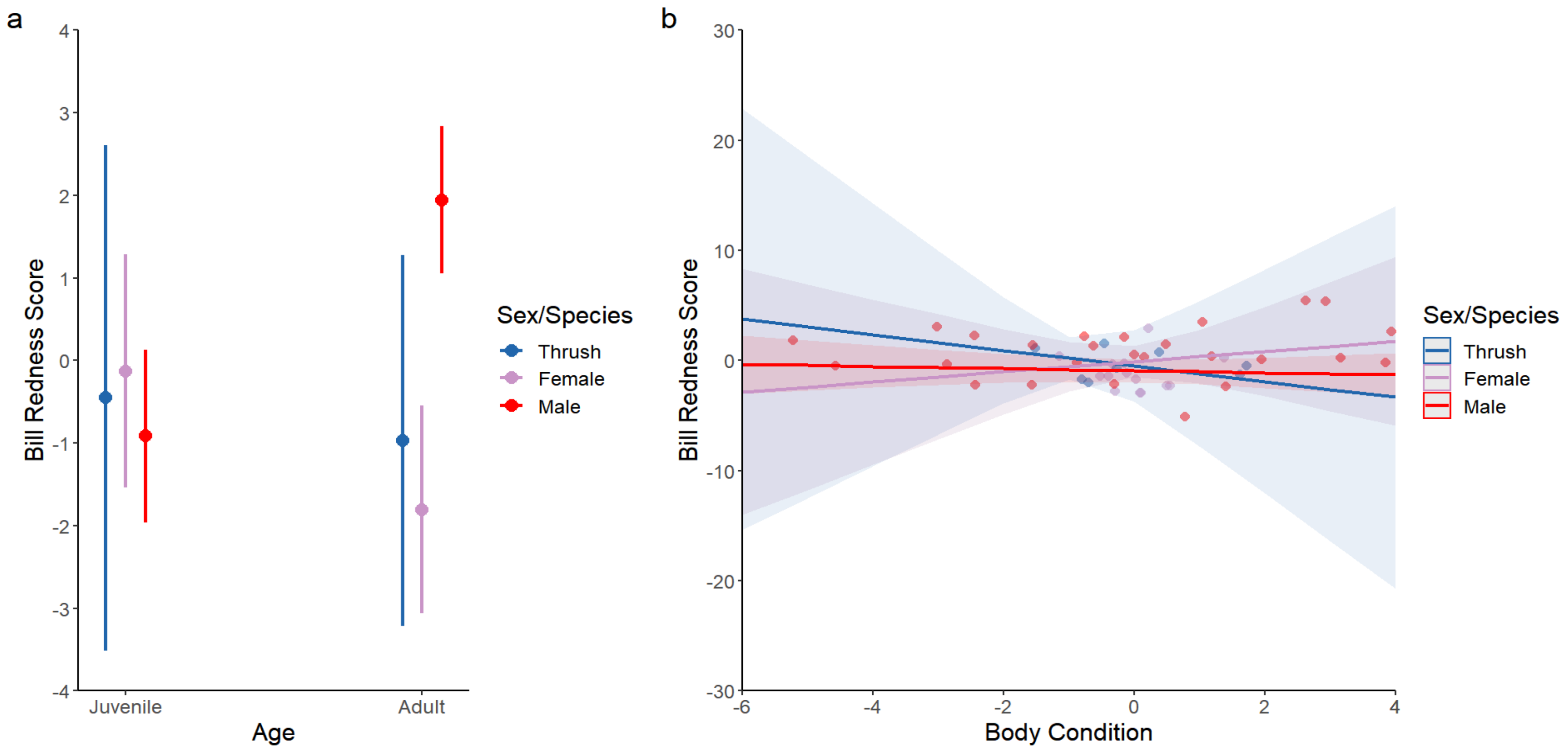

Figure 3.6. Predicted bill redness scores of Eurasian blackbirds and song thrushes. Bill redness score was obtained from a Principal Component Analysis (PCA), with higher values representing redder bills. Sex/species was either male (male blackbird), female (female blackbird), or thrush (song thrush). Figures represent predicted relationships after controlling for other factors in the model. a) Predicted bill redness scores based on a bird's sex/species and age. Juveniles were birds in their first year of life, while adults were older than a year. The lines represent 95% confidence intervals around the means indicated by the points. b) Predicted bill redness scores based on a bird's sex/species and body condition. Body condition was mass - Scaled Mass Index (SMI; Peig & Green, 2009). The ribbons represent 95% confidence intervals around the mean values illustrated by the trendlines.

Table 3.6. Results of a linear model testing for relationships between bill redness score and sex/species, body condition, and age of Eurasian blackbirds and song thrushes. Bill redness score was obtained from a Principal Component Analysis (PCA), with higher values representing redder bills. Body condition was mass - Scaled Mass Index (SMI; Peig & Green, 2009). Sex/species was either male (male blackbird), female (female blackbird), or thrush (song thrush), while age was either juvenile (birds in their first year of life) or adult (birds older than a year). Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	ColourScore ~ Sex*Condition*Age					
Predictors	*Estimates*	*CI*	*std. Error*	*df*	*Statistic*	*p*
(Intercept)	-0.96	-3.21 – 1.30	1.11	36.00	-0.86	0.395
Sex	-	-	-	-	5.35	**0.009 ** **
Sex [Female - Thrush]	-0.93	-3.52 – 1.65	1.27	36.00	-0.73	0.469
Sex [Male - Thrush]	2.93	0.49 – 5.36	1.20	36.00	2.44	**0.020 ***
Condition	0.27	-1.53 – 2.08	0.89	36.00	0.31	0.761
Age	-	-	-	-	2.66	0.112
Age [Adult - Juvenile]	-0.46	-4.51 – 3.59	2.00	36.00	-0.23	0.820
Sex × Condition	-	-	-	-	0.66	0.525
Sex [Female] × Condition	-1.56	-5.57 – 2.45	1.98	36.00	-0.79	0.436
Sex [Male] × Condition	0.11	-1.74 – 1.96	0.91	36.00	0.12	0.907
Sex × Age	-	-	-	-	8.34	**0.001 ** **
Sex [Female] × Age [Adult]	-1.33	-5.82 – 3.16	2.21	36.00	-0.60	0.552
Sex [Male] × Age [Adult]	3.35	-0.94 – 7.64	2.12	36.00	1.58	0.122
Condition × Age	-	-	-	-	2.41	0.130
Condition × Age [Adult]	0.98	-3.19 – 5.15	2.06	36.00	0.48	0.636

Sex × Condition × Age	-	-	-	-	0.64	0.535
Sex [Female] × Condition × Age [Adult]	-2.73	-8.55 – 3.10	2.87	36.00	-0.95	0.349
Sex [Male] × Condition × Age [Adult]	-0.50	-4.71 – 3.71	2.08	36.00	-0.24	0.809
Observations	48					
R^2 / R^2 adjusted	0.500 / 0.347					

3.4 Feather Colour

3.4.1 Relationships with bill colour, body condition, and age

Overall, only sex/species was significantly related to feather colour score ($p < 0.001$; Figure 3.7c; Table 3.7). Bill colour score ($p = 0.863$), body condition ($p = 0.644$), and age ($p = 0.424$) were all unrelated to feather colour score (Figure 3.7; Table 3.7). All interactions between factors were also non-significant and removed during model selection (Table 3.7). Post-hoc analyses indicated that male blackbirds had darker back feathers than female blackbirds ($p = 0.087$) and song thrushes ($p < 0.001$) on average (Table 6.18). Female blackbirds also had significantly darker back feathers than song thrushes ($p = 0.032$; Table 6.18).

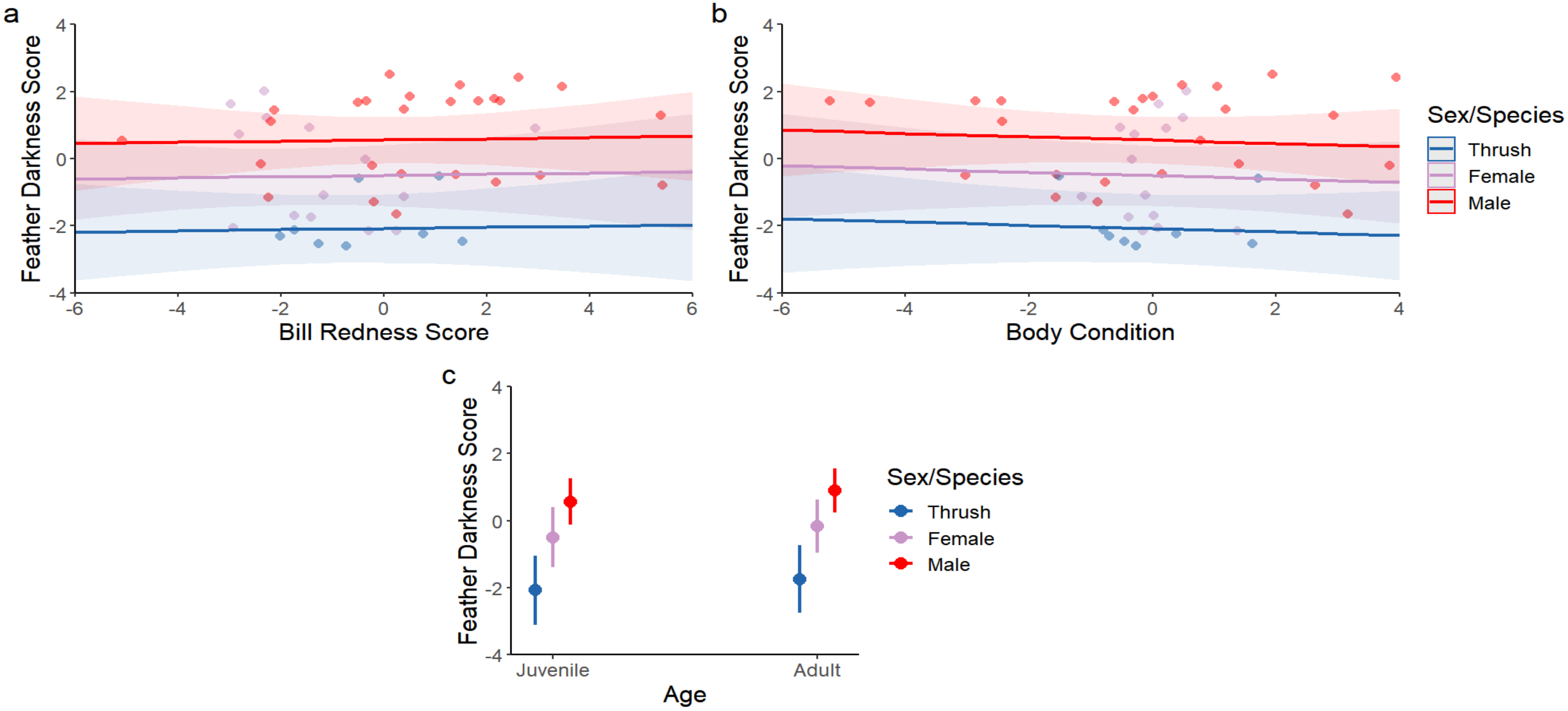

Figure 3.7. Predicted feather darkness scores of Eurasian blackbirds and song thrushes. Feather darkness score was obtained from a Principal Component Analysis (PCA), with higher values representing darker back feathers. Sex/species was either male (male blackbird), female (female blackbird), or thrush (song thrush). Figures represent predicted relationships after controlling for other factors in the model. Ribbons represent 95% confidence intervals around the mean values illustrated by the trendlines. a) Predicted feather darkness scores based on a bird’s sex/species and feather darkness score. Bill redness score was also obtained from a PCA, with higher values representing redder bills. b) Predicted feather darkness scores based on a bird’s sex/species and body condition. Body condition was mass - Scaled Mass Index (SMI; Peig & Green, 2009). c) Predicted feather darkness scores based on a bird’s sex/species and age. Juveniles were birds in their first year of life, while adults were older than a year. The lines represent 95% confidence intervals around the means indicated by the points.

Table 3.7. Results of a linear model testing for a relationship between feather darkness score and bill redness score, sex/species, body condition, and age of Eurasian blackbirds and song thrushes. Feather darkness score was obtained from a Principal Component Analysis (PCA), with higher values representing darker back feathers. Bill redness score (ColourScore) was also obtained from a PCA, with higher values representing redder bills. Body condition was mass - Scaled Mass Index (SMI; Peig & Green, 2009). Sex/species was either male (male blackbird), female (female blackbird), or thrush (song thrush), while age was either juvenile (birds in their first year of life) or adult (birds older than a year). Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	FeatherScore ~ ColourScore + Age + Condition + Sex					
Predictors	*Estimates*	*CI*	*std. Error*	*df*	*Statistic*	*p*
(Intercept)	-1.75	-2.79 – -0.70	0.52	42.00	-3.38	**0.002 ****
ColourScore	0.02	-0.19 – 0.22	0.10	42.00	0.17	0.863
Age	-	-	-	-	0.65	0.424
Age [Adult - Juvenile]	0.33	-0.48 – 1.15	0.40	42.00	0.82	0.414
Condition	-0.05	-0.27 – 0.17	0.11	42.00	-0.47	0.644
Sex	-	-	-	-	11.40	**<0.001 *****
Sex [Female - Thrush]	1.58	0.36 – 2.81	0.61	42.00	2.61	**0.013 ***
Sex [Male - Thrush]	2.64	1.51 – 3.76	0.56	42.00	4.73	**<0.001 *****
Observations	48					
R^2 / R^2 adjusted	0.385 / 0.312					
Terms dropped (in order): ColourScore:Sex:Age, ColourScore:Sex:Condition, ColourScore:Sex, ColourScore:Condition:Age, Condition:ColourScore, Age:ColourScore, Sex:Condition:Age, Sex:Condition, Age:Sex, Age:Condition						

3.5 Colour, condition, and age

3.5.1 Relationships with vigilance score

The relationship between vigilance score and bill redness was sex and age dependent (p = 0.032; Table 3.8). There was little association between bill redness and vigilance in juvenile birds, while the relationship was sex-specific in adults (Figure 3.8b). Adult female blackbirds with redder bills were less vigilant, while there appears to be little relationship between bill redness and vigilance in males (Figure 3.8b). The two-way interaction between bill redness score and age was marginally non-significant in the model (p = 0.109; Table 3.8), with vigilance tending to decrease more with bill redness score in adults than juveniles. The two-way interaction between sex and age was also significant in the model (p = 0.043; Table 3.8). Post-hoc analyses indicated that juvenile females were more vigilant than juvenile males (p = 0.056; Table 6.18). None of the other sex-age comparisons were significantly different (Table 6.18), although there was greater variation in vigilance scores among adult females compared to the other sex-age combinations (Figure 3.8a).

Vigilance score was also related to the interactions between feather darkness score and age (p = 0.018; Table 3.8) and feather darkness score and season (p = 0.062; Table 3.8). There was little relationship between vigilance and feather darkness in the non-breeding season, while birds with darker feathers were more vigilant in the breeding season (Figure 3.8d). Furthermore, vigilance score increases slightly with feather darkness in juvenile blackbirds but decreases with feather darkness in adult blackbirds (Figure 3.8c). There were no significant associations between vigilance score and body condition (p = 0.936; Table 3.8) or bill redness score alone (p = 0.829; Table 3.8). There was a weak relationship with feather darkness, with birds with darker feathers being more vigilant (p = 0.084; Table 3.8). Age alone was not a significant term in the model (p = 0.204; Table 3.8), although there was a suggestion that juvenile birds had higher vigilance than adults (p = 0.062; Table 3.8). Finally, there were also significant relationships between the vigilance of banded blackbirds and runtime, number of pauses, and the interaction between sex and season, as well as a weakly significant effect of cover (Table 3.8). However, these terms were only included in this model to control for their potential effects, so these relationships are not discussed further in this thesis.

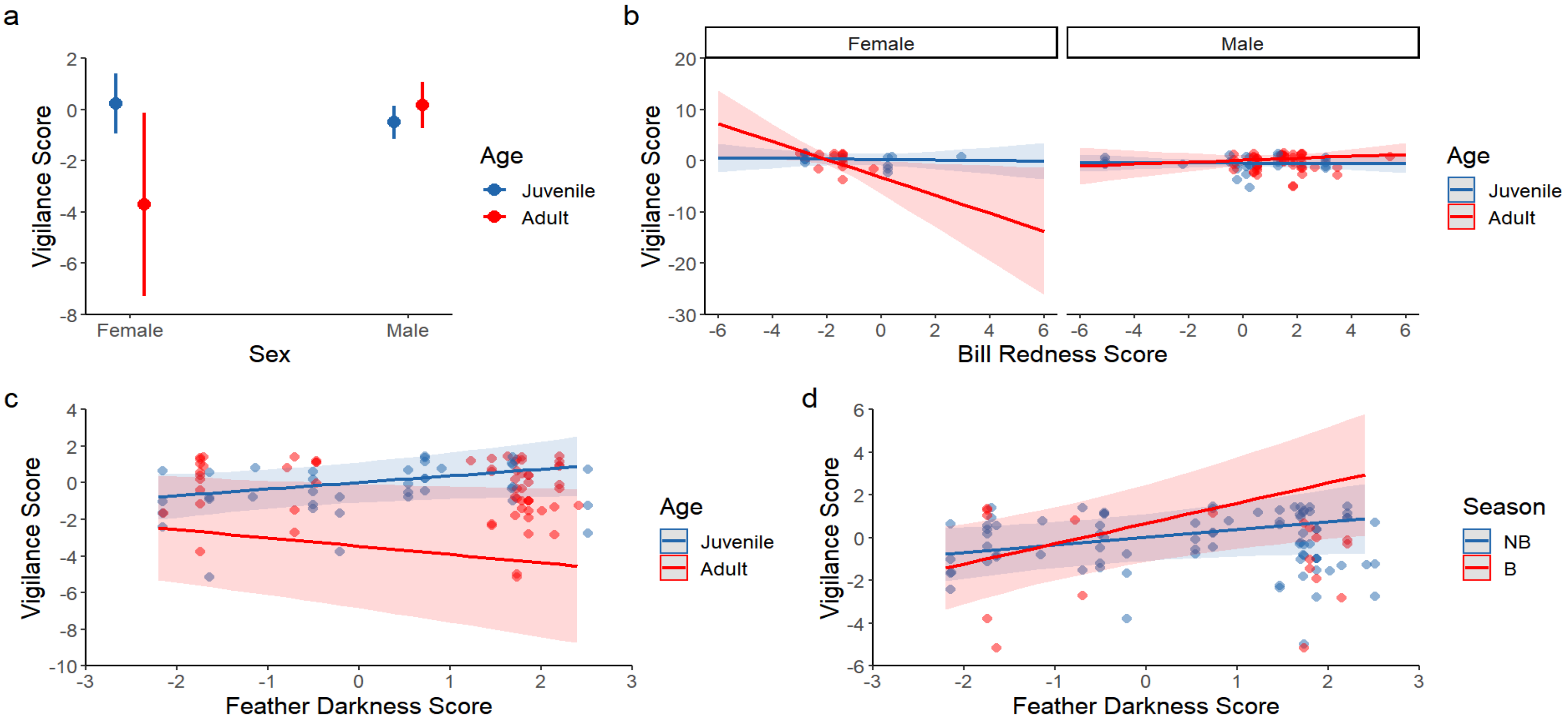

Figure 3.8. Predicted vigilance of foraging Eurasian blackbirds. Vigilance is a vigilance score obtained from a Principal Component Analysis (PCA), with higher values representing greater vigilance. Season was either B (breeding) or NB (non-breeding), while age was either juvenile (birds in their first year of life) or adult (birds older than a year). The feather darkness and bill redness scores were also obtained from PCAs, with higher values representing darker back feathers and redder bill colouration, respectively. Figures represent predicted relationships after controlling for other factors in the model. Ribbons represent 95% confidence intervals around the mean values illustrated by the trendlines. a) Predicted vigilance scores based on a bird's sex and age. The lines represent 95% confidence intervals around the means indicated by the points. b) Predicted vigilance scores based on a bird's sex, age, and bill redness score. c) Predicted vigilance scores based on a bird's age and feather darkness score. d) Predicted vigilance scores based on a bird's feather darkness score and the season.

