

Variation in the effect of corvid predation on songbird populations



Submitted by Lucy Capstick to the University of Exeter as a thesis for the degree of
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ABSTRACT

Populations of farmland songbirds have declined rapidly in the UK in recent decades. Over the same period the populations of predators which take songbird eggs and chicks from the nest (nest predators), have increased. For example, the numbers of corvids on farmland have grown steeply since the 1950s. Although, meta-analyses have suggested that, in general, predators do not limit bird populations, in some cases the removal of corvid predators has led to improved breeding success of songbirds, and increased songbird breeding population numbers. In this thesis, I explored potential explanations for this variation in the impact of corvids on songbird populations. Firstly, I examined how variation in the ecology and behaviour of songbirds influenced their susceptibility to nest predation by corvids, and conversely how variation in the ecology and behaviour of corvids affected the extent to which they predated the nests of songbirds. Secondly, I investigated how variation in the habitat use of both songbirds and corvids, affected the likelihood of corvids encountering and predated songbird nests.

I showed that the breeding biology of songbird species significantly affected their risk of nest predation by corvids. Species that nested in open nests, placed low in the shrub, and with higher breeding season overlap with the breeding season of magpies, were particularly susceptible. It might be expected that population numbers of these vulnerable species would be more likely to decline in response to corvid population increase. I found that species which were susceptible to corvid nest predation did suffer higher egg and chick mortality, suggesting that higher corvid predation could be a driver of higher mortality in the nesting period. However, populations of songbird species with higher nesting mortality were not more likely to have declined over a time period when corvid numbers were increasing. Additional mortality during the nesting period does not appear to limit breeding population numbers of these songbird species. Mortality at other life history stages, such as overwinter, may be more likely to limit their populations.

Variation in the ecology and behaviour of corvids also affected the extent to which they predated songbird nests. Predation of artificial nests by magpies was greater inside magpie territories late in the breeding season, but nests inside specific magpie territories suffered particularly high rates of predation. Territory owners may have differed in their propensity to predate nests, either because of internal

differences between territorial magpies, or differences between the territories they owned.

Finally, the effect of corvid predation on songbird species was found to be affected by the habitat context. By examining the habitat selection of both predators and prey, I could ascertain how songbird prey utilised habitat variation to avoid corvid predation. Songbirds chose to nest in particularly dense, inaccessible hedgerows, away from the most frequently occupied magpie nest sites. Therefore, magpies may have indirectly had a negative effect on songbirds, even though magpies did not appear to select habitat based on songbird presence. If good quality habitat is limited, songbirds avoiding magpies may be forced into using sub-optimal sites.

Examining the different sources of variation in the corvid-songbird relationship also provided insight into factors causing variation in predator-prey relationships more broadly. I therefore concluded by analysing the implications of this thesis for management of predator-prey relationships in general, and for the corvid-songbird relationship in particular. In the case of the latter, I considered how the findings of this thesis could inform management strategies which might reduce the effect of corvid nest predation on songbird populations. Management could be targeted towards specific songbird species which are susceptible to predation or particular habitats where songbird nests are likely to be vulnerable. Conversely it may be possible to identify, and concentrate management on, particular corvid territories in which nest predation risk is high and/or particular corvid territory holders who are likely to predate nests. Using this targeted management could increase the productivity and breeding population numbers of farmland songbirds, a group of species in long-term decline.

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DECLARATION

The five data chapters of this thesis were each written separately, in the format of manuscript for publication, therefore some information is repeated across chapters. The candidate made substantial contributions to all manuscripts and is responsible for the work presented in this thesis. However, when the first person is used in the manuscripts it is used in the plural ('we') to reflect contributions from co-authors and /or field assistants. Contributions are detailed for each manuscript below. Dr Joah Madden was involved in designing the project, helped guide data collection and provided comments on drafts of all chapters. All data used in this thesis was collected during the period of the project (2014-2017).

Chapter 2 Factors predicting the susceptibility of songbirds to nest predation by corvids

Capstick, LA., Madden, JR.

The candidate, with guidance from Dr Joah Madden, carried out the data collection, analysed the data, and wrote the manuscript. Dr Joah Madden, Dr Rufus Sage and Dr Tim Fawcett provided feedback on previous drafts. This paper was submitted to *Ibis* in December 2016 and two anonymous reviewers provided comments. Following these comments this paper was re-submitted to *Ibis* in November 2017.

Chapter 3 Variation in the effect of corvid predation on songbird population numbers

Capstick, LA., Madden, JR.

The candidate carried out the data collection, analysed the data, and wrote the manuscript. Dr Joah Madden provided guidance on data collection and comments on drafts of this chapter.

Chapter 4 Variation in magpie predation of artificial nests

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The candidate, with guidance from Dr Joah Madden, carried out the majority of data collection, analysed the data, and wrote the manuscript. Daniel Walker, Maria Christou, Keith Cowieson and particularly Rebecca Pinkham contributed to data collection. All authors, and Dr Mark Whiteside, provided comments on drafts.

Chapter 5 Effect of magpie ecology and habitat variation on farmland songbird nest site choice and nest success

Capstick, LA., Sage, RS., Madden, JR.

The candidate, with guidance from Dr Joah Madden, carried out the vast majority of data collection, analysed the data, and wrote the manuscript. Tony Powell and Dr Mark Whiteside contributed to data collection. All authors provided comments on drafts.

Chapter 6 Factors affecting magpie (*Pica pica*) habitat use in farmland

Capstick, LA., Sage, RS., Madden, JR.

The candidate, with guidance from Dr Joah Madden, carried out the vast majority of data collection, analysed the data, and wrote the manuscript. Maria Christou and Rebecca Pinkham contributed to data collection. Dr Mark Whiteside provided comments on drafts of this chapter. All authors provided feedback on drafts.

Chapter One

Variation in the effect of predators on bird prey species



1.1 INTRODUCTION

The populations of many farmland songbird species have declined rapidly since the 1950s in both Europe and North America (Voříšek et al., 2008; Brennan & Kuvlesky, 2005). In the United Kingdom this decline in population numbers has been particularly marked, with a fall of 54% between 1970 and 2014 (DEFRA, 2016), and consequently the UK populations of several farmland songbird species are now considered threatened (Eaton et al., 2015). Identifying and understanding the causes of their decline is therefore of critical importance in preventing further local loss of these birds (Krebs et al., 1999). This period of songbird decline has also seen a number of changes in agricultural management, specifically technological and scientific developments which, when combined with government policies that incentivised production, have led to unprecedented intensification (Benton et al., 2003). This agricultural intensification has modified farmland management in many ways, several of which have had negative effects on songbird species which specialise on this habitat (Chamberlain et al., 2000; O'Connor & Shrubbs, 1986; Donald et al., 2001). For example, field sizes have been enlarged to maximise production, but this has resulted in the loss of hedgerows and marginal areas, which are used as nesting sites (Robinson & Sutherland, 2002; Hinsley & Bellamy, 2000; Stoate et al., 1998), and foraging locations for farmland songbirds (Hallmann et al., 2014; Taylor et al., 2006; Mchugh et al., 2016).

The conservation of farmland songbird numbers is considered a priority in the UK, and over the last 30 years agri-environment schemes, which financially reward farmers for managing their land in an environmentally sensitive way, have been implemented across the UK in response to songbird decline (Davey et al., 2010; Natural England, 2009). These schemes include many management options designed specifically to increase the availability of resources which may be limiting farmland bird populations (Smallshire et al., 2004). Although this management has had a positive effect on local populations of some species, such as corn buntings (*Emberiza calandra*) in South-West England (Setchfield et al., 2012) or ciril buntings (*Emberiza cirilus*) in Devon (Peach et al., 2001), the national decline in farmland songbird species has continued (DEFRA, 2016). It has, therefore, frequently been suggested that other factors, including an increase in predation pressure, may have

also played a role in songbird population decline (Fuller et al., 1995; Nicoll & Norris, 2010; Dunn, 2009).