Table 3.8. Results of a Linear Mixed Model (LMM) testing for relationships between factors and the vigilance of Eurasian blackbirds while foraging. Vigilance is a vigilance score (PC1) obtained from a Principal Component Analysis (PCA), with higher values representing greater vigilance. Variance attributed to the random effects of individual ID and date of observation is also presented. Factors include age (juvenile; birds in their first year of life, or adult; birds older than a year), ColourScore (bill redness; higher values indicate redder bills), FeatherScore (back feather darkness; higher values indicate darker feathers), season (breeding/B or non-breeding/NB), condition (body condition; mass - Scaled Mass Index (SMI; Peig & Green, 2009)), cover (cover or open), runtime (the length of the observation, in seconds), and pause (the number of times the observation was paused). ColourScore and FeatherScore were obtained from PCAs. Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	PC1 ~ Sex*Age*ColourScore + Age*FeatherScore + Season*FeatherScore + Sex*Season + Condition + Cover + Runtime + Pause + (1|ID) + (1|Date)					
Predictors	*Estimates*	*CI*	*std. Error*	*df*	*Statistic*	*p*
(Intercept)	0.51	-0.98 – 2.00	0.75	80.00	0.68	0.496
Sex	-	-	-	-	0.00	0.982
Sex [Male - Female]	-0.73	-2.02 – 0.55	0.65	80.00	-1.13	0.260
Age	-	-	-	-	1.68	0.204
Age [Adult - Juvenile]	-3.03	-6.22 – 0.16	1.60	80.00	-1.89	**0.062 .**
ColourScore	-0.05	-0.56 – 0.45	0.25	80.00	-0.22	0.829
FeatherScore	0.36	-0.05 – 0.77	0.21	80.00	1.75	**0.084 .**
Season	-	-	-	-	2.66	0.107
Season [B - NB]	0.65	-0.92 – 2.23	0.79	80.00	0.83	0.410
Condition	-0.01	-0.18 – 0.17	0.09	80.00	-0.08	0.936
Cover	-	-	-	-	2.96	**0.089 .**
Cover [Cover - Open]	-0.79	-1.70 – 0.12	0.46	80.00	-1.72	**0.089 .**
Runtime	-0.00	-0.01 – -0.00	0.00	80.00	-2.53	**0.013 ***

Pause	0.61	0.13 – 1.09	0.24	80.00	2.51	**0.014 ***
Sex × Age	-	-	-	-	4.47	**0.043 ***
Sex [Male] × Age [Adult]	4.11	0.24 – 7.97	1.94	80.00	2.11	**0.038 ***
Sex × ColourScore	-	-	-	-	5.40	**0.025 ***
Sex [Male] × ColourScore	0.04	-0.52 – 0.61	0.28	80.00	0.15	0.884
Age × ColourScore	-	-	-	-	2.68	0.109
Age [Adult] × ColourScore	-1.69	-3.36 – -0.02	0.84	80.00	-2.02	**0.047 ***
Age × FeatherScore	-	-	-	-	6.60	**0.018 ***
Age [Adult] × FeatherScore	-0.81	-1.45 – -0.18	0.32	80.00	-2.57	**0.012 ***
Season × FeatherScore	-	-	-	-	3.58	**0.062 .**
Season [B] × FeatherScore	0.59	-0.03 – 1.20	0.31	80.00	1.89	**0.062 .**
Sex × Season	-	-	-	-	5.80	**0.018 ***
Sex [Male] × Season [B]	-2.69	-4.91 – -0.47	1.12	80.00	-2.41	**0.018 ***
Sex × Age × ColourScore	-	-	-	-	4.90	**0.032 ***
Sex [Male] × Age [Adult] × ColourScore	1.90	0.19 – 3.60	0.86	80.00	2.21	**0.030 ***

Random Effects

Residual effect	1.67
Date effect	0.00
ID effect	0.26
Observations	100

Marginal R^2 / Conditional R^2	0.320 / NA
Terms dropped (in order): DateCap, Mass, ColourScore:FeatherScore:Condition, ColourScore:FeatherScore, Sex:Age:FeatherScore, Temp, ColourScore:Condition, Sex:Season:ColourScore, ColourScore:Season, Sex:FeatherScore:Season, Sex:FeatherScore, FeatherScore:Condition, Sex:Season:Condition, Sex:Condition, Time, Season:Condition	

3.5.2 Relationships with FID

There was a significant relationship between FID and the interaction between sex and bill redness score in blackbirds ($p = 0.017$; Table 3.9). Specifically, female blackbirds with redder bills had lower FIDs, while there was little relationship between FID and bill redness in male blackbirds (Figure 3.9a). The FIDs of male banded blackbirds were also 6.73 metres ($p = 0.05$) higher, on average, than those of females (Table 3.9). Bill redness score ($p = 0.028$) and feather darkness score ($p = 0.030$) were both significantly negatively associated with FID, with birds with redder bills and darker back feathers having lower FIDs on average (Table 3.9). However, the relationship between feather darkness and FID did not depend on sex (Figure 3.9b; Table 3.9). Adult birds also had lower FIDs than juveniles, fleeing when I was an average of 3.79 metres ($p = 0.035$) closer to them (Figure 3.9c; Table 3.9). Finally, body condition did not have any significant relationship with FID ($p = 0.455$) and the significant association between FID and starting distance found in the analysis of the full dataset was retained (Table 3.9).

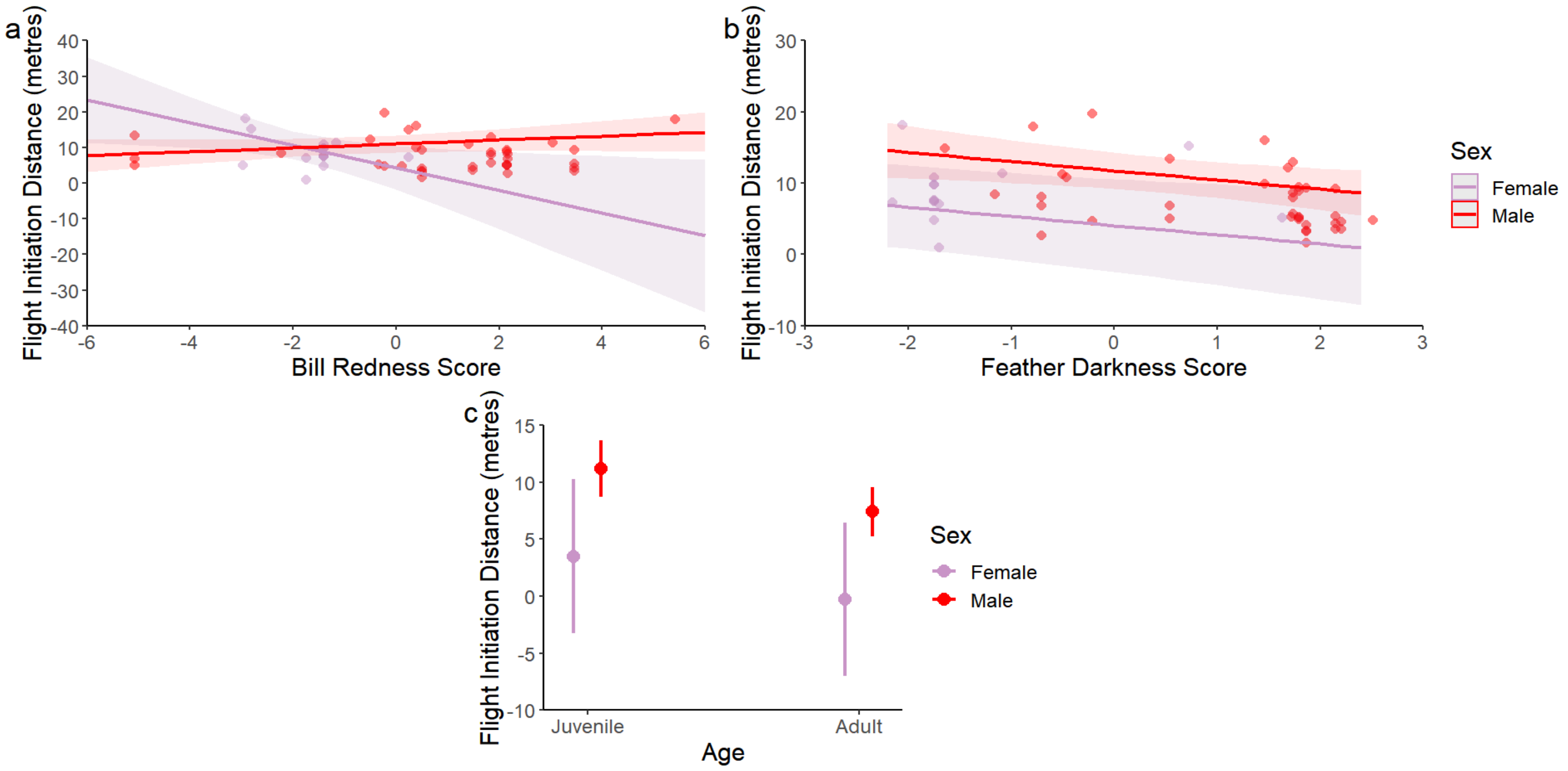

Figure 3.9. Predicted Flight Initiation Distances (FIDs) of Eurasian blackbirds. FID represents the distance between a blackbird and an approaching human at which the bird first took evasive action such as running or flying away. The feather darkness and bill redness scores were obtained from PCAs, with higher values representing darker back feathers and redder bill colouration, respectively. Juvenile birds were in their first year of life, while adult birds were older than one year. Figures represent predicted relationships after controlling for other factors in the model. Ribbons represent 95% confidence intervals around the mean values illustrated by the trendlines (although note that FIDs below 0 are impossible in reality). a) Predicted FIDs based on a bird’s sex and bill redness score. b) Predicted FIDs based on a bird’s sex and feather darkness score. c) Predicted FIDs based on a bird’s age and sex. The lines represent 95% confidence intervals around the means indicated by the points.

Table 3.9. Results of a Linear Mixed Model (LMM) testing for relationships between factors and the Flight Initiation Distances (FIDs) of Eurasian blackbirds, alongside variance attributed to the random effects of individual ID and date of observation. FID represents the distance between a blackbird and an approaching human at which the bird first took evasive action such as running or flying away. Factors include StartDist (starting distance; the distance between the bird and the human at the beginning of their approach), condition (body condition; mass - Scaled Mass Index (SMI; Peig & Green, 2009)), age (juvenile; birds in their first year of life, or adult; birds older than a year), ColourScore (bill redness; higher values indicate redder bills), and FeatherScore (back feather darkness; higher values indicate darker feathers). ColourScore and FeatherScore were obtained from Principal Component Analyses (PCAs). Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	FID ~ StartDist + Condition + Age + Sex*ColourScore + FeatherScore + (1|ID) + (1|Date)					
Predictors	*Estimates*	*CI*	*std. Error*	*df*	*Statistic*	*p*
(Intercept)	2.31	-4.13 – 8.75	3.14	28.40	0.74	0.468
StartDist	0.13	0.02 – 0.25	0.05	35.43	2.49	**0.018 ***
Condition	-0.24	-0.92 – 0.43	0.32	14.69	-0.77	0.455
Age	-	-	-	-	5.11	**0.035 ***
Age [Adult - Juvenile]	-3.79	-7.28 – -0.30	1.68	20.45	-2.26	**0.035 ***
Sex	-	-	-	-	4.28	**0.050 ***
Sex [Male - Female]	6.73	0.01 – 13.45	3.25	23.86	2.07	**0.050 ***
ColourScore	-3.19	-6.00 – -0.37	1.38	28.29	-2.31	**0.028 ***
FeatherScore	-1.29	-2.44 – -0.14	0.55	18.92	-2.35	**0.030 ***
Sex × ColourScore	-	-	-	-	6.45	**0.017 ***
Sex [Male] × ColourScore	3.73	0.71 – 6.75	1.47	25.86	2.54	**0.017 ***
Random Effects						
Residual effect	8.99					
ID effect	3.81					

Date effect	1.70
Observations	52
Marginal R^2 / Conditional R^2	0.342 / 0.592

Terms dropped (in order): DateCap, Distance, Season:Condition, Mass, Season:ColourScore, Season:FeatherScore, Sex:StartDist, StartDist:Age, ColourScore:FeatherScore, Sex:Age:FeatherScore, Age:FeatherScore, Sex:Age:ColourScore, Sex:Condition, Age:ColourScore, Sex:Age, Sex:FeatherScore, Season:StartDist, Season

3.5.3 Relationships with distance moved

There was a significant relationship between distance moved and the interaction between age and FID ($p = 0.045$; Table 3.10). There was no apparent association between FID and distance moved in adult blackbirds, while juvenile birds with shorter FIDs moved shorter distances after fleeing (Figure 3.10d). For each one metre increase in FID, the distance moved by a bird decreased by 0.6 metres more, on average, if that bird was a juvenile than if it was an adult ($p = 0.045$; Table 3.10). Adult birds also moved 10.46 metres less after fleeing than juveniles on average ($p = 0.007$; Table 3.10). There was an indication that blackbirds with redder bills moved further after fleeing, regardless of their sex ($p = 0.095$; Figure 3.10a; Table 3.10). Furthermore, there was a significant association between mass and distance moved, with heavier birds moving longer distances regardless of sex (Figure 3.10c). For each one gram increase in its mass, a blackbird is expected to move 0.43 metres further after fleeing ($p = 0.023$; Table 3.10). Body condition ($p = 0.891$) and feather darkness score ($p = 0.830$) do not appear to have any relationship with distance moved (Figure 3.10b; Table 3.10). The significant associations between FID and distance moved, and type of movement and distance moved found when the full dataset was analysed were retained in this model.

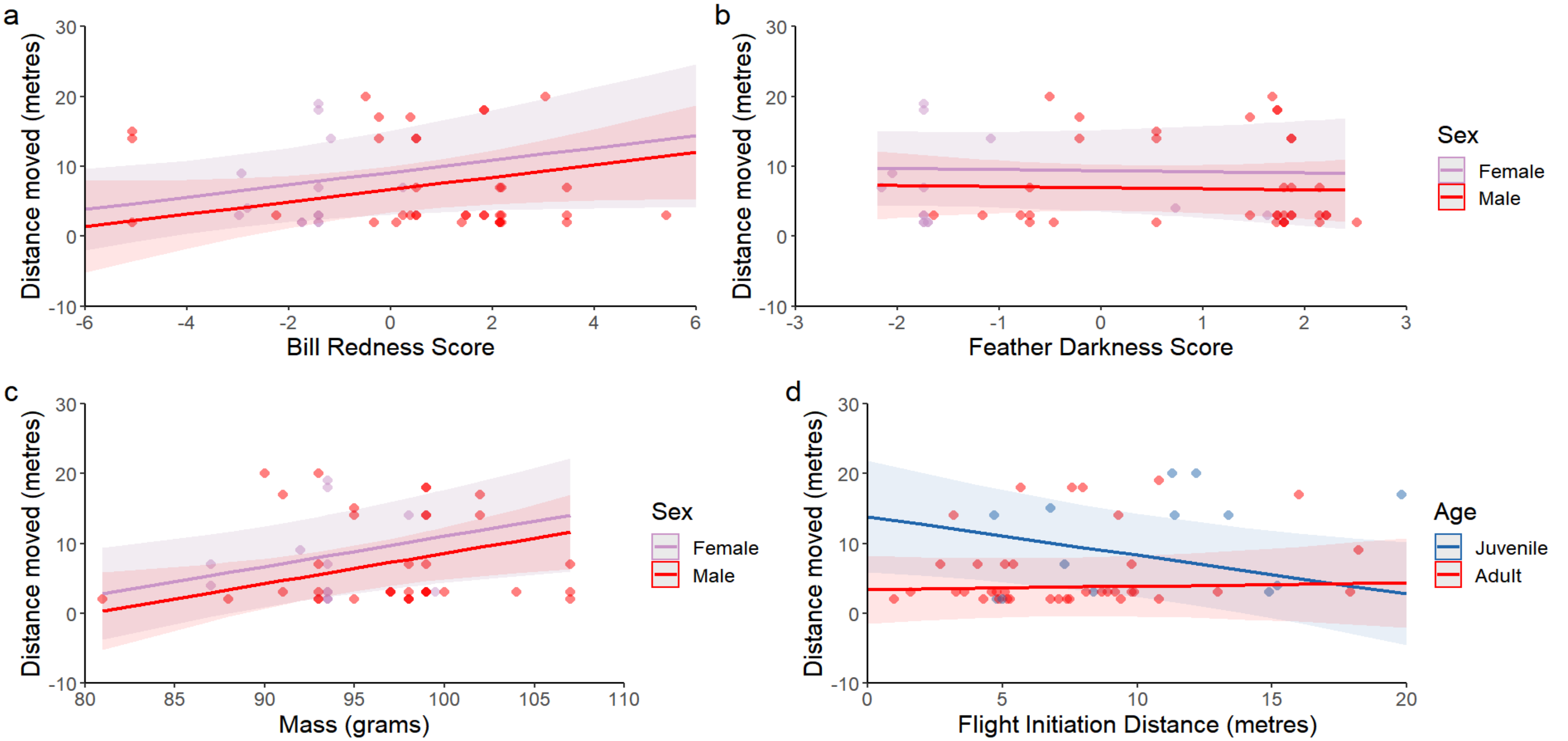

Figure 3.10. Predicted distances moved after fleeing an approaching human (in metres) of Eurasian blackbirds. Figures represent predicted relationships after controlling for other factors in the model. Ribbons represent 95% confidence intervals around the mean values illustrated by the trendlines (although note that distances moved below 0 are impossible in reality). a) Predicted distances moved based on a bird's sex and bill redness score. Bill redness score was obtained from a Principal Component Analysis (PCA), with higher values representing redder bills. b) Predicted distances moved based on a bird's sex and feather darkness score. Feather darkness score was also obtained from a PCA, with higher values representing darker back feathers. c) Predicted distances moved based on a bird's mass (its weight, in grams) and sex. d) Predicted distances moved based on a bird's age and its Flight Initiation Distance (FID). FID represents the distance between a blackbird and the approaching human at which the bird first took evasive action such as running or flying away. Juvenile birds were in their first year of life, while adult birds were older than one year.

Table 3.10. Results of a Linear Mixed Model (LMM) testing for relationships between factors and the distances moved after fleeing an approaching human (in metres) of Eurasian blackbirds, alongside variance attributed to the random effects of individual ID and date of observation. Factors include type (the type of movement; hop or fly), age (juvenile; birds in their first year of life, or adult; birds older than a year), FID (Flight Initiation Distance; the distance between a blackbird and the approaching human at which the bird first took evasive action), mass (the weight of the bird, in grams), ColourScore (bill redness; higher values indicate redder bills), FeatherScore (back feather darkness; higher values indicate darker feathers), and condition (body condition; mass - Scaled Mass Index (SMI; Peig & Green, 2009)). ColourScore and FeatherScore were obtained from Principal Component Analyses (PCAs). Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	Move ~ Type + Age*FID + Mass + Sex + ColourScore + FeatherScore + Condition + (1|ID) + (1|Date)					
Predictors	*Estimates*	*CI*	*std. Error*	*df*	*Statistic*	*p*
(Intercept)	-27.88	-61.11 – 5.34	15.44	13.57	-1.81	**0.093 .**
Type	-	-	-	-	75.85	**<0.001 *****
Type [Fly - Hop]	13.24	10.10 – 16.38	1.52	23.67	8.71	**<0.001 *****
Age	-	-	-	-	8.21	**0.007 ****
Age [Adult - Juvenile]	-10.46	-17.84 – -3.07	3.65	37.98	-2.87	**0.007 ****
FID	-0.55	-1.06 – -0.05	0.24	26.97	-2.26	**0.032 ***
Mass	0.43	0.07 – 0.80	0.17	14.14	2.54	**0.023 ***
Sex	-	-	-	-	0.75	0.404
Sex [Male - Female]	-2.43	-8.54 – 3.68	2.81	12.25	-0.86	0.404
ColourScore	0.88	-0.18 – 1.94	0.49	12.99	1.80	**0.095 .**
FeatherScore	-0.16	-1.73 – 1.41	0.73	12.88	-0.22	0.830
Condition	-0.06	-1.01 – 0.89	0.43	12.14	-0.14	0.891
Age × FID	-	-	-	-	4.31	**0.045 ***
Age [Adult] × FID	0.60	0.02 – 1.19	0.29	38.22	2.08	**0.045 ***

Random Effects	
Residual effect	7.16
ID effect	12.40
Date effect	1.83
Observations	51
Marginal R^2 / Conditional R^2	0.590 / 0.863

Terms dropped: Season:Condition, FID:StartDist, FeatherScore:Season, Cover, ColourScore:FeatherScore, Age:Sex:FID, Sex:FID, Age:Sex:Type, Age:Sex:ColourScore, Age:Sex:FeatherScore, ColourScore:Season, Season, Type:Sex, DateCap, Age:Type, Sex:Condition, Age:Sex:StartDist, Age:StartDist, Sex:StartDist, StartDist, Sex*FeatherScore, Age:Sex, Age:FeatherScore, Age:ColourScore, Sex:ColourScore

Chapter 4 Discussion

The major goal of this thesis was to test the caloric requirements and compensation hypotheses, to gain insight into the factors which drive the evolution of bird colouration and antipredator behaviour. This was done by comparing the cautiousness (vigilance, proportion of complete observations, and elements of escape behaviour) of birds which differed in colouration across seasons. Birds were generally less cautious in the breeding than the non-breeding season, particularly female blackbirds (Table 4.1), which supports the caloric requirements hypothesis. Female blackbirds with redder bills also tended to be less cautious (more vigilant and shorter FIDs; Table 4.1), further supporting the caloric requirements hypothesis. Song thrushes were more vigilant than blackbirds and there were few significant differences in cautiousness between male and female blackbirds (Table 4.1), which does not support the compensation hypothesis. Birds with redder bills or darker feathers were more cautious in some cases (Table 4.1), which could support the compensation hypothesis, but this was inconclusive. Overall, the results discussed below support the caloric requirements hypothesis more than the compensation hypothesis, but it is possible both influence antipredator behaviour in blackbirds and song thrushes.

Table 4.1. Summary results of this thesis. Red plus (+) symbols indicate higher cautiousness, blue (-) minus symbols indicate lower cautiousness, and black equal (=) symbols indicate equal cautiousness. ♂ represents males, ♀ represents females. See Chapter 2 (Methodology) for descriptions of the metrics of caution used.

	Species	**Season**	**Sex**	**Bill colour (♂ blackbird)**	**Bill colour** (♀ blackbird)	**Feather colour** (♂ blackbird)	**Feather colour** (♀ blackbird**)**
	Blackbird (BB) vs Song Thrush (ST)	Breeding (B) vs Non-breeding (NB)	Blackbird (♂ vs ♀**)**	Redder bills	Redder bills	Darker feathers	Darker feathers
Vigilance	- BB + ST	- B + NB [2]	=	=	- [4]	+	+
Proportion incomplete	=	- B + NB	=				
FID	=	- B + NB	=	=	-	-	-
Distance moved	= [1]	=	- ♀ + ♂	+ [5]	+ [5]	=	=
Odds of flying	=	=	+ ♀ - ♂ [3]				

Notes: [1] Although female blackbirds tended to move further than thrushes, [2] Significant in female blackbirds only, [3] In the breeding season only, [4] In adult females only, [5] weak relationship.

4.1 Species differences in antipredator behaviour

Song thrushes, the less conspicuous species, were more vigilant than blackbirds in both seasons. Song thrushes also tended towards being more cautious than blackbirds across some of the other metrics; they had the longest FIDs (although not significantly different to those of blackbirds) and moved further than female (but not male) blackbirds after fleeing. These results are counter to the compensation hypothesis, which predicts that less conspicuous birds should be less cautious (Pascual et al., 2014a, 2014b). Previous studies have found that more conspicuous bird species tend to have shorter foraging bouts (Silva et al., 2008) and respond more strongly to playbacks of predator vocalisations (Journey et al., 2013), which supports the compensation hypothesis and is counter to my results. As I compared the cautiousness of only two species, I had limited power to detect a broad relationship between species colouration and cautiousness. It may also be that this relationship differs between metrics of cautiousness, as Hensley et al. (2015) found no relationship between plumage conspicuousness and FID despite comparing 136 species.

Song thrushes may be more cautious than blackbirds because they are smaller. Smaller animals are thought to be more cautious due to being vulnerable to a wider range of predators, although the evidence for this is mixed (reviewed in Beauchamp, 2010). However, the size difference between blackbirds and song thrushes is small (~0-30 grams on average; Congdon, 2010; Higgins et al., 2006) and all the likely predators at my study site are known to attack both species (Busbridge & Stewart, 2018; Congdon, 2010; Higgins, 1999; Higgins et al., 2006; van Heezik et al., 2010). Therefore, it seems improbable that blackbirds and song thrushes are experiencing major differences in predation pressure at the study site. It is possible that song thrushes are innately more cautious than blackbirds due to being vulnerable to a wider range of predators in their native range, but as antipredator behaviour tends to be plastic and sensitive to predation risk in the specific environment (Lima & Dill, 1990; Mikula, 2014; Rodriguez-Prieto et al., 2009), this seems unlikely.

A potential explanation for the difference in vigilance between blackbirds and song thrushes is differences in dominance and foraging niche. Blackbirds tend to be dominant over song thrushes, often chasing them out of their territories and sometimes stealing their food (Higgins et al., 2008; pers. obs.). Therefore, song thrushes may have been vigilant to avoid aggressive interactions with blackbirds, which are costly in terms of energy expended in fleeing, loss of food and foraging time, and potential for injury (Gaglio et al., 2018; Kenyon & Martin, 2022; Robertson et al., 1986). Indeed, monitoring competitors often contributes to vigilance in birds (Askenmo et al., 1992; Beauchamp, 2017, 2019; Krebs, 1980; McQueen et al., 2017). It is even possible that the colouration of song thrushes has evolved to reduce conspicuousness to blackbirds, or to mimic female blackbirds to reduce aggression from males (interspecific social dominance mimicry; Prum, 2014). Song thrushes may also be less vigilant than blackbirds due to differences in their foraging behaviour. Blackbirds tend to forage more vigorously than song thrushes while on the ground, actively digging into soil and turning over leaf litter (Higgins et al., 2006; pers. obs.), during which it may be difficult or costly to remain vigilant. Conversely, song thrushes mainly pick off invertebrates from on or near the surface of the ground (Higgins et al., 2006; pers. obs.), allowing them to combine vigilance with breaks between pecks. Barbosa (1995) found that wading birds with a similar foraging strategy to song thrushes had higher scanning rates than waders with other foraging strategies, probably because they were more able to maintain vigilance while foraging. Therefore, the observation that song thrushes are more vigilant than blackbirds may be related to them being the less dominant species or be an artefact of differences in foraging behaviour.

However, differences in foraging behaviour do not explain the trend towards song thrushes selecting more cautious escape behaviours than blackbirds. One possibility is that song thrushes are less habituated to humans than blackbirds, as they tend to spend less time foraging in open areas and avoid people more (Higgins et al., 2008; pers. obs.). Greater habituation to humans has been shown to reduce FID in blackbirds (Rodriguez-Prieto et al., 2009) and other birds (Hall et al., 2020; Mikula, 2014), so the same may be true of song thrushes. Furthermore, blackbirds often excavate and forage in the same patch for extended periods (Higgins et al., 2006; pers. obs.), so they may risk losing that patch to a competitor or it being backfilled by wind if they abandon it to flee a potential predator. Therefore, it may be more costly for blackbirds to flee perceived threats than song thrushes, which do not usually excavate patches (Higgins et al., 2006; pers. obs.). Overall, it is likely that song thrushes are more cautious than blackbirds due to some combination of differences in foraging niche, dominance, and responsiveness to humans, none of which are related to differences in conspicuousness to predators.

4.2 Sex and seasonal differences in antipredator behaviour

Female blackbirds, but not males, were significantly less vigilant while foraging in the breeding than the non-breeding season. This result is in line with the caloric requirements hypothesis, which predicts that female birds in the breeding season should be less cautious than in the non-breeding season due to higher caloric requirements associated with egg production, incubation, and provisioning offspring (Diniz, 2011; Fogg et al., 2013; Post & Götmark, 2006a, 2006b). The only other major sex-specific difference in cautiousness across seasons was that male blackbirds tended to be less likely to fly (rather than hop or run) in the breeding season than the non-breeding season. Flight is energetically expensive for birds (Norberg, 1996; Nudds & Bryant, 2000) and male birds are also expected to have higher energetic requirements in the breeding season than the non-breeding season due to the demands of reproduction and territory defence (Askenmo et al., 1992; Bryant, 1997; McQueen et al., 2021b; Schartz & Zimmerman, 1971; Vezina & Salvante, 2010). Therefore, male blackbirds could be attempting to conserve energy by flying less often in the breeding season, even though flying away from a predator probably reduces predation risk more than hopping or running (Martín et al., 2008). If true, this finding also supports the caloric requirements hypothesis. However, an alternative explanation is that male blackbirds were less likely to fly in the breeding than the non-breeding season because they were less willing to abandon their mate or territory (Cooper, 1999). Birds which flew moved an average of ~9 metres further than those which hopped, and often flew into cover (pers. obs.), potentially leaving their mate or territory unguarded. As extra-pair paternity occurs in blackbirds (Creighton, 2000a), males which abandon their territories while their mates are fertile risk losing paternity to rival males. Therefore, it is unclear whether the reduction in likelihood of male blackbirds flying in the breeding compared to the non-breeding season supports the caloric requirements hypothesis.

There was a general reduction in cautiousness across various metrics in both blackbirds and song thrushes in the breeding season, compared with the non-breeding season, which also supports the caloric requirements hypothesis. While the difference in caloric requirements between seasons is expected to be larger in females than males, birds of both sexes are expected to have higher caloric requirements in the breeding season due to the energetic demands of reproduction (Askenmo et al., 1992; Bryant, 1997; Diniz, 2011; Fogg et al., 2013; McQueen et al., 2021b; Post & Götmark, 2006a, 2006b; Schartz & Zimmerman, 1971; Vezina & Salvante, 2010). Indeed, birds had shorter FIDs and observations were less likely to be complete (indicating shorter foraging bout lengths) in the breeding season than the non-breeding season. Song thrushes and blackbirds of both sexes were also less vigilant in the breeding than the non-breeding season, although the difference was only significant in female blackbirds. It is possible that predation risk was higher in the non-breeding than the breeding season, resulting in increased cautiousness. However, bird predation by cats in Aotearoa (van Heezik et al., 2010) and elsewhere (Krauze-Gryz et al., 2017; Loss et al., 2013) tends to be highest in spring and summer (i.e., the breeding season), although this may partially reflect increased predation of nestlings and fledglings rather than adults. As cats are probably the most common predator of birds in Pukekawa, there is no reason to suppose predation risk for blackbirds and song thrushes was higher in the non-breeding than the breeding season (and indeed the reverse may be true). Therefore, the most likely explanation for the reduction in cautiousness during the breeding season is that birds were prioritising foraging over cautiousness due to their increased caloric requirements. The apparent reduction in foraging bout length may also be due to birds foraging for shorter periods because they needed to return to the nest to incubate, brood, or feed young (Fogg et al., 2013; Post & Götmark, 2006b). My results are opposite to those of Reboreda and Fernandez (1997), who found greater rhea *Rhea americana* of both sexes were more vigilant in the breeding than the non-breeding season, which they attribute to either greater resource availability or increased intrasexual competition. It is possible that greater rhea are less resource limited or under higher predation risk in the breeding season, or prioritise monitoring conspecifics while breeding more than blackbirds and song thrushes, any of which could explain the differing seasonal patterns in vigilance behaviour. Interestingly, there was no overall seasonal effect on distance moved after fleeing or the type of movement. Perhaps caloric requirement differences have a larger impact on vigilance and the decision to flee than decisions made after fleeing, such as how far to move and which type of movement to perform, although this remains to be tested.

The relationship between sex and cautiousness in blackbirds was not consistent across metrics. Male blackbirds moved further after fleeing than females and flew longer distances when they chose to fly. Female blackbirds were less vigilant, had a lower proportion of complete observations, and had shorter FIDs than males, but none of these differences were statistically significant. Conversely, female blackbirds were more likely to fly than males, which was significant in the breeding but not the non-breeding season. The overall pattern of these results suggests that female blackbirds are less cautious than males, which could support either the caloric requirements or the compensation hypothesis. However, under the caloric requirements hypothesis female blackbirds would be expected to be less cautious relative to males in the breeding season (Diniz, 2011; Post & Götmark, 2006a, 2006b), while under the compensation hypothesis female blackbirds should be consistently less cautious than males (Pascual et al., 2014a, 2014b). As there was no evidence that the difference in cautiousness between the sexes depended on the season (except for likelihood of flying), these results provide some evidence for the compensation hypothesis. This is in line with other studies which found that female birds were less cautious than males when males were the more conspicuously coloured sex (Balph, 1977; Diniz, 2011; Hart & Freed, 2005; McQueen et al., 2017; Møller et al., 2019; Pascual et al., 2014a), which is generally attributed to the compensation hypothesis. The only result contradicting this was that female blackbirds were more likely than males to fly in the breeding season. However, male blackbirds in the breeding season also tended to fly less often than males in the non-breeding season, so this pattern appears to be driven by a general unwillingness of male blackbirds to fly in the breeding season, rather than female blackbirds being more cautious than males.