Predation can limit bird population numbers if the mortality caused by predators is additional to mortality caused by other factors, such as starvation (Lack, 1954). For many bird species predation is the greatest cause of mortality of eggs and chicks (Martin, 1993), and the predation of eggs and chicks in the nest, hereafter referred to as nest predation, is a disproportionate cause of mortality compared to predation of juvenile or adult birds (Newton, 1998). This means the effect of predators which take eggs and chicks (hereafter nest predators), rather than the effect of predators of adults birds, is more commonly considered when attempting to link predator effects to bird population declines (Gibbons et al., 2007).

The fall in numbers of farmland songbirds has coincided with the population growth of many mammalian and avian nest predators (Fuller et al., 1995) (*Figure 1.1*). Reasons for these large increases in nest predators, such as foxes (*Vulpes Vulpes*) from the 1960s to the 1990s and grey squirrels (*Sciurus carolinensis*) from the 1970s to the 2000s (Battersby, 2005), include the widespread decrease in number of gamekeepers (Nicoll & Norris, 2010) and an increase in anthropogenic food sources, such as waste from urban areas (Fuller & Gough, 1999; Rodewald et al., 2011).

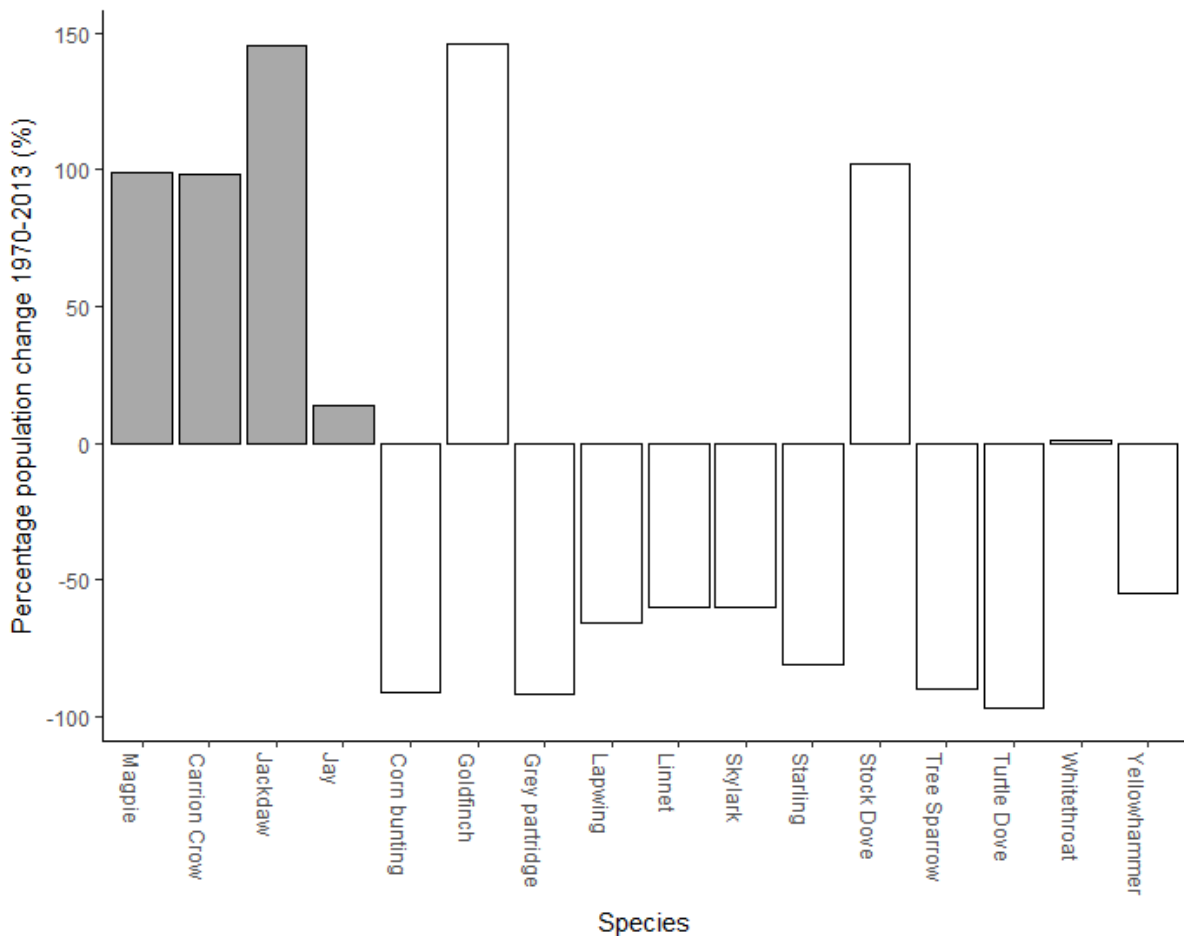


Figure 1.1: Percentage population change of corvid nest predators (grey bars) and birds which comprise the specialist farmland species included in the DEFRA farmland bird index* (white bars) between 1970 and 2013. Percentage change data is based on smoothed population trends produced by the BTO, smoothing removes between variation caused by weather or sampling effects (DEFRA, 2015).

* This index measures changes in populations of several farmland species, relative to population numbers in 1970. It used by DEFRA as a measure of government progress towards biodiversity recovery targets.

Corvids are known to predate eggs and chicks of songbirds in the nest (Coates & Delehanty, 2010; Weidinger, 2010). They have been directly observed taking eggs and chicks from the nest (Mallord et al., 2012; Stevens et al., 2008) and passerine remains have been identified in dietary analysis of adult magpies (*Pica pica*), carrion crows (*Corvus corone*) and jays (*Garrulus glandarius*) (Cotgreave, 1995; Holyoak, 1968; Tatner, 1980), and nestling magpies and carrion crows (Krystofkova et al., 2011; Yom-Tov, 1975; Tatner, 1980). The growth of corvid populations in the UK, again attributed to reduced predator control and increased food availability (Gregory & Marchant, 1996), was particularly prolific in the latter half of the 20th century. The population densities of jays, magpies, jackdaws (*Corvus monedula*), and carrion crows increased by more than 50% on farmland from 1964-

1993 (Gregory & Marchant, 1996). Magpie numbers in particular increased by 240% over this period, and despite the fact that population growth plateaued around the late 1980s (BTO, 2016), their population density remains high compared to historic levels (*Figure 1.1*).

The high density of magpies, may be detrimental to hedgerow nesting farmland songbird species. Although, mammals can be significant songbird nest predators, many mammal species, such as badgers (*Meles meles*), foxes and brown rats (*Rattus rattus*) are more likely to predate nests on the ground (Morris & Gilroy, 2008; Siriwardena, 2006). Conversely, corvids have been shown to be more frequent predators of nests above the ground, (Weidinger, 2002; Söderström et al., 1998) including those in farmland environments (Hatchwell et al., 1996; Luginbuhl et al., 2001). Farmland songbirds are less vulnerable to predation by the jay which is more commonly found in woodland habitats (Schaefer, 2004; Weidinger, 2009). Magpies and crows however are both found in farmland, but there is a substantial size difference between the two species, carrion crows, which have an average weight for both male and females of 510g, are approximately twice as big as magpies, which have an average weight for males of 240g and for females of 200g (Robinson, 2005). This means that some songbird nests, such as those located in hedgerows or dense shrub are more accessible to the smaller bodied magpie (Dunn et al., 2016; Weidinger, 2009). Magpies may pose a particular predation threat to hedgerow nesting farmland songbirds, many of which have suffered large population declines. Therefore, the effect of magpie predation on these songbirds merits particular focus.