While compensation is a plausible explanation for the observed trend towards female blackbirds being less cautious than males, there is an alternative view in support of the caloric requirements hypothesis. Female birds may have higher caloric requirements than males even outside of the breeding season, due to the need to recover mass lost in the last breeding season and prepare for the next (Arizmendi-Mejía et al., 2013; Nagy et al., 2007; Powolny et al., 2014). This possibility is supported by studies which show female skylarks *Alaudia arvensis* and evening grosbeaks *Hesperiphona vespertina* are less cautious than males even in the non-breeding season (Balph, 1977; Powolny et al., 2014). Skylarks are also sexually monochromatic, meaning that this difference cannot be attributed to the compensation hypothesis (Powolny et al., 2014). Therefore, female birds may be less cautious than males year-round to allow them to meet their higher caloric requirements. It is particularly interesting that the only statistically significant difference between male and female blackbirds was in distance moved (particularly distance flown) after fleeing. As flying is energetically costly for birds (Norberg, 1996; Nudds & Bryant, 2000), moving shorter distances when fleeing a potential threat may allow female blackbirds to conserve energy. It is also important to note that while I did not find female blackbirds were more cautious, relative to males, in the breeding season than the non-breeding season, this does not necessarily refute the caloric requirements hypothesis. It is possible that the caloric requirements of male and female blackbirds are actually similar in the breeding season, with females investing more in egg production, nest building, and incubation (Askenmo et al., 1992; Diniz, 2011; Fogg et al., 2013; Martin & Badyaev, 1996; Post & Götmark, 2006a, 2006b), while males invest more in sperm production, conspicuous colouration, and mate and territory defence (Askenmo et al., 1992; Bryant, 1997; McQueen et al., 2021b; Schartz & Zimmerman, 1971; Vezina & Salvante, 2010). Furthermore, I observed blackbirds throughout the breeding season, rather than just during the nest-building, egg-laying, and incubation period. This means the caloric requirements of male and female blackbirds may have been similar for much of the observation period because both sexes were feeding nestlings and fledglings (Creighton, 2000a; Halupka & Wysocki, 2004; Higgins et al., 2006; Ibáñez-Álamo & Soler, 2017). This explanation seems particularly likely considering blackbirds of both sexes were less cautious in the breeding than the non-breeding season, which may be due to increased caloric requirements. Overall, my results provide some evidence for both the compensation and caloric requirements hypotheses and highlight the importance of considering both hypotheses when examining relationships between sex, colouration, season, and cautiousness.

4.3 Individual variation in colouration

4.3.1 Age, sex, and colouration

Most of the relationships between age, sex, species, and bill colouration were unsurprising. Adult male blackbirds are known to accumulate carotenoids in their bills, making them appear yellow or orange (Baeta et al., 2008; Delhey et al., 2010; Faivre et al., 2001, 2003; Negro et al., 2018), and adult male blackbirds had the highest bill redness scores. The bills of some female blackbirds also appear yellow or orange (Higgins et al., 2006), indicating the presence of carotenoids (Delhey et al., 2010; Weaver et al., 2018), but adult female blackbirds still had significantly lower bill redness scores than males. Adult male blackbirds also had significantly higher bill redness scores than juvenile males, which is unsurprising as male blackbirds usually do not develop full bill colouration until their first or second breeding season (Grégoire et al., 2004; Higgins et al., 2006). Age and sex/species did not significantly affect bill colouration outside of interactions, probably because juvenile blackbirds, some female blackbirds, and song thrushes had similar bill redness scores. A previous study did find that female blackbirds in their first year had less intense bill colouration than those older than a year (Hatchwell et al., 2001), perhaps because their larger sample size allowed them to detect this relationship. My sample sizes of song thrushes and female blackbirds were limited, resulting in high variability of bill redness scores which may have obscured significant differences.

Male blackbirds had higher feather darkness scores than females, and blackbirds of both sexes had higher feather darkness scores than song thrushes. This is consistent with descriptions of these species (Bright & Waas, 2002; Delhey et al., 2010; Faivre et al., 2001; Higgins et al., 2006), as well as their appearance in the field. Interestingly, the difference in feather darkness score between male and female blackbirds was only weakly significant (p = 0.087). This is probably because male blackbirds retain brown back feathers until they have gone through their second moult (Higgins et al., 2006; Khokhlova, 2009) and may have similar feather colouration to females until this point. With this in mind, it is perhaps surprising that feather colouration did not depend on an interaction between age and sex/species, and juvenile male blackbirds appear to have similar feather darkness scores to adult males. As male blackbirds which have been through their first moult retain a variable proportion of brown feathers (Higgins et al., 2006; Khokhlova, 2009), it is possible both juvenile brown and adult black feathers were collected from birds classed as juveniles, obscuring any difference between age classes. Aging was also made more complicated due to many of the birds being actively in moult when captured, which may have resulted in misclassifications.

4.3.2 Colouration and body condition

There was no relationship between body condition and feather darkness score. Feather darkness score did not appear especially variable within sex/species groups, so it is possible it does not differ enough between individuals to be associated with condition. As blackbirds and song thrushes have uniformly melanin-based plumage, rather than a discrete area such as a breast patch, it is also possible that plumage darkness does not have any role in intraspecific signalling or indicate anything about individual quality or personality in these species. Furthermore, even in species where melanin-based colouration is confirmed to be involved in intraspecific signalling, it is common to find no relationship between individual colouration intensity and metrics of quality such as body condition (Ducrest et al., 2008; Griffith et al., 2006; Grffith et al., 1999; Roulin, 2016; Senar et al., 2003). It appears that any association between melanin-based colouration intensity and individual quality is dependent on the context, time of measurement, and metric of quality used (Ducrest et al., 2008; Griffith et al., 2006; Grffith et al., 1999; Roulin, 2009, 2016). It is also possible that feather darkness is related to individual condition at the time the feathers are moulted, but since some of the feathers sampled were probably from the previous moult (up to a year earlier) this may have resulted in no association between feather darkness and body condition at the time of sampling (Roulin, 2016; Svobodová et al., 2013; Vergara & Fargallo, 2011).

There was also no association between bill redness score and body condition in blackbirds and song thrushes. Song thrushes possess only limited yellow colouration on their bills (Higgins et al., 2006) and the sample size was small (n = 8), so it is perhaps unsurprising there was no relationship between their bill redness scores and body condition. However, the bill colouration of male (and some female) blackbirds is carotenoid-based (Baeta et al., 2008; Delhey et al., 2010; Faivre et al., 2001, 2003; Negro et al., 2018), and carotenoid-based colouration is often thought to signal individual quality (Griffith et al., 2006; Koch & Hill, 2018; Weaver et al., 2018). Therefore, a relationship between bill redness score and metrics of individual quality such as body condition is expected in blackbirds, though a previous study also found no relationship between bill colouration intensity and body condition (Faivre et al., 2001). Evidence for a relationship between blackbird bill colouration intensity and other metrics of individual quality, such as immune function and cloacal protuberance diameter, is also mixed (Baeta et al., 2008; Bright et al., 2004; Faivre et al., 2003). Therefore, it is unclear whether bill colouration signals individual quality in blackbirds.

Female blackbirds also appear not to directly prefer males with more orange bills (Bright & Waas, 2002; Grégoire et al., 2004; Préault et al., 2002), yet males with more orange bills obtain mates in better body condition (Faivre et al., 2001). One possible explanation is that male blackbirds with more orange bills possess higher quality territories, which are settled on independently by higher quality females (Bright et al., 2004; Faivre et al., 2001). Males with more orange bills might be more successful in male-male competition, allowing them to obtain higher quality territories (Bright & Waas, 2002; Bright et al., 2004; Faivre et al., 2001), or only high-quality territories may provide male blackbirds with the resources required to have bright orange bills (Bright et al., 2004; Faivre et al., 2001). Furthermore, male blackbirds with more orange bills tend to raise more offspring successfully (Préault et al., 2005). It seems likely that bill colouration in male blackbirds is somehow related to individual quality, but this relationship is complex and indirect, resulting in non-significant associations between bill colouration and metrics of quality. The same may be true of female bill colouration in blackbirds, but this has rarely been measured or linked to individual quality (but see Delhey et al., 2010; Hatchwell et al., 2001).

It is also important to note that it is very common to obtain no relationship between individual carotenoid-based colouration intensity and metrics of individual quality in birds (Amundsen, 2000; Griffith et al., 2006; Koch & Hill, 2018; Møller et al., 2000; Weaver et al., 2018). The relationship between carotenoid-based colouration intensity and individual quality appears to be complex and dependent on the metric of quality used and the type of colouration (Koch & Hill, 2018; Møller et al., 2000; Weaver et al., 2018). Carotenoid-based (and melanin-based) colouration intensity may also not be related to measures of body condition such as SMI, which correct body mass for body size, even if they are related to other metrics such as immune function. Overall, it appears the relationship between individual condition or quality and colouration is complicated, and may be indirect or even non-existent.

4.3.3 Bill and feather colouration

There was no significant relationship between the bill redness and feather darkness scores of blackbirds or song thrushes, regardless of sex. Other studies which tested for a relationship between melanin-based and carotenoid-based colouration intensity in birds have also found no relationship, which they attribute to the two types of colouration being associated with different individual behaviours or traits (Senar et al., 2003; Svobodová et al., 2013; Vergara & Fargallo, 2011; but see Hegyi et al., 2008). As the signalling function of feather darkness in blackbirds and song thrushes (if any) is unknown, it is entirely possible that bill and feather colouration are related to different individual characteristics in these species, rather than to each other. In blackbirds, bill colouration probably has some role in signalling individual quality, while feather colouration may have no relationship with quality or be associated with a different aspect of quality (see Section 4.3.2). In song thrushes, the small sample size may have prevented any relationships being detected, and there is currently no evidence that either bill or feather colouration have any role in intraspecific signalling. Relationships between colouration intensity and individual quality or traits are complex (see Section 4.3.2), so it is perhaps unsurprising that relationships between different types of colouration are equally complex.

Another possibility is that the different methodology I used to measure bill and feather colouration (colour photography and spectrometry, respectively) obscured any relationship between the two, even though colour photography has been shown to produce comparable results to spectrometry in previous studies (Stevens et al., 2009; Troscianko & Stevens, 2015; Yang et al., 2021). Finally, it is possible that bill redness and feather darkness were uncorrelated because the former is a dynamic signal associated with individual quality at the time of capture, while the latter is a more static signal which indicated quality back at the time of moulting (Roulin, 2016; Svobodová et al., 2013; Vergara & Fargallo, 2011). In support of this, Hegyi et al. (2008) found that the correlation between the brightness of carotenoid-based and melanin-based colouration spectra in great tits *Parus major* was only significant soon after moult. Ultimately there are many possible explanations for the lack of relationship between bill redness and feather darkness score in blackbirds, demonstrating the complexity associated with studying colouration in birds. Future research exploring whether there are signalling functions of feather darkness in blackbirds and song thrushes, and bill colouration in song thrushes, may simplify interpretation of these results.

4.4 Individual colouration and cautiousness

It is important to note that I collected the bill and feather colouration data prior to either of the observation periods. The bill and feather colouration of blackbirds of both sexes has been shown to change considerably through the year (Delhey et al., 2010). This is particularly true of male bill colouration, which is the most intense at the start of the breeding season (Delhey et al., 2010). This means that the blackbirds may not have been captured when variation in colouration between individuals was the greatest, and their colouration is likely to have changed between measurement and the observation periods. These limitations were unavoidable due to the timeframe and budget constraints of a Masters project, which did not allow large numbers of birds to be caught in both seasons. However, there is evidence that individual birds are consistent in the intensity of their colouration, relative to that of other individuals in the population, over months or years. This is true for both carotenoid-based (Pérez-Rodríguez, 2008; Quesada & Senar, 2006b) and melanin-based (Quesada & Senar, 2006b) colouration. Therefore, it was reasonable to assume that the blackbirds with more intense colouration (redder bills and darker feathers) at the time of measurement were those with more intense colouration during the observation periods. The results of the colour-cautiousness comparisons should also be interpreted with caution because the sample sizes were fairly small, since we could only catch a limited number of blackbirds and not all of these were located again during the cautiousness observations. In particular, some banded juveniles probably left the study site as part of post-breeding season dispersal (Higgins et al., 2006).

4.4.1 Feather colouration and cautiousness

There was a weak trend towards blackbirds with darker feathers being more vigilant, which was stronger in the breeding than the non-breeding season, and in juveniles than adults. This could support the compensation hypothesis, if darker blackbirds are under greater risk of predation, and are more vigilant as a means of compensating for this. Similarly, previous studies testing for a relationship between individual colouration and metrics of cautiousness (such as vigilance) have found that more conspicuously coloured individuals were more cautious (Cabido et al., 2009; Martín & López, 1999; McQueen et al., 2017; Pascual et al., 2014a, 2014b). It is possible that this relationship was stronger in juveniles because juvenile birds are often under higher risk of predation than adults (Clewley et al., 2018; Genovart et al., 2010; Hoy et al., 2015), so they may need to compensate more strongly than adults for any additional factors which increase their predation risk. However, there is no evidence that predation risk was higher in the breeding than the non-breeding season (see Section 4.2), so compensation does not explain why the relationship between vigilance and feather darkness was stronger in the breeding season. Darker individuals may be more aggressive, dominant, and involved in intrasexual competition (Ducrest et al., 2008; Jawor & Breitwisch, 2003; Grffith et al., 1999; Roulin, 2016). Therefore, as observing conspecifics is often a component of vigilance (Askenmo et al., 1992; Beauchamp, 2017, 2019; Krebs, 1980; McQueen et al., 2017), it is possible that individuals with darker feathers were more vigilant as they spent more time monitoring the behaviour of other birds. This may explain the seasonal difference in the relationship between feather darkness and vigilance, as the need to monitor conspecifics is expected to be stronger in the breeding season due to greater intrasexual competition and the risk of extrapair paternity (Creighton, 2000a; Halupka & Wysocki, 2004; Reboreda and Fernandez, 1997). Juvenile blackbirds with darker feathers may also have resembled adult blackbirds more, causing them to receive more aggression from adults (Coady & Dawson, 2013; Ligon & Hill, 2009; VanderWerf & Freed, 2003). Therefore, darker juvenile blackbirds may have been more vigilant to monitor adults to avoid aggressive interactions. Darker juveniles may also be more aggressive or dominant themselves and spend more time monitoring conspecifics as a result.

While birds with darker feathers were more vigilant while foraging, they initiated FID later in response to my approach. It is possible that there is a trade-off between these two metrics of cautiousness. Birds which are more vigilant may detect potential predators earlier, meaning they can monitor their approach without needing to flee as early (Hensley et al., 2015). Vigilance and fleeing approaching predators are both costly in terms of energy and lost foraging time (Fortin et al., 2004; Fritz et al., 2002; Lima & Dill, 1990; Martín et al., 2008; McQueen et al., 2017; Rodriguez-Prieto et al., 2009), so it may be advantageous for birds to prioritise one over the other. It is even possible that darker birds prioritise vigilance over FID because they can also monitor conspecifics while vigilant, assuming darker birds are more aggressive (Ducrest et al., 2008; Jawor & Breitwisch, 2003; Grffith et al., 1999; Roulin, 2016). Darker birds may also be less willing to abandon their territories by fleeing, if they have higher quality mates or resources to guard (Cooper, 1999). Similarly, numerous studies have found that birds with darker melanin-based colouration are bolder when responding to predators or novel situations (e.g., Costanzo et al., 2018; Mateos-Gonzalez & Senar, 2012; Quesada & Senar, 2007; van den Brink et al., 2012), so they may have simply been less threatened by my approach. Finally, it is possible that darker birds have higher caloric requirements and are prioritising remaining in a foraging area over fleeing a possible threat, in line with the caloric requirements hypothesis. Further research will be required to tease apart these possibilities.

There was no relationship between feather darkness and distance moved after fleeing. More conspicuously coloured birds may modify other aspects of their behaviour (such as vigilance and FID) because they believe themselves to be more likely to be detected and attacked by a predator, while their conspicuousness may not affect decisions they make after they have already decided to flee. Distance moved may instead be more closely related to other aspects of the escape response, such as FID and type of movement (see Section 4.5.4). Distance moved after fleeing may also have depended on a bird's level of habituation to humans (Bar-Ziv et al., 2023; Tätte et al., 2018), which may be unrelated to its feather colouration.

4.4.2 Bill colouration and cautiousness

Adult female blackbirds with redder bills were less vigilant while foraging and initiated flight later than females with less red bills. These results are counter to the compensation hypothesis, under which female blackbirds with redder bills would be expected to be more cautious to compensate for being more conspicuousness to predators. Other studies which tested for a relationship between individual colouration and cautiousness supported the compensation hypothesis, finding more conspicuous males were more cautious (Cabido et al., 2009; Martín & López, 1999; McQueen et al., 2017; Pascual et al., 2014a, 2014b). However, there was no relationship between cautiousness and individual colouration in female Spanish terrapins, despite males with brighter limb colouration being more cautious (Cabido et al., 2009). None of the other studies tested for a relationship between female colouration and cautiousness. Therefore, my results, alongside those of Cabido et al. (2009), suggest that the relationship between cautiousness and colouration intensity may differ between male and female animals. In female blackbirds, the caloric requirements hypothesis may be responsible for individuals with redder bills being less cautious. Carotenoids must be obtained by foraging (Koch & Hill, 2018; Møller et al., 2000; Weaver et al., 2018) and require energy to absorb, store, transport, and deposit in the relevant tissues (Hill, 2000). Therefore, female blackbirds with redder bills may need to forage more and conserve energy by fleeing later to obtain the carotenoids and energy required for their bill colouration. It is possible female blackbirds with redder bills fled later because they had higher quality mates or territories to defend, and were less willing to leave them (Cooper, 1999). However, they were also less vigilant, which suggests they were not monitoring conspecifics more than females with less red bills (Askenmo et al., 1992; Beauchamp, 2017, 2019; Krebs, 1980; McQueen et al., 2017), as would be expected if they were more involved in territory defence.

Interestingly, there were no relationships between bill colouration and FID or vigilance in male blackbirds. This may indicate that only female blackbirds experience an energetic cost to having redder coloured bills, which supports the caloric requirements hypothesis. Female birds probably have higher energetic requirements than males due to the costs of reproduction (Arizmendi-Mejía et al., 2013; Diniz, 2011; Fogg et al., 2013; Nagy et al., 2007; Post & Götmark, 2006a, 2006b; Powolny et al., 2014). Female birds also transfer large amounts of carotenoids to their eggs, which appears to protect them from oxidative damage (Blount, 2004; McGraw et al., 2005; Nordeide et al., 2013). Therefore, having redder bills may have a greater effect on cautiousness in female blackbirds than males because females require more energy and carotenoids generally. This may also explain why there was no relationship between vigilance and bill redness in juvenile female blackbirds, which may have had lower caloric requirements than adult females if they were not either breeding or recovering from breeding. If carotenoid-based colouration is more costly for female birds than males, this may partially explain why this colouration is usually more intense in males than females (Badyaev & Hill, 2000; Delhey & Peters, 2017). This has implications for the evolution of sexually dichromatic colouration in songbirds more broadly (see Section 4.6.3).

There are other possible explanations for female blackbirds with redder bills being less cautious, although most of these are still related to the caloric requirements hypothesis. Female blackbirds with redder bills may have invested more in reproduction than those with less red bills, resulting in them having higher caloric requirements and lower cautiousness. It is common for female birds with more intense carotenoid-based colouration to be better parents, produce more offspring, or have higher quality offspring (Garcia-Navas et al., 2012; McGraw et al., 2005; Nordeide et al., 2013; Weaver et al., 2018). It is also possible that bill colouration increases with age in female blackbirds, particularly as females in their first year have been shown to have less intense bill colouration than those older than a year (Hatchwell et al., 2001). In this case, female blackbirds with redder bills may invest more in reproduction (and therefore have higher caloric requirements) because they are older, so they have fewer potential breeding seasons left (the 'terminal investment hypothesis'; Clutton-Brock, 1984; Duffield et al., 2017; Velando et al., 2006). Older animals may also be less cautious because they are better at assessing predation risk (Kalb et al., 2019; Kullberg & Lind, 2002; Martín et al., 2008; Rajala et al., 2003). Therefore, it is possible that female blackbirds with redder bills tended to be less cautious because they were older. We were unable to age female blackbirds beyond being in their first year of life or older, so this cannot be ruled out. It is interesting that the relationship between bill redness and cautiousness did not differ by season, but this may have been due to small sample sizes of banded female blackbirds in the breeding season. It is also important to note that female birds may still have higher caloric requirements than males in the non-breeding season (Arizmendi-Mejía et al., 2013; Nagy et al., 2007; Powolny et al., 2014).

Considering the results of previous studies (Cabido et al., 2009; Martín & López, 1999; McQueen et al., 2017; Pascual et al., 2014a, 2014b), it is surprising that there was no relationship between bill redness and either vigilance or FID in male blackbirds. The compensation hypothesis assumes that individuals with more intense colouration perceive themselves as being under higher risk of predation due to being more visible to predators (Pascual et al., 2014a, 2014b). However, blackbird bill colouration may not vary enough between individuals to materially affect their conspicuousness or risk of predation. Therefore, male blackbirds may not need to compensate for having redder bills with increased cautiousness. Male blackbirds may also not be as energetically limited as females due to investing less in reproduction (Creighton, 2000a; Halupka & Wysocki, 2004; Higgins et al., 2006; Ibáñez-Álamo & Soler, 2017; Post & Götmark, 2006a), so males with redder bills may not need to forage or conserve energy more than those with less red bills. If neither caloric requirements nor compensation are influencing the relationship between bill colouration intensity and cautiousness in male blackbirds, the lack of association between the two seems sensible. It is also possible that male blackbirds with redder bills are more efficient foragers or possess higher quality food resources within their territories (Bright & Waas, 2002; Bright et al., 2004; Faivre et al., 2001), allowing them to express more intense bill colouration without reducing their cautiousness. Female blackbirds with redder bills may also be more efficient foragers or possess higher quality territories, but due to their higher caloric requirements this may not be sufficient to prevent them having to prioritise foraging and energy conservation over cautiousness to maintain their colouration.

There was also weak evidence that blackbirds with redder bills of both sexes and age classes moved further after fleeing than those with less red bills. It is possible that female blackbirds with redder bills were compensating for being less vigilant and having shorter FIDs by moving further after fleeing (Hensley et al., 2015; Martín & López, 2003; Martín et al., 2008; see Section 4.5.4). However, as the relationship between distance moved and bill redness did not depend on sex, this result may provide evidence for the compensation hypothesis. Blackbirds with redder bills may be (or perceive themselves to be) more conspicuous to predators than those with less red bills, causing them to move further away from potential threats in an effort to prevent themselves being detected again (Hensley et al., 2015). It may also be that distance moved and bill redness were both correlated with another factor not measured in this study, such as level of habituation to humans, which could have generated a positive relationship between the two.

4.5 Other factors affecting aspects of cautiousness

4.5.1 Body condition and cautiousness

There were no relationships between body condition and vigilance, FID, or distance moved after fleeing. Previous studies have found that animals in worse body condition are less vigilant and forage more, probably because they are attempting to improve their condition at the expense of cautiousness (Bachman, 1993; Fernández-Juricic & Beauchamp, 2008). One study did find a similar lack of relationship between body condition and vigilance, but they do not attempt to interpret this result (Whittingham et al., 2004). Conversely, animals in better body condition are usually found to have shorter FIDs, probably because they are either better able to escape predators at short distances or are investing more in energy in reproduction at the expense of cautiousness (Mohring et al., 2022; Seltmann et al., 2012; but see Kenward, 1978). As most of these studies also calculated body condition as mass corrected for body size (Fernández-Juricic & Beauchamp, 2008; Mohring et al., 2022; Seltmann et al., 2012), it seems unlikely I obtained no relationships between metrics of cautiousness and body condition due to my measure of body condition not being biologically relevant. To my knowledge, a relationship between body condition and distance moved has not previously been tested for in animals.

It is possible I found no relationship between body condition and cautiousness because body condition was measured 0-10 months before the behavioural observations. As body mass changes substantially throughout the year in birds (Arizmendi-Mejía et al., 2013; Askenmo et al., 1992; Nagy et al., 2007), including blackbirds (Lundberg, 1985), my body condition measurements may not have always reflected body condition at the time of observation. It is also possible that reduced cautiousness in birds in worse condition due to the need to forage more to improve their condition (Bachman, 1993; Fernández-Juricic & Beauchamp, 2008) and reduced cautiousness in birds in better condition due to greater investment in reproduction (Mohring et al., 2022; Seltmann et al., 2012) can balance out, resulting in no relationship between condition and cautiousness.

4.5.2 Age and cautiousness

Juvenile blackbirds were consistently more cautious than adults; they initiated flight earlier, moved further, and tended to be more vigilant. This contrasts with previous studies which have found juvenile birds (Boukhriss et al., 2007; Ferguson, 1987; Kalb et al., 2019) and other animals (reviewed in Arenz & Leger, 2000) are less cautious than adults. This is thought to be because they are less aware of danger due to being less experienced with predators (Kalb et al., 2019; Kullberg & Lind, 2002), although juveniles may also have higher nutritional requirements (Arenz & Leger, 2000) or be less territorial (Ferguson, 1987). However, the reverse pattern is also seen, with juvenile animals being more cautious than adults in some species (Arenz & Leger, 2000; Hope et al., 2014; Rajala et al., 2003), including blackbirds (Martín et al., 2008). Juvenile birds are often under higher risk of predation than adults (Clewley et al., 2018; Genovart et al., 2010; Hoy et al., 2015), so increased cautiousness may be a way of compensating for this (Rajala et al., 2003). Juvenile birds may also be less able to assess predation risk accurately than adults due to being less experienced, so it may be beneficial for them to be more cautious in all situations (Lima & Dill, 1990; Martín et al., 2008;

Rajala et al., 2003). Even if increased cautiousness comes at an energetic cost to juvenile birds, it may be worthwhile if it increases their likelihood of surviving to reproduce (Martín et al., 2008).

Interestingly, there was a stronger relationship between FID and distance moved in juvenile than adult blackbirds, with juveniles with shorter FIDs fleeing greater distances. If juvenile blackbirds have higher energetic requirements than adults (Arenz & Leger, 2000), they may trade-off energy expended in fleeing more often and fleeing greater distances more strongly (Martín & López, 2003; Martín et al., 2008). Juvenile female blackbirds were also more vigilant than juvenile males, although the sample sizes were fairly small. Juvenile female blackbirds may be less dominant than juvenile males (Grubb & Woodrey, 1990; Lundberg, 1985) and use vigilance to avoid aggressive interactions with juvenile males or adults. Juvenile male blackbirds also could have had higher caloric requirements than females if they were developing adult bill and feather colouration, which differs from juvenile colouration more than in females (Higgins et al., 2006) and is probably costly to produce (Griffith et al., 2006; Koch & Hill, 2018; Hill, 2000; Møller et al., 2000; Roulin, 2016; Weaver et al., 2018). Therefore, juvenile male blackbirds may have been prioritising foraging over vigilance to obtain the energy required to develop adult colouration.

4.5.3 Habitat cover and cautiousness

There were some effects of habitat cover on metrics of cautiousness in blackbirds and song thrushes. Birds in the open were more vigilant than those in cover. Many studies have found birds are more vigilant when further from cover, which is assumed to be because they perceive themselves as being under higher risk of predation due to being further from safety (Lazarus & Symonds, 1992; Lima & Dill, 1990; Pascual & Senar, 2013). Similarly, birds tended to move further after fleeing when they were in the open than in cover. This may again have been due to birds in the open perceiving themselves as being under greater risk of predation, particularly if they chose to stay in the open rather than fleeing to cover (Stankowich & Blumstein 2005; Wilson & Cooper, 2007). Birds in the open may also have simply needed to flee further to reach protective cover than those already in some type of cover (Tatte et al., 2018). Counter to these results, and most of the literature (Samia et al., 2016; Stankowich & Blumstein 2005), blackbirds and song thrushes initiated flight sooner (had longer FIDs) when they were closer to cover. Birds which were closer to cover may have been those which were more cautious generally or less habituated to humans, causing them to respond more strongly to my approach. It is also possible that birds further from cover compensated for their greater vigilance and distances moved with shorter FIDs (Hensley et al., 2015; Martín & López, 2003; Martín et al., 2008). Finally, fleeing may have been less energetically costly for birds closer to cover because they did not need to move as far to reach safety, allowing them to flee potential threats earlier.

There was also a species difference in the relationship between cover and odds of flying. Blackbirds were more likely to fly (rather than run or hop) when they were further from cover. This may have been because they perceived themselves as being under greater risk of predation when further from cover (Stankowich & Blumstein 2005; Wilson & Cooper, 2007). Martín et al. (2008) also found that blackbirds were more likely to fly when further from cover, although this was non-significant in their study. I found the opposite pattern in song thrushes, in which the odds of flying tended to increase when they were closer to cover. Song thrushes which were foraging nearer to cover may have been those which were more cautious or less habituated to humans than those foraging further away, causing them to respond to my approach more strongly. It is also possible that short flights into cover were less energetically costly for song thrushes than blackbirds because they are smaller and lighter (Congdon, 2010; Higgins et al., 2006; Nudds & Bryant, 2000; Witter & Cuthill, 1993).

4.5.4 Relationships between elements of escape behaviour

There were several significant relationships between the elements of the escape response; starting distance, FID, distance moved, and type of movement. I found a positive relationship between FID and starting distance, as expected from previous studies of birds (Blumstein, 2003, 2010), including blackbirds (Martín et al., 2008; Rodriguez-Prieto et al., 2009). It is thought that FID is related to starting distance because it is beneficial for birds to flee soon after detecting a potential threat to avoid the costs of sustained threat monitoring and of having to use more costly escape strategies (Blumstein, 2003, 2010). The relationship between FID and starting distance was stronger in song thrushes than blackbirds, possibly because they were the more cautious species overall. This relationship was also stronger in the breeding than the non-breeding season, which appears to have been driven by some birds in the breeding season having short FIDs despite long starting distances (Figure 3.3b). These short FIDs may reflect blackbirds and song thrushes generally being less cautious in the breeding than the non-breeding season (see Section 4.2).

Birds with shorter FIDs moved further after fleeing. A negative relationship between FID and distance moved has been obtained in previous studies, although this was either indirect (Martín et al., 2008), or context-dependent (Martín & López, 2003), and is not the norm (Cooper, 2006; Tätte et al., 2018; Wilson & Cooper, 2007). It is possible that blackbirds and song thrushes trade-off FID and distance moved against each other, as higher values of either should reduce predation risk but increase energy expenditure (Martín & López, 2003; Martín et al., 2008). Birds which flee potential threats later (i.e., have shorter FIDs) may also perceive them as more threatening because they are closer, and move further away as a result (Martín et al., 2008). Interestingly, the relationship between FID and distance moved was positive in female blackbirds, while it was negative in male blackbirds and song thrushes. Perhaps female blackbirds which fled earlier moved greater distances because they were generally more cautious individuals (Cooper, 2006; Tätte et al., 2018; Wilson & Cooper, 2007), while male blackbirds and song thrushes trade-off the two elements of the escape response against each other.

Birds which chose to fly, rather than hop or run, moved greater distances, as in Martín et al. (2008). These individuals may have been those which were more cautious in general, opting to reduce predation risk by both flying and moving longer distances (Martín et al., 2008). It also seems sensible that once at bird has decided to fly, which is more energetically costly than running (Butler, 1991), it should maximise the reduction in predation risk it obtains by expending this energy by moving further away from a potential threat. Interestingly, the type of movement selected did not depend on FID. This is contrary to the results of Martín et al. (2008), who found that blackbirds with shorter FIDs were more likely to fly than those with longer FIDs. However, there was still an indirect relationship between FID and type of movement in my study, as birds with shorter FIDs and birds that chose to fly both moved further. This probably reflects a trade-off between different behaviours which reduce predation risk but are energetically costly (Martín & López, 2003; Martín et al., 2008).

4.5.5 Banded status and cautiousness

While vigilance and FID were not affected by banded status, unbanded birds moved further after fleeing than banded birds. It is possible that banded birds represented a subset of the population which was less cautious, more habituated to humans, or were otherwise both more likely to be caught and less responsive to my approach (Perrins, 1971; Remsen & Good, 1996). Birds which were ‘flightier’ (i.e., flew more often) may have been more likely to be caught in the nets (Remsen & Good, 1996) and also to move further after fleeing (as birds which fled by flying moved further than birds which hopped or ran in my study). Banded birds may also have responded less strongly to my approach specifically because they had survived an encounter with me before, although to my knowledge this possibility has not been tested.

4.5.6 Mass and cautiousness

There was no effect of mass on vigilance or FID, but heavier birds moved further after fleeing. This was not because heavier birds were in better condition, as there was no relationship between body condition and distance moved. However, it is possible that heavier birds had greater energy reserves (Labocha & Hayes, 2012; Lima, 1986; Witter & Cuthill, 1993), making it less costly for them to move further away from a potential predator. Within a species, heavier birds are also thought to be easier for predators to catch due to having poorer escape ability (Gosler et al., 1995; Lima, 1986; Witter & Cuthill, 1993). Therefore, heavier blackbirds may have wanted to move further away from a potential predator to deter pursuit or remove themselves from its line of sight. This is similar to the finding that heavier zebra finches *Taeniopygia guttata* increased their flight speed when alarmed, relative to the speed of their routine flights, more than lighter finches (Veasey et al., 1998). Heavier zebra finches, and blackbirds, may perceive themselves as being under higher risk of predation, and compensate for this by responding more strongly when fleeing potential threats.

4.5.7 Visible *Turdus* spp. and cautiousness

There were no relationships between the number of blackbirds and song thrushes visible to the focal bird and any metric of cautiousness. Vigilance often decreases with group size in birds, which is generally attributed to detection and dilution effects (reviewed in Beauchamp, 2003). Birds may also be less cautious in their escape behaviours (such as FID) if they perceive themselves as being safer when there are more conspecifics around (Martín et al., 2008). However, while blackbirds and song thrushes sometimes forage in flocks in Aotearoa, they are territorial for most of the year (Gurr, 1954; Higgins et al., 2006). Blackbirds and song thrushes may have perceived other individuals as a threat most of the time, and any reduction in vigilance due to their presence may have been balanced or exceeded by increased vigilance to monitor their behaviour (Beauchamp, 2017, 2019; Krebs, 1980).

4.5.8 Pause, runtime, and vigilance while foraging

Blackbirds and song thrushes were more vigilant when there were more pauses in the observation. Observations with pauses tended to be those where the focal bird was either highly mobile or encountered a disturbance (e.g., a nearby pedestrian), causing it to move out of my sight temporarily at least once. As human disturbances cause increased vigilance in birds (Fernández-Juricic & Telleria, 2000; Randler, 2006; Ward & Low, 1997), and blackbirds and song thrushes which were very mobile were probably foraging less, it is unsurprising that vigilance increased with the number of pauses in the observation. Similarly, blackbirds and song thrushes tended to be less vigilant during longer observations. Longer observations may have been of birds which were less cautious generally, and therefore both less vigilant and less likely to leave the observation area in response to a disturbance. Birds which did not encounter a disturbance during the observation period may also have both stayed in the area longer and been less vigilant (Fernández-Juricic & Telleria, 2000; Randler, 2006; Ward & Low, 1997). Finally, longer observations may have been those of birds which were settled in a high-quality foraging patch, making them both less likely to leave the area and less vigilant (Lagos et al., 2009; Pays et al., 2012).

4.5.9 Temperature, time of day, and vigilance while foraging

Blackbirds and song thrushes tended to be more vigilant when air temperatures were higher. This is unsurprising, as birds have higher energetic requirements at colder temperatures, causing them to need to forage more at the expense of vigilance (Askenmo et al., 1992; Caraco et al., 1990; Powolny et al., 2014; Pravosudov & Grubb, 1995). Blackbirds and song thrushes were also less vigilant later in the day, although the effect size was small. This may reflect intense foraging late in the afternoon in preparation for dusk (Bonter et al., 2013; McNamara et al., 1994). As I did not begin observations until 2-3 hours after dawn, it is unknown whether the blackbirds and song thrushes in my study exhibited bimodal foraging patterns with peaks at dawn and dusk (McNamara et al., 1994), or foraged consistently through the day until a peak before dusk (Bonter et al., 2013).

4.6 Implications and conclusions

4.6.1 The caloric requirements hypothesis

The majority of my findings provide compelling evidence for what I have termed the caloric requirements hypothesis. Female blackbirds were less vigilant in the breeding than the non-breeding season, which is most logically explained by them needing to forage more to meet elevated caloric requirements associated with reproduction. Male blackbirds and song thrushes also tended to be less cautious in the breeding season, which is unsurprising as birds of both sexes are expected to have higher caloric requirements while breeding than outside of the breeding season. Finally, female blackbirds with redder bills were generally less cautious (lower vigilance and shorter FIDs) than those with less red bills. This was probably because female blackbirds with redder bills had higher caloric requirements in some way. The findings that only female blackbirds were significantly less cautious in the breeding season, and that only female blackbirds with redder bills were less cautious, can be readily explained by female birds having higher caloric requirements associated with reproduction than males. Blackbirds with darker feathers also had shorter FIDs, which could be explained by the caloric requirements hypothesis if they are attempting to conserve energy to compensate for the costs of producing and maintaining this colouration.