Studies which have investigated the potential correlation between corvid population growth and songbird population decline have not found clear evidence of cause and effect. Gooch et al. (1991) found no relationship between changes in magpie density on farmland and the nest success of fifteen songbird species, and Thomson et al. (1998) found that inter-annual variation in the populations of twenty-three songbird species at a given site was generally unrelated to the presence or absence of magpies. Most recently Newson et al. (2010) did not detect negative associations between population change in corvids in the UK (including carrion crow, magpie and jay) and population change in twenty-nine passerine species. These national scale correlative studies seem to suggest no general link between corvid population growth and songbird decline. However, it may be that such coarse-scale

studies do not always detect local fine-scale effects of predators on prey species (Aebischer et al., 2015).

The most effective way of measuring the effect of corvids on songbirds is by carrying out removal studies. These studies generally involve trapping, or actively culling, the corvids at a given site, and monitoring the response of the songbird population. However, the results of these removal studies do not reveal a general pattern; the effect of corvid removal on songbird populations is not consistent. Corvid removal has increased songbird breeding success and breeding population numbers, of blackbird, dunnoek (*Prunella modularis*) and yellowhammer (*Emberiza citrinella*) on lowland farmland (Stoate & Szczur, 2001a; Baláz et al., 2007), and breeding success of meadow pipit (*Anthus pratensis*) on upland grouse moor (Fletcher et al., 2010). Yet magpie removal did not have an overall positive effect on communities of songbirds in suburban parks (Chiron & Julliard, 2007). A meta-analysis of studies which assessed the effect of changes in corvid abundance on their prey species, found that corvids often, but not always, had no effect on passerine species' abundance or productivity (Madden et al., 2015). Therefore, it appears that the effect of corvid predation on songbird populations varies. Understanding the causes of this variation could facilitate the identification of situations when removal of corvid predators might have a positive effect on songbird prey populations (Newton, 1994a; Aebischer et al., 2015; Côté & Sutherland, 1997). This is important because, the removal of corvids is controversial, costly, and has animal welfare implications (Smith et al., 2010) and therefore should only be implemented when there is a high likelihood that removal will led to prey population increases.

Several meta-analyses have attempted to identify which factors lead to variation in the effect of predator removal on bird populations more generally. These studies found varying explanations for the differing impact of predators on bird populations. For example, post-breeding population numbers following predator removal were greater on mainland habitats than those on islands (Smith et al., 2010). However, the studies included in these meta-analyses were biased towards those studies which remove predators in an attempt to improve breeding success of ground nesting waders and gamebird species (Holt et al., 2008), and few focused on farmland songbirds. This means this type of study may be unlikely to identify factors

pertinent to the response of farmland songbirds to corvid removal. In general, when multiple predatory and prey species studied across a diverse set of habitats, are considered in large, regional, or national scale studies or meta-analyses, more subtle and changeable interactions between predators and their prey may be lost. Conversely, more fine-scale research (for example, a field study focused on a particular community in one site) may illuminate factors, such as between species variation in response to predators, or habitat moderation, which might affect the response of specific songbird species to the removal of particular predator species.

In the introduction to this thesis I will examine factors which have been shown to cause variation in predator-prey interactions in general. I will explore factors which are likely to cause variation in the impact of predators on bird prey, highlighting those factors which are likely to cause variation in the impact of magpies on farmland songbirds specifically. Finally, I will detail the work that will be carried out as part of this thesis, which will include fine-scale study of a specific community of magpies and farmland songbirds, to further investigate the factors identified as likely to cause variation in the relationship between magpies and farmland songbirds.

Firstly, I will consider differences between and within prey species, and separately differences between and within predator species, which could affect the predator-prey relationship. I will report differences between prey species in their vulnerability to nest predation (1.2.1). This could explain differential changes in breeding success following predator removal. Prey species may also differ in the effect of egg and chick mortality, compared to mortality at other life history stages, on overall population trends. This may explain the different response of prey populations to changing predator numbers (1.2.2). Predator species may vary in their propensity to take specific prey, due to differences in their foraging ecology. Individual predators may also differ in their predation behaviour depending on availability of alternative food sources, restrictions in other resources, or individual differences in foraging preferences (1.2.3).

Secondly, I will explore how habitat variation can act to moderate these predator-prey interactions (Evans, 2004; Dunn et al., 2010) (1.3). Habitat differences may influence prey species' ability to avoid predation (1.3.1) and affect predator species' chance of encountering prey (1.3.2). For example, habitat factors could

facilitate high population density of predators at a landscape scale, and so increasing rates of predator-prey encounters (1.3.2.1). At a local scale, predators may be more likely to establish territories in particular habitats and consequently predation may be higher near these predator breeding sites (1.3.2.2). Even within their territories individual predators may favour certain habitats and prey in those favoured areas could be particularly vulnerable (1.3.2.3).

1.2 THE EFFECT OF DIFFERENCES IN PREDATOR AND PREY ECOLOGY AND BEHAVIOUR ON THE PREDATOR-PREY RELATIONSHIP

Prey species vary in their conspicuousness, nest-defence behaviour and habitat use and these differences can affect their susceptibility to predation. Predators also differ in prey preference, breeding system and foraging behaviour and this can affect their propensity to take certain prey. Such differences interact to ensure that particular prey species are differentially susceptible to different species or classes of predator. For example, wheatear nests (*Oenanthe oenanthe*) are located in holes on or near the ground, and can be accessed by mammals and snakes, but not corvids (Pärt, 2001). Some predator and prey species may have coevolved and this may have determined both the antipredator behaviour of the prey species, and the foraging ecology and behaviour of the predator species (Anson & Dickman, 2013).

Alternatively, some prey species may have evolved rapidly in response to a specific predation threat. For example, forest songbirds in Hawaii have evolved to nest higher in the canopy in response to the invasion of black rats and so have increased their nest success (Vanderwerf, 2012). Understanding these differences in predators and prey, and how they interact and influence each other, may provide insight into situations where prey are likely to be vulnerable to predation by particular predators (Juskaitis, 1995).

1.2.1 Differences in prey breeding ecology and behaviour

Bird prey species have responded differently, in terms of both breeding success and breeding populations numbers, to experimental predator removal (Fletcher et al., 2010; Chiron & Julliard, 2007). These removal studies often suggest habitat or site-specific explanatory factors to account for these differential responses between species (White et al., 2014; Baines, 1990). White et al. (2014) attributed the finding that improvements in nest success, following predator removal, were seen in

blackbird and chaffinch but not whitethroat, to the fact that overwinter habitat management at the site had a positive effect on the resident blackbird and chaffinch, rather than the migrant whitethroat. However, there has been limited exploration of fundamental differences between species which might influence their response to predator removal. Species differ in their breeding biology in terms of nest site, nesting materials, breeding phenology and the behaviour of the adults (and chicks) at the nest. All these factors may affect the predation risk faced by a species.

One distinct difference in breeding biology of birds which is likely to influence their risk of predation is their nest location. Crudely, some species nest on the ground (such as gamebirds) while others nest above the ground. Although meta-analyses of predator removal studies have not found variation in response to predator removal between gamebirds or non-gamebirds (Côté & Sutherland, 1997), between ground nesters or non-ground nesters (Smith et al., 2010), or between gamebirds, passerines and waders (Madden et al., 2015), these analyses have only looked at differences between broad groups of species. It may be that more detailed species-specific, variation in breeding biology does influence the relative effect of predator removal on their breeding success.