However, I did not find support for all the predictions of the caloric requirements hypothesis. Blackbirds with darker feathers were not consistently less cautious, and blackbirds with redder bills moved further after fleeing. This may have been due to trade-offs between different types of antipredator behaviour, or some effect of the compensation hypothesis. There were also few significant differences in antipredator behaviour between male and female blackbirds, although females tended to be less cautious than males. This may have been due to the sexes having similar caloric requirements during some of the year, particularly while feeding nestlings and fledglings. Finally, the difference in cautiousness between male and female blackbirds did not increase in the breeding season, relative to the non-breeding season. What my results suggest instead is that both sexes had higher caloric requirements in the breeding season, maintaining a similar relationship between sex and cautiousness across seasons. However, the caloric requirements of female blackbirds do appear to change across seasons more than in males, as only female blackbirds were significantly less vigilant in the breeding than the non-breeding season.

4.6.2 The compensation hypothesis

My evidence for the compensation hypothesis was mixed and inconclusive. Song thrushes were more cautious than blackbirds, despite being the less conspicuous species. Female blackbirds tended to be less cautious than males, which could support the compensation hypothesis, but may just as easily be the result of caloric requirement differences. Blackbirds with darker feathers were more vigilant while foraging, and blackbirds with redder bills moved further after fleeing, but blackbirds with redder bills and darker feathers were not consistently less cautious across all metrics tested (vigilance, FID, and distance moved). My thesis certainly does not disprove the compensation hypothesis, particularly as there is already extensive evidence from the literature that more conspicuously coloured species, sexes, and individuals are more cautious. However, it also fails to find unequivocal evidence in support of it in blackbirds and song thrushes. Perhaps stronger evidence for the compensation hypothesis will be found in species where sexes and individuals differ more in colouration, as blackbirds only possess “intermediate” sexual dichromatism (Armenta et al., 2008; Ibáñez-Álamo & Soler, 2017) and intrasexual differences in colouration are not as drastic as in species where there are multiple colour morphs. As there was only mixed evidence that more conspicuous birds were more cautious, my thesis also fails to conclusively support the idea that more conspicuous birds use their colouration to signal that they are more difficult to catch (which would fall under the unprofitable prey hypothesis).

While my results did not strongly support the compensation hypothesis, they do not refute the idea that the combined compensation-caloric requirements hypothesis represents an additional cost of conspicuous colouration to female birds. As female blackbirds with redder bills were less cautious than those with less red bills, these individuals may indeed have been unable to increase their cautiousness to compensate for any additional conspicuousness conferred by their colouration. This was not something I was able to directly test for in my thesis but represents an interesting direction for future work.

4.6.3 The evolution of sexual dichromatism

Recent analyses indicate that females are less colourful and there is greater sexual dichromatism in bird species where males contribute less to parental care (Dale et al., 2015; Dunn et al., 2015; Fargevieille et al., 2023; but see Matysioková et al., 2017). However, attempts to provide a mechanism for this finding have been inconclusive, particularly in socially monogamous species. Evidence for the nest predation hypothesis is mixed, and nest location or time spent by each sex at the nest are not consistently related to the level of sexual dichromatism in birds (Dunn et al., 2015; Fargevieille et al., 2023; Haskell, 1996; Matysioková et al., 2017; Soler & Moreno, 2012). My results support the caloric requirements hypothesis as a potential mechanism for the evolution of sexual dichromatism and female colouration in birds. Female birds may be unable to bear the costs of both conspicuous colouration and high caloric requirements when males contribute little to parental care. However, the reproductive caloric requirements of female birds are expected to decrease when males contribute more to parental care, which may allow them to express more conspicuous colouration. Therefore, the caloric requirements hypothesis can explain the negative relationship between the extent of sexual dichromatism and the level of male parental care. There is less evidence for the combined caloric requirements-compensation hypothesis from my results, although it may also influence the evolution of sexual dichromatism.

Female birds tend to be more colourful and sexual dichromatism lower in the tropics (Dale et al., 2015; Dunn et al., 2015; Macedo et al., 2008). This can be attributed to greater social selection on tropical females due to increased resource competition and male mate choice (Dunn et al., 2015; Macedo et al., 2008). However, it is also possible that caloric requirements are less limiting on female birds in the tropics than in temperate regions because they lay smaller clutches, receive more parental assistance from males, and have stable year-round access to resources (Dale et al., 2015; Dunn et al., 2015; Macedo et al., 2008). Female birds in the tropics may be more colourful because they are under greater social selection but may only be able to actually evolve conspicuous colouration because they are less constrained by caloric requirements. A recent analysis by Fargevieille et al. (2023) found that female chromaticity increases with the extent of male parental care when egg production is low. However, female birds appear to eventually reach a point where they can no longer keep increasing egg production without becoming less colourful, regardless of the level of male parental investment. This strongly suggests some role of caloric requirements in the evolution of female colouration. Female birds are able to be more colourful when males assist more in parental care, reducing their reproductive caloric requirements, but eventually the caloric requirements involved with egg production will trade-off with those associated with producing and maintaining that colouration. Of course, caloric requirements are probably not the only determinant of the extent of sexual dichromatism in birds, with factors such as whether the species is migratory and the strength of sexual selection probably relevant too (Dale et al., 2015; Dunn et al., 2015; Fargevieille et al., 2023; Macedo et al., 2008; Matysioková et al., 2017).

It is interesting that only carotenoid-based colouration appears to be more costly for female blackbirds than males. Female blackbirds may be generally more carotenoid-limited than males due to allocating carotenoids to egg production, with no such difference in melanin requirements. Birds must also obtain carotenoids from their diet, while they can synthesise melanins themselves. Therefore, it is possible that only carotenoid-based colouration forces female birds to forage more, at the expense of cautiousness. Carotenoid-based colouration may also be more costly for birds, including blackbirds, to produce and maintain than melanin-based colouration, although this claim is debated (Griffith et al., 2006). Finally, bill colouration is the most intense early in the breeding season in male blackbirds (Delhey et al., 2010), and probably also in females, which coincides with the time when the reproductive caloric requirements of females are probably highest. Conversely, blackbirds moult in late summer and autumn in Aotearoa, after the breeding season (Gurr, 1954; Higgins et al., 2006), so carotenoid-based colouration may be more costly for female blackbirds to produce than melanin-based colouration simply due to the timing of investment. Regardless of the mechanism, my results indicate that expressing and maintaining carotenoid-based colouration is more costly for female birds than melanin-based colouration. This may explain why sexual dichromatism driven by carotenoid colouration is usually more extreme than that driven by melanin-based colouration in birds (Badyaev & Hill, 2000; Delhey & Peters, 2017). As melanin-based colouration is usually lighter in female birds than males, there may also be some difference in the costs of producing this colouration between the sexes, which I was unable to detect in this thesis. Perhaps, as darker birds are usually more aggressive and probably receive more aggression from conspecifics themselves, female birds tend to be lighter as a way of avoiding aggression from males.

4.6.4 Individual colouration, quality, and honest signalling

Carotenoid-based colouration appears costly for female blackbirds, so it may be an honest indication of female quality. Only female blackbirds which are efficient foragers, possess high quality territories, or are otherwise high quality may be able to express high levels of carotenoid-based colouration in their bills due to these costs. Female birds with more intense carotenoid-based colouration do tend to be more successful in reproduction, perhaps due to their higher quality (Garcia-Navas et al., 2012; McGraw et al., 2005; Nordeide et al., 2013; Weaver et al., 2018). This should favour the evolution of male mate choice for females with intensely coloured bills, which has not been tested for in blackbirds. My thesis did not find evidence that melanin-based colouration in blackbirds of both sexes, or carotenoid-based bill colouration in male blackbirds, was similarly costly to female bill colouration. There was also no relationship between carotenoid-based or melanin-based colouration in blackbirds and one index of individual quality, body condition. Despite this, previous work suggests that bill colouration in male blackbirds may be costly and signal individual quality in some way; this may just be unrelated to cautiousness and foraging behaviour. If darker feather colouration in blackbirds is not costly to produce or associated with individual quality in any way, it is unlikely to have evolved as a signal of quality or to play any role in intraspecific interactions. As feather darkness did not vary much between individuals of the same sex and species in my study, variation may simply be genetic or related to time since moult. However, I cannot rule out that darker feathers are costly for blackbirds in another way, especially since producing and maintaining melanin-based colouration is thought to have some costs for birds.

4.6.5 Future directions

This thesis highlights several areas for future research. To better understand the role of carotenoid-based and melanin-based colouration in blackbirds, more research examining whether female bill colouration and feather darkness in either sex are related to mate choice, dominance in intrasexual interactions, and/or individual quality is necessary. In birds more broadly, more studies which test the caloric requirements hypothesis are required. Most of the evidence that female birds have higher caloric requirements than males or while breeding (including that presented in this thesis) is indirect, relying on inferences from antipredator and foraging behaviour. Research which models or measures the caloric requirements of male and female birds during both the breeding and non-breeding seasons may be able to provide more direct evidence for caloric requirement differences. Alongside this, more studies should record foraging behaviour and cautiousness in the same population of birds in both the breeding and non-breeding seasons, which allows more conclusive (although still indirect) evidence for the caloric requirements hypothesis to be gathered. As my thesis is the first to test for a relationship between female colouration intensity and cautiousness in birds, future research is also required on this topic. If the results of these studies confirm that female birds tend to have higher caloric requirements than males, and conspicuous colouration is more costly for female birds than males, the caloric requirements hypothesis may be a powerful mechanism to explain patterns of sexual dichromatism and female colouration in birds. Finally, I would like to stress the importance of considering both the caloric requirements and compensation hypotheses when studying the effect of colouration on antipredator cautiousness. Studies which can conclusively attribute their results to one or the other, or both acting together, will be particularly valuable in understanding the relationships between colouration, predation, and cautiousness in animals.

4.6.6 Conclusion

Overall, my thesis provides compelling evidence for the caloric requirements hypothesis. Female birds are less cautious while breeding and when they have more intense carotenoid-based bill colouration than the reverse. I found more mixed support for the compensation hypothesis, but do not rule out the possibility that both the compensation and caloric requirements hypothesis are influencing antipredator behaviour in blackbirds. I suggest that it is more costly for female birds than males to express intense colouration because they already face higher caloric requirements. Therefore, it may be less beneficial for female birds to express intense colouration than males, even when they stand to benefit from this colouration through social selection. This may contribute to the evolution of sexual dichromatism in birds and help to explain why males are often more colourful even in socially monogamous songbirds. Colouration intensity, particularly of carotenoid-based colouration, may also be a particularly honest signal of quality in female birds due to being costly to express.

Chapter 5 References

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Chapter 6 Supplementary Information

6.1 Principal Component Analyses (PCAs)

6.1.1 Bill colouration

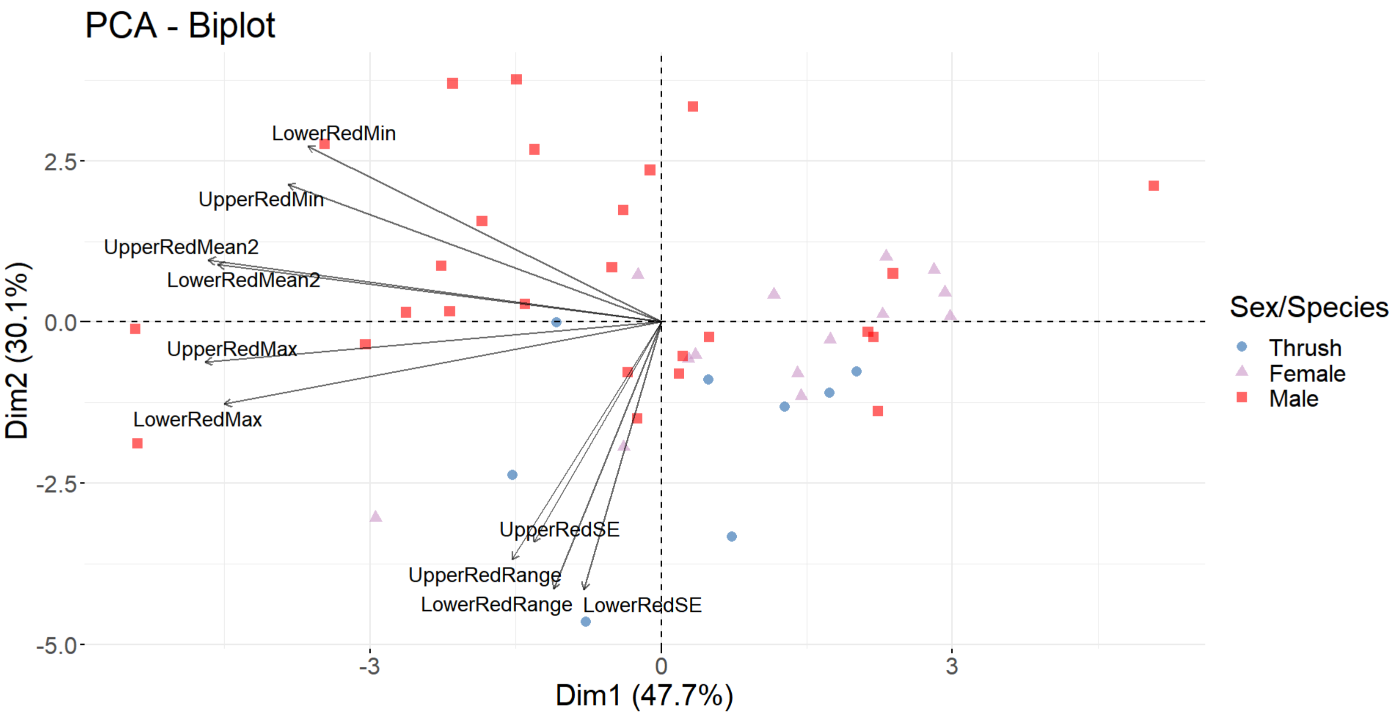

Figure 6.1. Biplot of a Principal Component Analysis (PCA) run on bill colouration data collected from Eurasian blackbirds and song thrushes. The arrows represent summary statistics calculated from red reflectances measured from photographs of the bird's bills using the micaToolbox (Troscianko & Stevens, 2015), see Section 2.7 for details. These summary statistics were mean, minimum (Min), maximum (Max), range, and standard error of the mean (SE), which were calculated for each mandible (upper and lower) of each bird. Dimension one was considered to represent a bill 'redness' score, due to higher values of this component being associated with lower values of most of these metrics, and thus less red bills. The sign of this score was reversed for analyses so that higher values were associated with redder bills.

Table 6.1. Eigenvalues, percentages of variance explained, and cumulative percentages of variance explained for each dimension of a Principal Component Analysis (PCA) run on bill colouration data collected from Eurasian blackbirds and song thrushes.

	Eigenvalue	Variance (%)	Cumulative Variance (%)
Dim 1	4.768	47.676	47.676
Dim 2	3.014	30.144	77.820
Dim 3	1.600	15.999	93.819
Dim 4	0.539	5.385	99.204
Dim 5	0.030	0.300	99.504
Dim 6	0.020	0.202	99.706
Dim 7	0.017	0.171	99.878
Dim 8	0.012	0.122	100
Dim 9	0	0	100
Dim 10	0	0	100

Table 6.2. Percentage contributions of each variable to each dimension in a Principal Component Analysis (PCA) run on bill colouration data collected from Eurasian blackbirds and song thrushes. The bill colouration variables measured were mean (Mean2), minimum (Min), maximum (Max), range, and standard error of the mean (SE) for both mandibles (upper and lower) of each individual bird.

	Dim 1	Dim 2	Dim 3	Dim 4	Dim 5	Dim 6	Dim 7	Dim 8	Dim 9	Dim 10
UpperRedMean2	18.294	1.235	0.138	13.667	16.709	38.330	11.613	0.013	0	0
UpperRedSE	1.453	15.486	27.904	1.348	2.776	21.187	29.495	0.350	0	0
UpperRedMax	18.543	0.506	0.326	16.835	7.848	2.503	10.898	0.593	5.904	36.044
UpperRedMin	12.427	6.066	8.710	15.006	2.843	18.028	0.00004	0.077	5.186	31.657
UpperRedRange	1.988	18.033	22.023	0.442	2.950	11.366	21.476	0.514	2.985	18.224
LowerRedMean2	17.535	1.054	0.234	21.650	22.648	4.217	5.252	27.410	0	0
LowerRedSE	0.540	22.840	16.721	1.413	14.848	2.157	13.055	28.425	0	0
LowerRedMax	17.036	2.150	2.281	15.397	1.452	0.038	0.098	25.532	30.947	5.070
LowerRedMin	11.145	9.862	5.535	14.101	18.419	1.281	4.647	2.410	28.012	4.589
LowerRedRange	1.039	22.767	16.127	0.142	9.507	0.894	3.466	14.676	26.965	4.417

6.1.2 Feather colouration

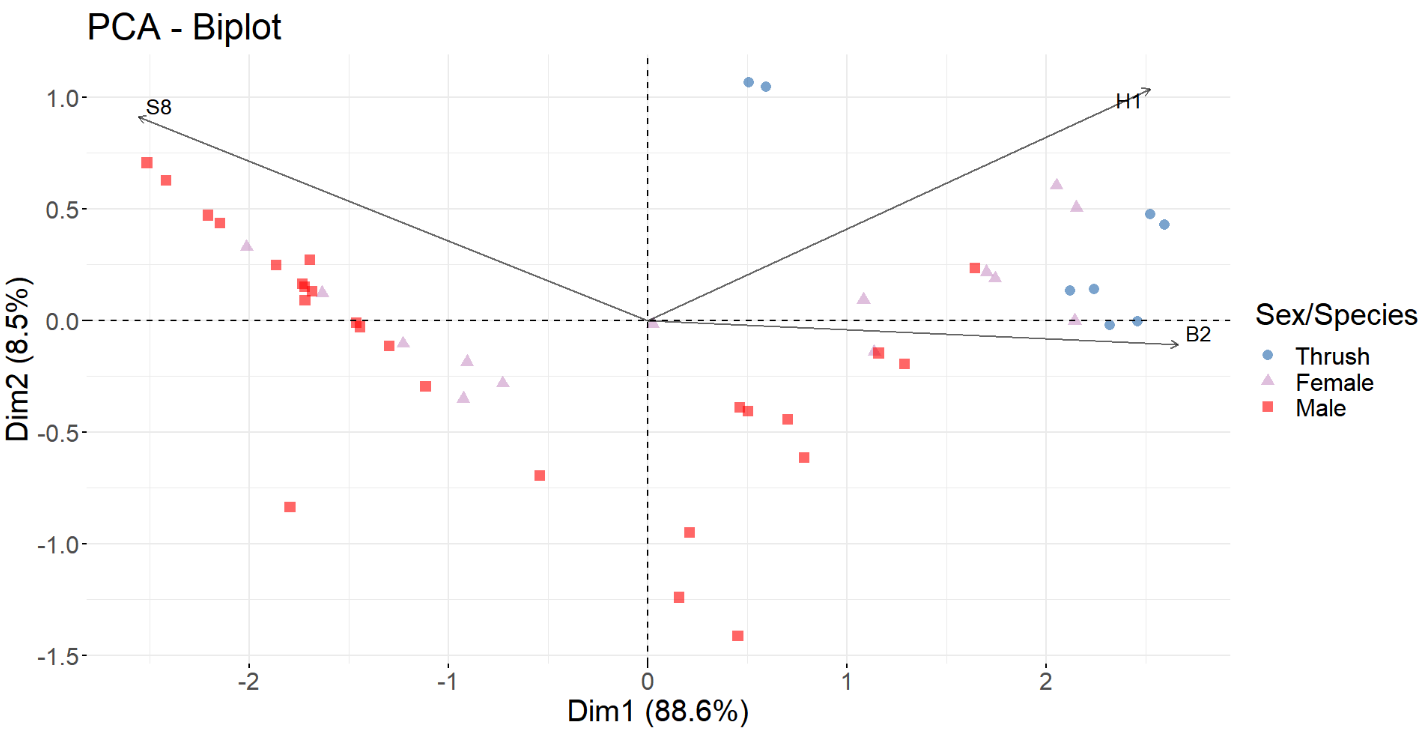

Figure 6.2. Biplot of a Principal Component Analysis (PCA) run on feather colouration data collected from Eurasian blackbirds and song thrushes (see Section 2.8 for details). The arrows represent chroma (S8), hue (H1), and mean brightness (B2), computed using the 'pavo' (Maia et al., 2019) package in R. Dimension one was considered to represent a feather 'darkness' score, due to higher values being associated with higher brightness and hue, and lower chroma. The sign of this score was reversed for analyses so that higher values were associated with darker feathers.

Table 6.3. Eigenvalues, percentages of variance explained, and cumulative percentages of variance explained for each dimension of a Principal Component Analysis (PCA) run on feather colouration data collected from Eurasian blackbirds and song thrushes.

	Eigenvalue	Variance (%)	Cumulative Variance (%)
Dim 1	2.659	88.639	88.639
Dim 2	0.256	8.520	97.159
Dim 3	0.085	2.841	100

Table 6.4. Percentage contributions of variables to each dimension in a Principal Component Analysis (PCA) run on feather colouration data collected from Eurasian blackbirds and song thrushes. The variables were mean brightness (B2), chroma (S8), and hue (H1).

	Dim1	Dim2	Dim3
B2	35.500	0.594	63.906
S8	32.669	43.372	23.959
H1	31.831	56.034	12.135

6.1.3 Vigilance

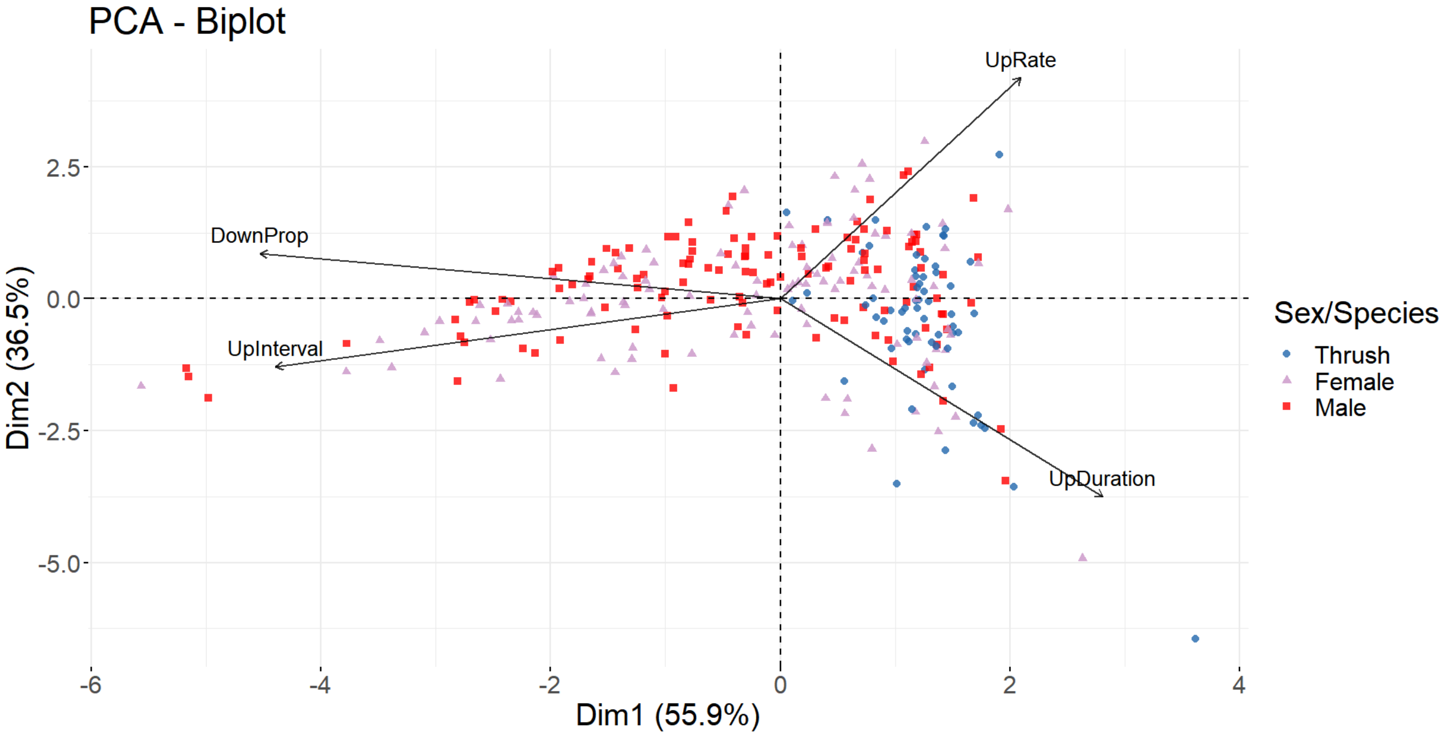

Figure 6.3. Biplot of a Principal Component Analysis (PCA) run on vigilance data collected from foraging Eurasian blackbirds and song thrushes. The arrows represent DownProp (proportion of time with head down), UpRate (average head up rate; raises per minute), UpInterval (average interval between head raises, in seconds), and UpDuration (average head up duration, in seconds). Dimension one was considered to represent a ‘vigilance score’, as higher values are associated with higher head up rates, longer head up durations, shorter head up intervals, and less time with head down.

Table 6.5. Eigenvalues, percentages of variance explained, and cumulative percentages of variance explained for each dimension of a Principal Component Analysis (PCA) run on vigilance data collected from foraging Eurasian blackbirds and song thrushes.

	Eigenvalue	Variance (%)	Cumulative Variance (%)
Dim 1	2.237	55.913	55.913
Dim 2	1.460	36.511	92.424
Dim 3	0.172	4.302	96.727
Dim 4	0.131	3.273	100

Table 6.6. Percentage contributions of each variable to each dimension in a Principal Component Analysis (PCA) run on vigilance data collected from foraging Eurasian blackbirds and song thrushes. The variables were DownProp (proportion of time with head down), UpRate (average head up rate; raises per minute), UpInterval (average interval between head raises, in seconds), and UpDuration (average head up duration, in seconds).

	Dim 1	Dim 2	Dim 3	Dim 4
DownProp	39.378	2.175	26.765	31.683
UpRate	8.410	51.570	15.415	24.604
UpInterval	37.065	4.888	57.470	0.577
UpDuration	15.147	41.367	0.350	43.136

6.2 Head down proportion analysis

Table 6.7. Results of a Linear Mixed Model (LMM) testing for relationships between factors and the proportions of time Eurasian blackbirds and song thrushes spent with their heads down while foraging, alongside variance attributed to the random effects of individual ID and date of observation. Factors include sex/species (male blackbird, female blackbird, or song thrush), season (breeding/B or non-breeding/NB), cover (open or cover), pause (the number of times the observation was paused), temp (air temperature, in °C), and time (the time the observation began, in minutes since midnight). Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	DownProp ~ Sex*Season + Cover + Pause + Temp*Time + (1|ID) + (1|Date)					
Predictors	*Estimates*	*CI*	*std. Error*	*df*	*Statistic*	*p*
(Intercept)	1.08	0.25 – 1.91	0.42	268.60	2.57	**0.011 ***
Sex	-	-	-	-	42.66	**<0.001 *****
Sex [Female - Thrush]	0.29	0.20 – 0.37	0.04	256.02	6.96	**<0.001 *****
Sex [Male - Thrush]	0.32	0.24 – 0.40	0.04	208.18	7.75	**<0.001 *****
Season	-	-	-	-	4.90	**0.031 ***
Season [B - NB]	0.10	-0.05 – 0.26	0.08	154.29	1.30	0.197
Cover	-	-	-	-	25.51	**<0.001 *****
Cover [Cover - Open]	0.19	0.11 – 0.26	0.04	273.24	5.05	**<0.001 *****
Pause	-0.07	-0.10 – -0.03	0.02	275.10	-3.94	**<0.001 *****
Temp	-0.06	-0.10 – -0.01	0.02	269.43	-2.51	**0.013 ***
Time	-0.00	-0.00 – 0.00	0.00	272.64	-1.32	0.189
Sex × Season	-	-	-	-	2.28	0.104
Sex [Female] × Season [B]	0.09	-0.05 – 0.24	0.07	262.48	1.26	0.209

Sex [Male] × Season [B]	-0.03	-0.17 – 0.12	0.07	262.18	-0.34	0.730
Temp × Time	0.00	-0.00 – 0.00	0.00	275.17	1.91	**0.057 .**
Random Effects						
Residual effect	0.04					
ID effect	0.00					
Date effect	0.01					
Observations	287					
Marginal R^2 / Conditional R^2	0.367 / 0.504					
Terms dropped (in order): Location, Weather, Sex:Cover, Sex:Distance, Season:Time:Temp, Runtime, PauseProp, SameSpecies, Banded OtherSpecies, Season:Time, Distance, Season:Temp						

6.3 Head up rate analysis

Table 6.8. Results of a Linear Mixed Model (LMM) testing for relationships between factors and the head up rates (number of head raises per minute) of foraging Eurasian blackbirds and song thrushes, alongside variance attributed to the random effects of individual ID and date of observation. Factors include sex/species (male blackbird, female blackbird, or song thrush), season (breeding/B or non-breeding/NB), cover (open or cover), runtime (the length of the observation, in seconds), pause (the number of times the observation was paused), otherspecies (the number of individuals of the other *Turdus* species (blackbird or song thrush) visible to the focal individual during the observation period), and temp (air temperature, in °C). Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	UpRate ~ Sex*Season + Cover + Runtime + Pause + OtherSpecies + Season*Temp + (1|ID) + (1|Date)					
Predictors	*Estimates*	*CI*	*std. Error*	*df*	*Statistic*	*p*
(Intercept)	4.00	2.55 – 5.45	0.73	86.66	5.49	**<0.001 *** **
Sex	-	-	-	-	2.16	0.119
Sex [Female - Thrush]	0.28	-0.29 – 0.85	0.29	239.70	0.97	0.333
Sex [Male - Thrush]	0.41	-0.16 – 0.97	0.29	201.22	1.43	0.155
Season	-	-	-	-	3.64	**0.059 .**
Season [B - NB]	-2.92	-5.92 – 0.08	1.51	95.99	-1.93	**0.056 .**
Cover	-	-	-	-	4.99	**0.026 ***
Cover [Cover - Open]	-0.48	-0.91 – -0.06	0.22	266.93	-2.23	**0.026 ***
Runtime	-0.00	-0.00 – -0.00	0.00	255.08	-3.77	**<0.001 *** **
Pause	0.62	0.43 – 0.82	0.10	259.40	6.27	**<0.001 *** **
OtherSpecies	0.22	0.02 – 0.43	0.10	265.01	2.18	**0.030 ***
Temp	-0.05	-0.13 – 0.03	0.04	61.41	-1.29	0.202

Sex × Season	-	-	-	-	0.18	0.833
Sex [Female] × Season [B]	0.01	-0.86 – 0.88	0.44	257.87	0.03	0.980
Sex [Male] × Season [B]	0.19	-0.66 – 1.04	0.43	255.12	0.45	0.656
Season × Temp	-	-	-	-	3.37	**0.070 .**
Season [B] × Temp	0.13	-0.01 – 0.27	0.07	86.09	1.84	**0.070 .**
Random Effects						
Residual effect	1.19					
ID effect	0.20					
Date effect	0.09					
Observations	279					
Marginal R^2 / Conditional R^2	0.200 / 0.360					
Terms dropped (in order): Location, Weather, Sex:Distance, Sex:Cover, SameSpecies, Season:Time:Temp, Season:Time, Temp:Time, Time, PauseProp, Banded, Distance						

6.4 Head up interval analysis

Table 6.9. Results of a Linear Mixed Model (LMM) testing for relationships between factors and the average head up intervals (number of seconds between head raises) of foraging Eurasian blackbirds and song thrushes, alongside variance attributed to the random effects of individual ID and date of observation. Factors include sex/species (male blackbird, female blackbird, or song thrush), season (breeding/B or non-breeding/NB), cover (open or cover), runtime (the length of the observation, in seconds), pause (the number of times the observation was paused), temp (air temperature, in °C), and time (the time the observation began, in minutes since midnight). The values in the table have been back-transformed from the log scale. Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

	log(UpInterval) ~ Sex*Season + Cover + Runtime + Pause + Season*Temp + Temp*Time + (1|ID) + (1|Date)					
Predictors	*Estimates*	*CI*	*std. Error*	*df*	*Statistic*	*p*
(Intercept)	27.82	1.72 – 450.91	39.36	263.20	2.35	**0.019 ***
Sex	-	-	-	-	29.87	**<0.001 *****
Sex [Female - Thrush]	2.23	1.69 – 2.94	0.31	257.05	5.73	**<0.001 *****
Sex [Male - Thrush]	2.16	1.64 – 2.85	0.30	209.49	5.47	**<0.001 *****
Season	-	-	-	-	7.21	**0.008 ****
Season [B - NB]	10.72	1.62 – 70.88	10.22	112.09	2.49	**0.014 ***
Cover	-	-	-	-	15.92	**<0.001 *****
Cover [Cover - Open]	1.66	1.29 – 2.13	0.21	272.93	3.99	**<0.001 *****
Runtime	1.00	1.00 – 1.00	0.00	263.82	1.89	**0.060 .**
Pause	0.69	0.61 – 0.77	0.04	271.96	-6.51	**<0.001**
Temp	0.87	0.75 – 1.01	0.07	262.05	-1.78	**0.075 .**
Time	1.00	0.99 – 1.00	0.00	264.00	-1.29	0.199
Sex × Season	-	-	-	-	0.99	0.373

Sex [Female] × Season [B]	1.40	0.85 – 2.30	0.35	263.44	1.33	0.184
Sex [Male] × Season [B]	1.17	0.71 – 1.90	0.29	263.89	0.62	0.538
Season × Temp	-	-	-	-	6.04	**0.016 ***
Season [B] × Temp	0.90	0.82 – 0.98	0.04	101.45	-2.46	**0.016 ***
Temp × Time	1.00	1.00 – 1.00	0.00	269.76	1.88	**0.061 .**
Random Effects						
Residual effect	0.40					
ID effect	0.06					
Date effect	0.06					
Observations	287					
Marginal R^2 / Conditional R^2	0.359 / 0.511					

Terms dropped (in order): Location, Weather, Sex:Distance, Season:Time:Temp, Season:Time, Sex:Cover, OtherSpecies, SameSpecies, Banded, Distance

6.5 Head up duration analysis

Table 6.10. Results of a Linear Mixed Model (LMM) testing for relationships between factors and the average head up durations (in seconds) of foraging Eurasian blackbirds and song thrushes, alongside variance attributed to the random effects of individual ID and date of observation. Factors include sex/species (male blackbird, female blackbird, or song thrush), season (breeding/B or non-breeding/NB), cover (open or cover), temp (air temperature, in °C), and time (the time the observation began, in minutes since midnight). The values in the table have been back-transformed from the log scale. Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	log(UpDuration) ~ Sex*Season + Cover + Temp*Time + (1|ID) + (1|Date)					
Predictors	*Estimates*	*CI*	*std. Error*	*df*	*Statistic*	*p*
(Intercept)	1.86	0.15 – 22.54	2.36	264.31	0.49	0.624
Sex	-	-	-	-	28.18	**<0.001 *** **
Sex [Female - Thrush]	0.55	0.43 – 0.71	0.07	251.26	-4.73	**<0.001 *** **
Sex [Male - Thrush]	0.44	0.35 – 0.57	0.05	182.73	-6.55	**<0.001 *** **
Season	-	-	-	-	4.43	**0.040 * **
Season [B - NB]	0.80	0.51 – 1.25	0.18	151.33	-0.99	0.325
Cover	-	-	-	-	13.44	**<0.001 *** **
Cover [Cover - Open]	0.66	0.53 – 0.83	0.07	276.07	-3.67	**<0.001 *** **
Temp	1.17	1.02 – 1.34	0.08	266.57	2.30	**0.022 * **
Time	1.00	1.00 – 1.00	0.00	269.35	1.16	0.248
Sex × Season	-	-	-	-	2.75	**0.066 .**
Sex [Female] × Season [B]	0.70	0.45 – 1.09	0.16	261.41	-1.58	0.116
Sex [Male] × Season [B]	1.03	0.67 – 1.59	0.23	259.51	0.13	0.895
Temp × Time	1.00	1.00 – 1.00	0.00	274.42	-1.72	**0.086 .**