Nest predation risk has been shown to vary in relation to a number of aspects of prey breeding biology (Newton, 1998). Several attributes of a species' nest site choice affect their predation risk. Some sites have greater physical protection from predators. For example, nests located in natural holes are less accessible to larger predators (Martin & Li, 1992) and tend to suffer lower rates of predation (Wesolowski & Stawarczyk, 1991; Willson et al., 2001). Nest cover (vegetation which conceals the nest site) may also provide protection from some predators. Wegrzyn & Leniowski (2011) found blackcap (*Sylvia atricapilla*) nest survival was lower at sites with less vegetation cover.

Egg size affects relative risk of predation. Corvids preferentially take eggs they can pick up and carry (Montevecchi, 1976) whereas small rodents can only predate the smallest eggs (Degraaf et al., 1999). Timing of breeding could also affect predation risk, for instance birds that nest earlier in the year may be more vulnerable due to the reduced vegetation cover available (Santos & Telleria, 1991; Mallord et al., 2008).

Species also differ in breeding behaviour at and around the nest. This too affects nest predation risk; for example, nest defence behaviour influences likelihood of nest predation (Goławski & Mitrus, 2008). The benefits of nest defence differs, being greater for thrushes, which have more conspicuous nests, than blackcaps, which have better concealed nests (Weidinger, 2002, 2009). Relatively smaller songbird species with less conspicuous nests are less likely to engage in active nest defence (Schaefer, 2004).

The effects of breeding ecology on predation risk differ depending on the composition of the predator community. It would be expected that due to the behaviour of visually oriented avian predators such as corvids, specific characteristics of prey breeding biology would influence corvid predation rates. For example, nests lower in shrub or hedgerows may be less visible to corvids such as magpies, than nests higher up (Remeš, 2005a; Colombelli-Négrel & Kleindorfer, 2009).

Using these findings, taken from a range of previous studies, broad inferences can be made about the impact of a songbird species' breeding biology on their risk of corvid nest predation. However, these previous analyses have not often assessed the effect of several different attributes of songbird breeding biology, and of the interactions between these different attributes, on predation risk.

In Chapter Two I examine how fine-scale differences in songbird species' biology influence predation by corvids. I will carry out an analysis of the literature which examines songbird species' reproduction, specifically investigating the proportion of reported egg and nestling losses attributed to predation by corvids. I will relate variation in these reported nest predation rates attributed to corvids to difference in breeding biology between songbird species. I can then identify farmland songbirds which are particularly vulnerable to corvid predation based on their breeding biology.

1.2.2 Differences in prey species' demography

If prey species differ in their vulnerability to predation it might be expected that they would also differ in their population response to predator removal. However, while predation by a particular predator at the nest stage may be a critical determinant of prey population numbers, other causes of mortality, and mortality at other life history

stages, can also affect population numbers. Therefore, the removal of a single (nest) predator species does not always result in the expected increase in the prey population, even when the prey species is known to be vulnerable to predation.

Firstly, it may depend on which predator species were removed and how this removal affected the predatory behaviour of the remaining predators. Decline in predation by one group of predators may simply facilitate predation by another group of uncontrolled predators (Ellis-Felege et al., 2012; Bodey et al., 2011; Norrdahl & Korpimäki, 1995).

Secondly, susceptibility to predation in general may not drive variation in mortality of eggs and chicks in the nests (hereafter nesting mortality); other causes of mortality such as starvation or exposure may be more important for some species, or populations (Kirkpatrick et al., 2009; Etterson et al., 2007; Ratcliffe et al., 2006; Kern, 2015). If nest predators take chicks or eggs which would otherwise have died due to different causes, the so-called 'doomed surplus', then reduction in predation rates may not reduce overall nesting mortality (Bolton et al., 2007b; Nordström et al., 2002; Errington, 1946b).

Finally, variability in nesting mortality may not influence overall population trends. Côté & Sutherland (1997) used a quantitative meta-analysis to compare the results of twenty studies investigating the effect of predator removal on target bird species, and they found removal of predators resulted in an increase in hatching success and post-breeding numbers, but not an increase in breeding populations in subsequent years. Populations may be better able to respond to losses in the early life history stages, especially if these losses can be made up by increased reproductive output (additional broods) or reductions in later density-dependent population losses (Martin, 1995). If populations can compensate for losses during early life history stages, then it may be that mortality at other life history stages is more influential in limiting population numbers. For example, for some farmland songbirds changes in overwinter survival, rather than changes in breeding success, have been found to correlate with changes in overall population numbers (Baillie & Peach, 1992). If populations are robust to changes in nesting mortality then removal of nest predators will not increase subsequent breeding numbers (Newton, 1998).

Previous studies have examined how mortality in the nesting period relates to overall population declines during periods of nest predator population increase (Siriwardena et al., 2000a; Baillie & Peach, 1992). However, these studies have not generally related this to a species' susceptibility to nest predation by particular nest predators. In Chapter Three of this thesis I will conduct a second analysis of data taken from the literature. In this analysis, I will extract reports of mortality at the egg and chick stage (nesting mortality). Firstly, I will ask whether nesting mortality is related specifically to susceptibility to corvid predation. Other predators may play a compensatory role. Secondly, if nesting mortality corresponds to variation in corvid predation, I will ask whether it is related to likelihood of a species' post-breeding population recovering following to corvid removal or natural decline. If species with high nesting mortality tend to have high susceptibility to corvid predation and are more likely to respond positively to corvid removal, then I propose that corvid predation could be limiting the post breeding numbers (autumn populations) of these species. Finally, I will ask if the breeding populations of species with high nesting mortality are also more likely to have declined during a period of corvid population growth (and supposed increase in nest predation by corvids). If so, it may be nest predation by corvids can limit overall breeding populations of these species, and that these species are more likely to benefit, in terms of increased breeding population numbers, from targeted corvid removal.

1.2.3 Differences in predator ecology and behaviour

Differences in prey ecology and behaviour do not explain all the variation in predator-prey relationships. Predators themselves differ between species in their effect on prey, and even within species the effect of a predator on a specific prey species may differ across time or space. Birds are predated by animals from many taxa including mammals, birds and reptiles (Steen & Haugvold, 2009; Draycott et al., 2008; Seymour et al., 2003; Spanhove et al., 2009; Best & Stauffer, 1980). These different predators vary in the number of prey they take across regions and across habitats (Angelstam, 1986; Söderström et al., 1998). For example, in urban areas, cats (*Felis catus*) are more frequent nest predators than other species (Baker et al., 2008). The effect of particular predatory species can also vary depending on external factors, such as habitat variation or availability of alternative prey (Newton, 1998), and internal factors, such as temporal variation in foraging requirements (Annett &

Pierotti, 1989) or individual variation in foraging preferences (Patrick & Weimerskirch, 2014).

Different predator species may be specialist or generalist in their prey choice. Some predator species are generalists; they switch to alternative prey readily and are less likely to have specialised predation behaviour. Conversely specialists eat a narrow range of prey and are likely to be adapted to taking specific prey (Andersson & Erlinge, 1977; Steenhof & Kochert, 1988). These specialists may persist in targeting specific prey even when they become rare (Dickman & Newsome, 2015), and so have a particularly detrimental effect on prey populations.

As well as differences between predator species, animals of the same species, even within the same population, can also differ in their predation behaviour (Bolnick et al., 2003). Some individuals may specialise on particular types of prey. For instance, within a population of urban cats some individuals were found to specialise on lizards while others specialised on birds (Dickman & Newsome, 2015), therefore specific individuals could be disproportionately responsible for a large amount of predation of particular prey (Linnell et al., 1999; Odden et al., 2002). The mixed outcome of predator removal studies may be partly explained by this paradigm; a failure to remove the specific individuals responsible for most of the predation will lead to a disparity between the number of predators removed and the increase in the prey species' population numbers.

The difference in predation behaviour between individual predators, or guilds of predators, may arise because individual predators differ in the chance of encountering prey species due to variation in their own ranging and foraging behaviour. Some individuals may be more likely to encounter the prey species (Linnell et al., 1999; Graham et al., 2011). For instance male lynx (*Lynx lynx*) ranged further than females and were more likely to encounter livestock and thus more likely to predate them (Odden et al., 2002). Within species that show territoriality, such as corvids (Birkhead, 1991), it may be that the breeding territorial individuals, who have greater knowledge of defined habitat patches, are likely to encounter concealed prey (such as nests). Conversely non-territorial individuals may range over a wider area and be less likely to find more inconspicuous prey (Sacks et al., 1999). For example, non-territorial corvids can range over an area three to four times larger than territory

holders (Birkhead, 1991). These territorial individuals, which are likely to more frequently encounter a specific prey type restricted to, or especially common in their territory, may also form a search image for that prey which increases the likelihood or efficiency of subsequent predation (Croze 1970 cited in Montevicchi, 1976). Møller (1988) found that predation on blackbird nests was disproportionately higher in habitat patches with a territorial pair of magpies present and, other studies have suggested nest predation rates are higher near corvid nests (Vigallon et al., 2005; Slagsvold, 1980a).

Other factors can also cause variation in foraging preferences. Predators may vary temporally in prey choice, species have been shown to switch to prey of higher nutritional value when they have dependent young, probably to facilitate growth of their young (Annett & Pierotti, 1989; Sasvari & Hegyi, 1998). The remains of eggs and chicks have been found in analyses of magpie diet during their own breeding season (Holyoak, 1968). This may be related to the greater availability of nests during this time, but it could also be because corvids choose a nutrient-rich food when provisioning young (Sasvari & Hegyi, 1998).

Finally, individuals may differ in their underlying behavioural types, and this may explain their different predatory choices. Animals can display consistent differences in behaviour across contexts (defined as an animal's personality), and this variation may influence their foraging behaviour (Biro & Stamps, 2008). Individuals within populations have been shown to vary along a proactive-reactive axis (Sih et al., 2004) and this difference in behaviour has been linked to variation in movement patterns, which may be directly linked to foraging strategies (Nilsson et al., 2014). For example bolder individuals could be more likely to exploit particular foraging habitats (Wolf & Weissing, 2012; Patrick & Weimerskirch, 2014). Differences in personality may therefore drive differences in behaviour which affect an individual's likelihood to predate nests, it may be that particular predators choose to forage in sites where nests are likely to occur.

Slagsvold (1980) suggested that particular individual hooded crows (*Corvus corone cornix*) specialised in predating fieldfare (*Turdus pilaris*) nests. The existence of individual specialisation is increasingly recognised in natural populations (Araújo et al., 2011), and as corvids have been shown to display individual differences in

other behaviours (Chiarati et al., 2012; Range et al., 2006), the likelihood of detecting individual differences in foraging behaviour seems reasonable.

Fine-scale analysis of magpie predation behaviour have rarely been conducted, particularly in UK farmland. Therefore, in Chapter Four I will conduct an experiment using the placement of artificial nests in a typical mixed agricultural environment to carry out a detailed and controlled examination of magpie predation behaviour. By placing the nests in different configurations, it will be possible to see how predation rates of nests are affected by presence of, and distance from, active magpie nests, as well as by time of year in relation to the magpies' breeding season. I will also characterise the magpie population on the site and colour ring territorial individuals. I will then assess individual differences in predation behaviour by using trail cameras to identify which colour ringed magpies are predating artificial nests. If some individuals are particularly predatory at specific times, and it is possible to identify them, precisely targeted control of disproportionately predatory individuals may be practicable.

1.3 THE EFFECT OF VARIATION IN HABITAT ON THE PREDATOR-PREY RELATIONSHIP

Variation in predator and prey ecology can affect the predator-prey relationship, but any predator-prey interaction is also moderated by the habitat in which the species exist (Newton, 1998). Habitat variation influences local density and distribution of prey and predator species, directly affecting the probability of predators encountering prey (Evans, 2004). Availability of habitat may also indirectly influence predator-prey interactions, by affecting how well prey are able to avoid local predators (Dunn et al., 2010). In Chapter Five I take the perspective of the prey (farmland songbirds) and explore how the local habitat affects prey vulnerability to nest predation (by magpies). In Chapter Six, I will take the perspective of the predator (magpies) and explore how the local habitat determines the movement of predators and hence their probability of encountering prey. By relating the habitat use of magpies to that of songbirds in a mixed farmland site I will be able to assess how habitat variation affects this specific predator-prey relationship. UK farmland habitat has undergone significant changes in recent decades, and these changes may have modified farmland songbird interactions with their predators, including magpies.

1.3.1 Habitat variation and prey species' vulnerability to predation

Habitat factors affect prey species' ability to respond to direct and indirect predation threats. Nest site choice, and resulting nest success, is thought to be at least partly based on the parents attempting to avoid predators (Eggers et al., 2005; Tryjanowski et al., 2002). The availability of nesting habitat is therefore likely to be important in facilitating this avoidance of predators (Newton 1994). Habitat factors and landscape structure are also likely to affect predator distribution within the habitat and thus the likelihood of a predator encountering a particular nest of its prey. The risk of predation can be higher for nests situated near predator breeding sites (Slagsvold, 1980a), near areas where predators prefer to forage (Pescador & Peris, 2007), or near routes predators use to move through the landscape (Morris & Gilroy, 2008).

Habitat attributes can reduce the risk of a nest being predated even when it is situated in areas where predators are likely to forage. Nests positioned in vegetation that provides greater cover and concealment are often less likely to be predated, particularly by visually oriented avian predators (Remeš, 2005a; Hatchwell et al., 1999; Kelleher & O'Halloran, 2007). For example, farmland songbirds had higher nest success in less accessible hedgerows (Dunn et al., 2016). Alternatively for species, such as lapwing (*Vanellus vanellus*), which rely on early detection of predators nest sites with sparser vegetation may be favoured (Wilson et al., 2005).

Other habitat characteristics, such as the proximity of the prey species' optimal foraging habitat can also indirectly affect the probability of predation of their nests (Brickle et al., 2000). Chick begging calls, which may increase when food is scarce, can attract the attention of predators (Ibáñez-Álamo et al., 2012; McDonald et al., 2009; Evans et al., 1997). Poor food availability can detrimentally affect parental condition, reducing the effectivity of their nest defence and chick provisioning behaviour (Hogstad, 1993). In a farmland environment, when food availability was low, yellowhammer (*Emberiza citrinella*) were unable to sufficiently provision large broods of chicks when corvid activity levels were high (Dunn et al., 2010).

Although, there is an extensive literature examining how habitat attributes affect breeding farmland songbirds (Newton, 2004; Aebischer et al., 2000; Browne & Aebischer, 2003; Bishton, 2001; Robinson et al., 2004). These studies have rarely

related these habitat factors directly to detailed knowledge of the ecology and ranging behaviour of the local predator population. In Chapter Five, I will examine the habitat selection of songbirds breeding on farmland whilst considering the distribution and foraging behaviour of the local magpies. I will examine how the specific nest sites chosen by hedgerow nesting songbirds are related to magpie breeding and foraging ecology, and to habitat factors which might influence predation risk, such as vegetation density. The results of the artificial nest experiments in Chapter Four will provide a measure of variation in nest predation between magpie territories, I will utilise this to examine whether songbird nest site choice relates to fine-scale variation in nest predation risk.