Random Effects	
Residual effect	0.34
ID effect	0.03
Date effect	0.05
Observations	287
Marginal R^2 / Conditional R^2	0.262 / 0.401

Terms dropped (in order): Weather, Location, Sex:Cover, Pause, Sex:Distance, Distance, Season:Time:Temp, SameSpecies, Banded, PauseProp, Season:Time, Season:Temp, Runtime, OtherSpecies

6.6 Vigilance score post-hoc analysis

Table 6.11. Post-hoc analysis of the relationships between the vigilance of foraging Eurasian blackbirds and song thrushes, their sex/species, and the season. Vigilance is a vigilance score (PC1) obtained from a Principal Component Analysis (PCA), with higher values representing greater vigilance. Sex/species was either male (male blackbird), female (female blackbird), or thrush (song thrush), while season was either B (breeding) or NB (non-breeding). p-values were computed based on a Linear Mixed Model (LMM), using the emm function from the 'emmeans' package within the glht function from the 'multcomp' package, with single-step adjustment for multiple comparisons. Post-hoc tests on sex and sex:season were run separately but are presented in a single table. Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	Estimate	lwr	upr	Std. Error	t value	Pr(> | t|)
Thrush - Female	1.563	1.041	2.085	0.221	7.060	**<0.001 *****
Thrush - Male	1.365	0.851	1.880	0.218	6.260	**<0.001 *****
Female - Male	-0.198	-0.603	0.207	0.172	-1.152	0.480
Thrush NB - Female NB	1.358	0.677	2.039	0.240	5.669	**<0.001 *****
Thrush NB - Male NB	1.480	0.804	2.156	0.238	6.229	**<0.001 *****
Thrush NB - Thrush B	0.677	-0.588	1.942	0.445	1.522	0.627
Thrush NB - Female B	2.445	1.350	3.540	0.385	6.353	**<0.001 *****
Thrush NB - Male B	1.927	0.879	2.976	0.369	5.229	**<0.001 *****
Female NB - Male NB	0.122	-0.486	0.731	0.214	0.572	0.992
Female NB - Thrush B	-0.681	-1.891	0.528	0.425	-1.602	0.573
Female NB - Female B	1.087	0.075	2.100	0.356	3.056	**0.028 ***
Female NB - Male B	0.569	-0.404	1.543	0.342	1.664	0.532
Male NB - Thrush B	-0.804	-2.038	0.431	0.434	-1.851	0.411
Male NB - Female B	0.965	-0.083	2.013	0.368	2.620	**0.089 .**
Male NB - Male B	0.447	-0.546	1.440	0.349	1.281	0.777
Thrush B - Female B	1.769	0.727	2.811	0.366	4.829	**<0.001 *****
Thrush B - Male B	1.251	0.229	2.273	0.359	3.481	**0.007 ****

Female B - Male B	-0.518	-1.259	0.223	0.260	-1.990	0.329

6.7 Proportion of observations complete post-hoc analysis

Table 6.12. Post-hoc analysis of the relationships between the proportions of complete vigilance observations (over three minutes in length) of foraging Eurasian blackbirds and song thrushes, their sex/species, and the season. Sex/species was either male (male blackbird), female (female blackbird), or thrush (song thrush), while season was either B (breeding) or NB (non-breeding). p-values were computed based on a linear model, using the emm function from the ‘emmeans’ package within the glht function from the ‘multcomp’ package, with single-step adjustment for multiple comparisons. Post-hoc tests on sex and sex:season were run separately but are presented in a single table. Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	Estimate	lwr	upr	Std. Error	t value	Pr(> | t|)
Female - Male	-0.021	-0.082	0.039	0.010	-2.076	0.297
Female - Thrush	-0.040	-0.101	0.020	0.010	-3.906	0.107
Male - Thrush	-0.019	-0.079	0.042	0.010	-1.830	0.352
Female B - Male B	-0.021	-0.095	0.052	0.010	-2.076	0.406
Female B - Thrush B	-0.040	-0.114	0.034	0.010	-3.906	0.153
Female B - Female NB	-0.081	-0.141	-0.021	0.008	-9.652	**0.028 ***
Female B - Male NB	-0.102	-0.198	-0.007	0.013	-7.713	**0.044 ***
Female B - Thrush NB	-0.121	-0.216	-0.026	0.013	-9.130	**0.031***
Male B - Thrush B	-0.019	-0.093	0.055	0.010	-1.830	0.473
Male B - Female NB	-0.060	-0.155	0.036	0.013	-4.496	0.120
Male B - Male NB	-0.081	-0.141	-0.021	0.008	-9.652	**0.028 ***
Male B - Thrush NB	-0.100	-0.195	-0.005	0.013	-7.522	**0.046 ***
Thrush B - Female NB	-0.041	-0.136	0.054	0.013	-3.079	0.229
Thrush B - Male NB	-0.062	-0.157	0.033	0.013	-4.687	0.111
Thrush B - Thrush NB	-0.081	-0.141	-0.021	0.008	-9.652	**0.028 ***
Female NB - Male NB	-0.021	-0.095	0.052	0.010	-2.076	0.406
Female NB - Thrush NB	-0.040	-0.114	0.034	0.010	-3.906	0.153
Male NB - Thrush NB	-0.019	-0.093	0.055	0.010	-1.830	0.473

6.8 FID post-hoc analysis

Table 6.13. Post-hoc analysis of the relationships between the Flight Initiation Distances (FIDs) of Eurasian blackbirds and song thrushes, their sex/species, and the season. FID represents the distance between a blackbird and an approaching human at which the bird first took evasive action such as running or flying away. Sex/species was either male (male blackbird), female (female blackbird), or thrush (song thrush), while season was either B (breeding) or NB (non-breeding). p-values were computed based on a Linear Mixed Model (LMM), using the emm function from the 'emmeans' package within the glht function from the 'multcomp' package, with single-step adjustment for multiple comparisons. Post-hoc tests on sex and sex:season were run separately but are presented in a single table. Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	Estimate	lwr	upr	Std. Error	t value	Pr(> | t|)
Thrush - Female	0.418	-1.759	2.596	0.920	0.455	0.892
Thrush - Male	0.106	-2.061	2.274	0.916	0.116	0.993
Female - Male	-0.312	-2.168	1.544	0.784	-0.398	0.916
Thrush NB - Female NB	1.239	-2.353	4.831	1.244	0.996	0.916
Thrush NB - Male NB	1.623	-1.917	5.163	1.226	1.324	0.766
Thrush NB - Thrush B	1.525	-2.734	5.784	1.475	1.034	0.903
Thrush NB - Female B	1.123	-2.222	4.467	1.158	0.969	0.925
Thrush NB - Male B	0.115	-3.120	3.350	1.120	0.103	1.000
Female NB - Male NB	0.384	-3.020	3.787	1.179	0.326	0.999
Female NB - Thrush B	0.286	-3.817	4.389	1.421	0.201	1.000
Female NB - Female B	-0.117	-3.157	2.924	1.053	-0.111	1.000
Female NB - Male B	-1.124	-4.170	1.921	1.055	-1.066	0.891
Male NB - Thrush B	-0.098	-4.211	4.015	1.425	-0.069	1.000
Male NB - Female B	-0.500	-3.625	2.625	1.082	-0.462	0.997
Male NB - Male B	-1.508	-4.369	1.353	0.991	-1.522	0.644
Thrush B - Female B	-0.403	-4.233	3.427	1.326	-0.304	1.000
Thrush B - Male B	-1.410	-5.200	2.380	1.313	-1.074	0.888
Female B - Male B	-1.008	-3.708	1.693	0.935	-1.077	0.886

6.9 Distance moved post-hoc analysis

Table 6.14. Post-hoc analysis of the relationships between the distance moved after fleeing an approaching human (to the nearest metre) of Eurasian blackbirds and song thrushes, their sex/species, and the season. Sex/species was either male (male blackbird), female (female blackbird), or thrush (song thrush), while season was either B (breeding) or NB (non-breeding). p-values were computed based on a Linear Mixed Model (LMM), using the emm function from the ‘emmeans’ package within the glht function from the ‘multcomp’ package, with single-step adjustment for multiple comparisons. Post-hoc tests on sex and sex:season were run separately but are presented in a single table. Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	Estimate	lwr	upr	Std. Error	t value	Pr(> | t|)
Thrush - Female	2.468	-0.191	5.126	1.123	2.198	**0.075 .**
Thrush - Male	-1.320	-4.073	1.432	1.162	-1.136	0.493
Female - Male	-3.788	-6.202	-1.374	1.019	-3.717	**<0.001 *****
Thrush NB - Female NB	2.978	-1.437	7.392	1.526	1.951	0.373
Thrush NB - Male NB	-1.476	-5.926	2.974	1.538	-0.960	0.928
Thrush NB - Thrush B	0.822	-3.857	5.502	1.617	0.509	0.996
Thrush NB - Female B	2.781	-1.119	6.680	1.348	2.063	0.310
Thrush NB - Male B	-0.342	-4.522	3.838	1.445	-0.237	1.000
Female NB - Male NB	-4.454	-8.684	-0.224	1.462	-3.046	**0.033 ***
Female NB - Thrush B	-2.155	-7.055	2.744	1.694	-1.273	0.796
Female NB - Female B	-0.197	-3.905	3.511	1.282	-0.154	1.000
Female NB - Male B	-3.320	-7.467	0.828	1.434	-2.315	0.194
Male NB - Thrush B	2.299	-2.589	7.186	1.689	1.361	0.747
Male NB - Female B	4.257	0.311	8.203	1.364	3.121	**0.027 ***
Male NB - Male B	1.134	-2.697	4.966	1.324	0.856	0.955
Thrush B - Female B	1.958	-2.417	6.333	1.512	1.295	0.784
Thrush B - Male B	-1.164	-5.707	3.379	1.570	-0.741	0.976
Female B - Male B	-3.122	-6.664	0.419	1.224	-2.551	0.117

Table 6.15. Post-hoc analysis of the relationships between the distance moved after fleeing an approaching human (to the nearest metre) of Eurasian blackbirds and song thrushes, their sex/species, and the type of movement (hop or fly) they selected. Sex/species was either male (male blackbird), female (female blackbird), or thrush (song thrush). p-values were computed based on a Linear Mixed Model (LMM), using the emmeans function from the 'emmeans' package, with mvt adjustment for multiple comparisons. Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

Type	Sex	contrast	estimate	lwr	upr	Std. Error	df	t value	Pr(> | t|)
Hop	.	Female - Thrush	1.055	-2.519	4.629	1.303	149.951	0.810	0.948
Hop	.	Female - Male	0.523	-2.448	3.493	1.084	161.598	0.482	0.995
Hop	.	Thrush - Male	-0.532	-3.958	2.894	1.247	147.737	-0.427	0.997
Fly	.	Female - Thrush	-1.957	-7.569	3.655	2.048	159.644	-0.956	0.901
Fly	.	Female - Male	-4.994	-9.890	-0.097	1.787	164.821	-2.795	**0.043 ***
Fly	.	Thrush - Male	-3.037	-8.759	2.686	2.089	165.783	-1.454	0.616
.	Female	Hop - Fly	-3.522	-7.781	0.737	1.551	139.958	-2.270	0.158
.	Thrush	Hop - Fly	-6.535	-11.799	-1.270	1.919	164.600	-3.405	**0.007 ****
.	Male	Hop - Fly	-9.039	-13.073	-5.004	1.472	165.332	-6.139	**<0.001 *****

6.10 Type of movement post-hoc analysis

Table 6.16. Post-hoc analysis of the relationships between the type of movement (fly or hop) selected by Eurasian blackbirds and song thrushes fleeing an approaching human, their sex/species, and the season. Sex/species was either male (male blackbird), female (female blackbird), or thrush (song thrush), while season was either B (breeding) or NB (non-breeding). p-values were computed based on a Generalised Linear Mixed Model (GLMM) with a binomial distribution and logit-link function, using the emm function from the 'emmeans' package within the glht function from the 'multcomp' package, with single-step adjustment for multiple comparisons. Estimates represent the log(odds) of a bird flying rather than hopping and were exponentiated when discussed in the main text. Post-hoc tests on sex and sex:season were run separately but are presented in a single table. Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	Estimate	lwr	upr	Std. Error	t value	Pr(> | t|)
Thrush - Female	0.267	-1.042	1.577	0.561	0.477	0.881
Thrush - Male	1.080	-0.443	2.603	0.652	1.657	0.219
Female - Male	0.813	-0.371	1.996	0.507	1.604	0.241
Thrush NB - Female NB	0.566	-1.628	2.760	0.773	0.732	0.977
Thrush NB - Male NB	0.292	-2.074	2.657	0.834	0.350	0.999
Thrush NB - Thrush B	0.351	-2.479	3.181	0.997	0.352	0.999
Thrush NB - Female B	0.320	-1.868	2.509	0.771	0.415	0.998
Thrush NB - Male B	2.220	-0.353	4.792	0.907	2.447	0.136
Female NB - Male NB	-0.274	-2.283	1.735	0.708	-0.387	0.999
Female NB - Thrush B	-0.215	-2.664	2.235	0.863	-0.249	1.000
Female NB - Female B	-0.246	-2.028	1.537	0.628	-0.391	0.999
Female NB - Male B	1.654	-0.499	3.806	0.759	2.180	0.241
Male NB - Thrush B	0.059	-2.549	2.668	0.919	0.065	1.000
Male NB - Female B	0.028	-1.879	1.935	0.672	0.042	1.000
Male NB - Male B	1.928	-0.236	4.091	0.763	2.528	0.112
Thrush B - Female B	-0.031	-2.418	2.356	0.841	-0.037	1
Thrush B - Male B	1.868	-0.843	4.580	0.956	1.955	0.361
Female B - Male B	1.899	-0.054	3.853	0.689	2.758	**0.062 .**

6.11 Bill colouration, sex, and age post-hoc analysis

Table 6.17. Post-hoc analysis of the relationships between the bill redness scores of blackbirds and song thrushes and their sex/species and age. Bill redness score was obtained from a Principal Component Analysis (PCA), with higher values representing redder bills. Sex/species was either male (male blackbird), female (female blackbird), or thrush (song thrush), while age was either juvenile (birds in their first year of life) or adult (birds older than a year). p-values were computed based on a linear model, using the emmeans function from the 'emmeans' package, with mvt adjustment for multiple comparisons. Post-hoc tests on sex and sex:age were run separately but are presented in a single table. Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

	Age	Sex	contrast	estimate	SE	df	lower.CL	upper.CL	t.ratio	p.value
1	.	.	Thrush - Female	0.255	1.082	36	-2.361	2.871	0.236	0.969
2	.	.	Thrush - Male	-1.228	1.029	36	-3.717	1.262	-1.193	0.454
3	.	.	Female - Male	-1.483	0.596	36	-2.926	-0.041	-2.487	**0.043 ***
1	Adult	.	Thrush - Female	0.834	1.314	36	-2.900	4.568	0.635	0.980
2	Adult	.	Thrush - Male	-2.918	1.233	36	-6.423	0.586	-2.367	0.143
3	Adult	.	Female - Male	-3.752	0.788	36	-5.991	-1.513	-4.763	**<0.001 *****
4	Juvenile	.	Thrush - Female	-0.323	1.719	36	-5.209	4.562	-0.188	1.000
5	Juvenile	.	Thrush - Male	0.463	1.649	36	-4.223	5.149	0.281	1.000
6	Juvenile	.	Female - Male	0.786	0.896	36	-1.760	3.332	0.878	0.925
7	.	Thrush	Adult - Juvenile	-0.520	1.936	36	-6.023	4.983	-0.269	1.000
8	.	Female	Adult - Juvenile	-1.677	0.965	36	-4.421	1.067	-1.737	0.430
9	.	Male	Adult - Juvenile	2.861	0.701	36	0.870	4.853	4.084	**0.002 ****

6.12 Feather colouration and sex/species post-hoc analysis

Table 6.18. Post-hoc analysis of the relationship between sex/species and feather darkness score in Eurasian blackbirds and song thrushes. Feather darkness score was extracted from a Principal Component Analysis (PCA), with higher values representing darker back feathers. Sex/species was either male (male blackbird), female (female blackbird), or thrush (song thrush). p-values were computed based on a linear model, using the emmeans function from the 'emmeans' package, with mvt adjustment for multiple comparisons. Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

contrast	estimate	SE	df	lower.CL	upper.CL	t.ratio	p.value
Thrush - Female	-1.582	0.606	42	-3.052	-0.112	-2.609	**0.032 ***
Thrush - Male	-2.639	0.558	42	-3.991	-1.287	-4.732	**<0.001 *****
Female - Male	-1.057	0.487	42	-2.239	0.124	-2.170	**0.087 .**

6.13 Vigilance score, sex, and age post-hoc analysis

Table 6.19. Post-hoc analysis of the relationships between the vigilance of foraging Eurasian blackbirds and song thrushes and their sex/species and age. Vigilance is a vigilance score (PC1) obtained from a Principal Component Analysis (PCA), with higher values representing greater vigilance. Sex/species was either male (male blackbird), female (female blackbird), or thrush (song thrush), while age was either juvenile (birds in their first year of life) or adult (birds older than a year). p-values were computed based on a Linear Mixed Model (LMM), using the emmeans function from the 'emmeans' package, with mvt adjustment for multiple comparisons. Note: p-values <0.10 are bolded and the significance level indicated with a full stop (< 0.10) or asterix (* p < 0.05, ** p < 0.01, *** p < 0.001).

Age	Sex	contrast	estimate	SE	df	lower.CL	upper.CL	t.ratio	p.value
First	.	Female - Male	2.066	0.832	38.586	-0.043	4.175	2.483	**0.056 .**
Adult	.	Female - Male	-2.540	2.092	28.662	-7.927	2.847	-1.214	0.553
.	Female	First - Adult	3.930	1.957	32.648	-1.073	8.933	2.008	0.158
.	Male	First - Adult	-0.676	0.575	12.341	-2.281	0.929	-1.175	0.588