Finally, I will examine how and whether songbird nest site choice relates to nest success in the songbird species on my field site. The link between where a prey species chooses to locate their nest and the fate of that nest is not always intuitive. This is because the cues songbirds use to select nest sites, and avoid predators, may not always be effective. If predator home ranges vary from year to year, then safer areas in one year may become vulnerable in following years. If farming practices alter then the attractiveness of the area to nest predators, may also change, meaning nests situated in an area become more likely to be encountered by predators. Changes in the farmland environment, caused by agricultural intensification, may mean that the relationship between the preferred nesting habitat of songbirds and the risk of nest predation by corvids has altered, such that preferred nest sites are actually lower quality and suffer increased predation risk (Battin, 2004). This would exacerbate the potential impact of increased corvid numbers on songbird breeding success. Conversely, songbirds could make nest site choices, or other modifications to their breeding behaviour (Remeš, 2005b), which minimise their risk of nest predation even in the presence of predators. In this case the effect of an increase in corvid numbers may not be as detrimental as expected.

1.3.2 Habitat variation and predator species' impact on prey

Prey species may be able to reduce their risk of nest predation through their own habitat use, but the chance of their nest being encountered by a predator is also likely to be affected by habitat use of the predator (Newton, 1998). Most obviously,

predators are more likely to encounter nests in habitat areas they utilise more frequently (Whittingham & Evans, 2004).

The selection of habitats, both by predators and their prey, occurs at a range of different spatial scales. At the landscape scale, individuals can choose between, for example, an area of mixed farmland or a suburban area. At local scale, such as within a farm, they may choose field margins or the middle of fields. At the field margin, they may discriminate between areas of dense tufted grass and areas of more open herbs as foraging or nesting sites. Habitat choice is likely to be scale-dependent: factors which influence the landscape scale distribution of a species may not determine use of habitat in a given area within this landscape. Landscape scale habitat variation affects species' population density and distribution at a regional level (for example at 10km² scale) whereas local scale variation is likely to affect predator habitat use within a landscape (<1km²), such as breeding or foraging site choice. For instance, Ravens (*Corvus corax*) suffered reduced breeding success when there was a higher proportion of coniferous-dominated forest in the area around the nest (1500m radius), but when choosing specific nest sites they preferred conifer trees (specifically, pine trees) (Mueller et al., 2009). Examining factors that determine species' distribution at various scales, and the interactions between these different scales, could explain regional and local differences in predator-prey interactions (Robinson et al., 2004). By understanding how corvids utilise habitat at different scales, I will identify areas within a mixed arable and pastoral farmland habitat where songbird nests are most vulnerable to nest predators (see *Chapter Five and Six*).

1.3.2.1 Landscape scale habitat variation

At a landscape scale, predator effect on prey can often be determined by the density of predators; in areas where predator densities are low then predator removal is less likely to influence bird abundance (Aebischer et al., 2015). This may be particularly relevant for generalist predators, whose population numbers are unlikely to be directly related to the availability of any single prey species (Gibbons et al., 2007), and at a landscape scale are likely to be limited by other resources (Newton 1998).

Recognising habitat factors which cause predators to exist at a high density at particular areas within a landscape could highlight areas where prey may be more

vulnerable to predation. For example, Steller's jays (*Cyanocitta stelleri*) exist at higher densities around specific anthropogenic food sources and so marbled murrelet nests (*Brachyramphus marmoratus*) in these areas may be more at risk of predation (West et al., 2016). While the abundance of mammalian nest predators in forest corridors was affected by broader habitat structure (forest corridor width) and wider landscape context (number of buildings in adjacent landscapes) (Sinclair et al., 2005).

The density of magpies in farmland is thought to be related to the availability of foraging habitat. Magpie population density may differ in association with broad variation in agricultural management (Gregory & Marchant, 1996). Magpies prefer to forage in grassland and this may lead to higher population densities in areas where pastoral farming dominates (Birkhead, 1991). However, we understand little about what predicts magpie population density in a landscape comprised of mixed farmland.

In Chapter Six I will extend my field site to assess landscape scale distribution of magpie nests. I will use density of magpie nests per km² as an indication of preferred magpie habitat within a landscape. This will allow me to examine which habitat characteristics (such as hedge length, road length, grass, and crop availability) predict favoured magpie habitat. These preferred habitats may indicate areas within a UK farming landscape where songbird nests may be more at risk of predation.

1.3.2.2 Local scale habitat variation

At the local scale, within a given landscape, habitat selection may be driven by different factors to those driving landscape scale habitat selection. For territorial nest predators determining the factors that drive breeding site choice, or territory establishment can be a useful indication of local areas where prey may be more vulnerable. For example, identifying the factors which drive nest site choice of corvids may provide an indication of areas corvids are likely to use. Corvids are often territorial and only forage in the vicinity of their own nests (Birkhead, 1991; Vines, 1981).

Nest site choice is influenced by a variety of interacting factors which vary between populations. For example, the availability of foraging habitat (Goldyn et al.,

2003; Kang et al., 2012) or nest site availability, may be limiting (Birkhead et al., 1986). In addition to these habitat factors, proximity of their own nest predators may also affect nest site choice. For instance, magpie nest success is reduced in areas near to carrion crow nests (Baeyens, 1981b).

The factors influencing magpie nest site choice are likely to differ in their relative influence depending on the configuration of the local habitat. In a rural environment magpie nest sites were further apart than predicted (>150m) and the population was possibly limited by presence of conspecifics (Vines, 1981) where as in an urban environment magpies existed at much higher densities (56.8 pairs/km²) and their breeding population size seemed to be limited by the availability of trees preferred for nesting (Antonov & Atanasova, 2002). In Chapter Six I will assess the relative influence of different factors (specifically availability of different foraging habitat, proximity of conspecifics, proximity of urban areas and availability of different tree species for nesting) on magpie nest site choice in a mixed agricultural habitat. This analysis will provide measure of magpie habitat use at a local scale which can be compared to the measure of habitat preferences at a landscape scale (1.3.2.1)

1.3.2.3 *Individual scale variation in habitat use*

Direct assessment of how predators move through their ranges or territories, and how they differentially utilise particular habitats within these areas, could provide further fine-scale identification of areas where predators may be more likely to encounter songbird nests. Mammalian species use the borders between two habitat types, such as grass field margins and crops, to move through habitats, and nests near these borders are more vulnerable to predation (Morris & Gilroy, 2008). Radio-tracked American crows (*Corvus brachyrhynchos*) were found to fly directly from nest sites (>5km away) to anthropogenic food sources (settlements and campgrounds) which lead to a higher abundance of crows in these areas. Species nesting around these food sources may therefore be particularly vulnerable to nest predation by these crows (Marzluff & Neatherlin, 2006).

In Chapter Six I will use two measures to examine habitat use at an individual level. Firstly, I will radio-track individual magpies to see which habitats are used most frequently. Previous radio-tracking studies of corvids have largely focused on other species (Smedshaug et al., 2002), and have not examined magpie habitat use in

mixed farmland. By comparing magpie use of particular habitats relative to their availability, I will be able to infer what types of habitats they prefer to utilize. I will support this inference of preferred habitats by presenting simulated territorial intrusions by (dummy) conspecifics and observing the strength of responses to these intrusions. More valued habitats may be more vigorously defended from intrusion. It might be magpie favoured foraging habitat (pasture) is considered more valuable and is more frequently used (Møller, 1982).

By using three scales (landscape, local and individual) to measure magpie habitat use, and considering habitat factors found to influence songbird nest site choice in Chapter Five, I will identify areas where magpies and songbird populations are most likely to overlap, and hence where magpies have the greatest opportunity to predate the nests of songbirds.

1.4 CONCLUSIONS

The influence of predators on prey populations can be moderated by multiple factors. The effect of these multiple, and interacting, sources of variation may explain why the relationship between populations of UK farmland nesting songbirds and an apparently common nest predator, the magpie, are so varied, and why the local control of magpies does not commonly lead to increases in the populations of their songbird prey. By studying a specific community of magpies and farmland songbirds at a fine-scale, I may be able to identify specific factors which affect the impact of magpie nest predation on farmland songbirds that have not been revealed through broader scale larger studies or meta-analyses.

Firstly, songbird species may vary in their susceptibility to predation; only vulnerable species are likely to respond to predator removal. I will assess which songbird prey species, because of their breeding biology, are most vulnerable to corvid predation in Chapter Two. I would expect that species which have particular attributes of breeding biology that make them especially susceptible to nest predation by magpies, for example those that have open nests at shrub height, to be those most likely to benefit from targeted removal of magpies.

Secondly, corvid predation may not contribute significantly to overall nesting mortality, or if it does, variation in nesting mortality may not affect overall population trends. I will examine this question in Chapter Three by comparing songbird species'

egg and chick mortality (as reported in the literature) to their susceptibility to corvid predation and overall population trends.

Thirdly, predators may vary, both between and within species, in the extent to which they predate particular prey species. In this case only removing individual predators responsible for most of the predation will lead to increase in the prey population. In Chapter Four I will analyse how variation in magpie ecology and behaviour can affect the extent to which they predate nests. In common with previous studies I might expect that territorial magpies predate disproportionately, particularly during their own breeding season. Additionally, more fine-scale inter-individual differences in nest predation behaviour may be identifiable.

Finally, habitat variation is likely to affect habitat use by both predator and prey species. If both predators and prey favour the same habitats, perhaps because the habitats provide foraging opportunities or cover, then prey may be more likely to be encountered by predators. Examining habitat factors that drive songbird nest site choice and nest success, in Chapter Five, and local magpie distribution and habitat use, in Chapter Six, could indicate how habitat and/or predator management might be used to reduce the direct and indirect effect of predation on songbird nests. I might expect magpies and songbirds to share broad habitat preferences, perhaps due to overlapping diet requirements. However, these coarse-grained overlaps may conceal fine-scale segregation which reduces magpie encounters with songbird nests.

The magpie songbird predator-prey relationship is of particular interest as farmland songbirds are species of conservation concern and magpies are apparently common nest predators in UK farmland. Better understanding of the factors modifying this relationship could indicate possible management interventions that may benefit songbird populations, and in Chapter Seven, I will summarise my results and set them in the context of previous research examining the relationship between corvid populations and songbird productivity. I will assess which factors I find to be influential in modifying the magpie-songbird relationship and consider how they could be applied to management. In Chapter Seven I will also explore how the findings of this thesis could be used to make some broader inferences about how variation in the above factors could influence predator-prey relationships more generally. For

example, better understanding of predator-prey dynamics may provide insight into how human modification of habitat and species' population numbers may be influencing these dynamics.

Chapter Two

Factors predicting the susceptibility of songbirds to nest predation by corvids



ABSTRACT

The effect of nest predation (predation of eggs and chicks in the nest) by corvids on songbird populations is unclear. Although several meta-analyses have suggested that in most cases nest predation does not limit bird populations, the response of songbirds to experimental nest predator removal has varied across studies. As an explanation for this mixed response we test the hypothesis that susceptibility to nest predation by corvids varies between species according to differences in their breeding biology. We conducted a wide review of studies detailing nest predation on UK songbirds and extracted the reported rates of nest predation from 83 papers which attempted to identify the predators responsible. We found that corvids were significant predators of songbird nests and that 25% of all nest predation was attributed to corvids. We used a generalised linear modelling approach to assess the effect of features of songbird species' breeding biology on rates of nest predation by corvids specifically. Several aspects of songbird breeding biology predicted corvid nest predation rates. Species that constructed open nests, positioned low in vegetation ($\leq 2\text{m}$ but above ground), and whose breeding season overlapped with the magpie's breeding season, were found to incur the highest nest predation rates. We then used the model with the best predictive ability to predict predation rates for UK breeding songbird species for which there was no empirical data. It was therefore possible to use the results of this analysis to assess the risk of nest predation by corvids according to songbird species' breeding biology. If species differ in their vulnerability to corvid predation then we should expect them to vary in response to corvid removal. We determined that in at least some cases, species we predicted to be more susceptible to corvid nest predation did indeed show increased breeding success or population abundance in response to corvid removal. Corvid removal could lead to increases in the breeding success of species that are likely to be especially vulnerable to predation. Therefore, targeted removal of corvids in circumstances where these species are threatened could have conservation benefits.

2.1 INTRODUCTION

The decline of farmland songbirds across Europe and North America is well-documented and even with widespread conservation efforts ongoing (Donald et al., 2006; Voříšek et al., 2008; Brennan & Kuvlesky, 2005; Donald et al., 2002). Agri-environment schemes are one of the main mechanisms which aim to deliver habitat management to halt this decline (Batáry et al., 2015). However, although specific targeted management options have been shown to benefit certain species at a local scale (McHugh et al., 2016; Perkins et al., 2011; Chamberlain et al., 2009), evidence for an overall positive impact of agri-environment schemes on farmland songbirds is limited (Kleijn et al., 2001; Bright et al., 2015). The implementation of wildlife friendly habitat management does not always lead to local population recovery (Tworek et al., 2017; Aebischer et al., 2015) and at a wider scale population declines continue; farmland bird numbers decreased by 57% between 1980 and 2014 across Europe (PECBMS, 2017). It has been suggested that habitat improvements have failed to reverse this population decline because the role of other factors, and the interactions between them, has been underplayed (Nicoll & Norris, 2010; White et al., 2008; Whittingham & Evans, 2004).

One of the most cited of these other factors is predation. Songbird decline has coincided with the reduction of widespread predator control (Douglas et al., 2014; Morris & Gilroy, 2008), an increase anthropogenic food source such as carrion (Gregory & Marchant, 1996) and the associated population growth of many generalist predators (Newson et al., 2010b; Battersby, 2005). Predation of eggs and chicks in the nest, hereafter nest predation, is commonly carried out by corvids (Shurulinkov, 2005; Desrochers & Magrath, 1993; Baláz et al., 2007), and although their numbers are now stabilising, corvid populations have increased substantially in recent decades; magpie (*Pica pica*) by 99% from 1970 to 2013 in the UK, carrion crow (*Corvus corone*) by 98% and jay (*Garrulus glandarius*) by 14% (DEFRA, 2015), with similar trends seen across Europe (Voříšek et al., 2008).

However, it is not clear that the relationship between falling songbird numbers and predator population growth is causal (Gibbons et al., 2007; Bell et al., 2010). Studies looking specifically at the correlation between corvid and songbird population change have found little evidence of predators limiting prey populations (Gooch et

al., 1991; Thomson et al., 1998). One explanation is that corvids predated nests are simply causing compensatory mortality, removing part of the population that would have died anyway (the so-called 'doomed surplus' Errington 1946). In this case, a growth in corvid numbers would not be expected to have a negative effect on the populations of birds whose nests they predate.

Alternatively, it could be that corvids are simply not predated many nests. Dietary studies have suggested that eggs and nestlings make up only a small proportion of the diet of corvids and their nestlings (Díaz-Ruiz et al., 2015; Holyoak, 1968) and they may attract undeserved blame for nest predation due to their conspicuous, diurnal activity (Birkhead, 1991). However, these hypotheses receive only mixed support from removal studies in which predator numbers are reduced in an area and the resulting breeding success of the prey species is monitored. For example, removal of a suite of predators, including corvids, did lead to an increase in breeding success in farmland songbirds when combined with sympathetic habitat management (White et al., 2014). Cessation of corvid control (as well as selective mammalian predator control) resulted in a mixed response across a guild of upland songbirds; skylark (*Alauda arvensis*) had lowered abundance whereas meadow pipits (*Anthus pratensis*) showed no response (Baines et al., 2008). Conversely, in one controlled experimental study where just magpies were removed no overall effect was found on the number of adult or juvenile songbirds (Chiron & Julliard, 2007). A recent systematic review drew together correlational and experimental studies from around the world to explore the effect of the removal of corvids on populations of their bird prey (Madden et al., 2015). They found that, in most but not all cases, corvids had no negative effect on the abundance or productivity of birds. An explanation for this apparent difference in songbird species response to corvid population increases, or to experimental corvid removal, within and across studies may be that particular songbird species are differentially predated by corvids. At present, there is no overview of how rates of nest predation by corvids differ between songbird species. Consequently, there is no way of determining whether removal of corvids is predicted to affect the breeding success or population dynamics of any particular songbird species.

Factors that influence the susceptibility of a particular species to nest predation by corvids are likely to relate to aspects of their breeding biology. Birds' breeding strategies vary in several ways which may affect nest predation in general, and nest predation by corvids particularly. The most striking difference in breeding biology is between hole and open-nesting species. Nest losses, particularly at the egg stage, have been shown to be fewer in species that nest in cavities or nest boxes, which offer greater physical protection than open nest sites (Martin & Li, 1992; Ricklefs, 1969). Corvid predators specifically have been found to be unable to access hole nests of some species, such as the northern wheatear (*Oenanthe oenanthe*) (Pärt 2001). Conversely, open-cup nesting farmland songbirds are affected detrimentally by corvids (Baláz et al., 2007; Slagsvold, 1980b; White et al., 2008). Other factors relating to nest position, such as nest height, also influence predation risk (Ludvig et al., 1995). Weidinger (2002) found that the poorly concealed nests of thrushes were more heavily predated by corvids than the nests of blackcaps (*Sylvia atricapilla*) which are well-concealed in the lower canopy.

Other aspects of songbird breeding biology can influence a predator's ability to predate the nest. Egg size affects rodent species ability to attack eggs (Degraaf & Maier, 1996; Degraaf et al., 1999) and corvid species predation strategy (Montevecchi, 1976). It has been suggested that because corvids preferentially remove eggs from the nest site, rather than consuming them in situ, they may favour predated species with smaller, lighter eggs (Haskell, 1995; Major, 1991).

Life history interactions between predators and prey could also be influential. Some species time their own breeding in accordance with the availability of specific prey, for example great tits (*Parus major*) have higher breeding success when caterpillar biomass is highest (Naef-Daenzer et al., 2000). Species which breed at the same time as their predators could therefore suffer increased nest predation.

We aimed to assess how variation in aspects of songbird breeding biology explained variation in rates of nest predation attributable to corvids. If a large number of potential prey species are not predated by corvids due to their breeding biology, then perhaps we should not be surprised if they do not respond to changes in corvid numbers. We concentrated on UK songbirds as there is a good understanding of their breeding biology (Cramp & Perrins, 1994; Cramp, 1992, 1988; Cramp et al.,

1994; Cramp & Perrins, 1993) and there are sufficient detailed previous studies of these species to attribute rates of nest predation to particular predators. UK songbirds merit focus as population declines are ongoing and a better understanding of the effect of predation on these species would provide further insight into this decline (Hayhow et al., 2015).

We also attempted to predict predation rates for each of the thirty-one UK breeding species for which we do not have empirical data using knowledge of their breeding biology. This in turn allowed us to examine the effects of breeding biology generally on corvid predation rates, and this may allow inferences to be made about non-UK species not included in this review. These results might permit us to ask which species are likely to be susceptible to nest predation by corvids and hence, which species might benefit from corvid removal.

2.2 METHODS

2.2.1 Literature search

A comprehensive search of the literature aimed to find any studies which reported nest predation rates of breeding UK songbirds. The search was limited to resident or migrant songbirds with more than 100 pairs breeding per year on average (Harrop et al., 2013). A total of 68 species were included. Details of the sources searched, and the criteria used, are provided as supporting information (*Appendix table A1*).

2.2.2 Analysis of papers

Over 5000 papers were initially screened through our literature search and results were extracted from 83 of them for this review (*Appendix table A2*). A small number of papers reported predation rates for multiple species ($n=13$) and rates for each species were extracted separately (hereafter referred to as cases). Sixty-nine papers provided just 1 case and 103 cases were included in total. We collected data for 37 of the original 68 species, with up to 10 separate studies contributing data to any one species. Twenty-five species were represented by just 1 or 2 cases. The 31 species for which no appropriate results were found included common species such as robin (*Erithacus rubecula*) and starling (*Sturnus vulgaris*) as well as birds which breed less frequently in the UK, such as the scottish crossbill (*Loxia scotica*). Despite there

being no time limit on the search 80% of studies that reported the required information were published from 1990 onwards.

2.2.3 Predation figures

Studies were only included if the nest predation rate could be extracted, either directly or by calculation, from the presented data. Nest predation rate was defined as the proportion of total breeding effort (eggs or nestlings) lost to predation. This was generally reported in studies as the number of nests predated out of the total number of nests monitored. To avoid false negatives, studies with a nest predation rate of 0 were only included when the authors explicitly stated that no predation had taken place. If no attempt was made to identify the predators responsible, then data was excluded. For example, in cases where predator identification methods (e.g. cameras) were only utilised for a sample of nests but no attempt was made to identify predators at other nests, then only a subset of the reported data was included. Some non-English language studies were included if the abstract was in English and the required detail could be extracted from the paper, for example Barkow (2005).

When studies manipulated aspects of breeding biology as part of their experimental protocol, for example Alatalo & Lundberg (1984) compared different nest box densities, results (total number of nests predated and total number of nests monitored) were summed across treatments. Within studies data was also summed across years when site and species were constant. This ensured consistency between studies as, due to variation in data presentation across sources, it was not always possible to separate data per year. Care was taken to avoid duplication; when the same data, or a subset of the same data, was reported across multiple studies the report with the clearest predator identification was used.

2.2.4 Predator identification

The proportion of predation attributed to different predators was directly extracted from the text where possible (67% of cases). In other cases, figures were estimated based on the information given (33% of cases), for example, 'most predation due to' was assumed conservatively to be 50% of predation. If no qualifiers were used to attribute predation to specific predators, then studies were excluded from further

analysis. Across all studies the difference between total predation events and predation events assigned to specific predator species were given a predator identity of 'unknown'.

Predator identification evidence quality was categorised and used to assess the reliability of the study's results. The studies which inferred the predators' identity from evidence at the nest, categorised as 'field signs', were considered separately to studies which observed predation, often using cameras, and were categorised as 'observed'. All other methods of identification, were considered generally less reliable, for example utilising information from previous studies of the site or knowledge of the local predator population, and were categorised as 'other'.

2.2.5 Prey species breeding biology parameters

Characteristics of the prey species' breeding biology considered likely to influence susceptibility to corvid nest predation were taken from Ferguson-Lees et al. (2011) and Harrison & Castell (2002). The first two characteristics that we considered affected the accessibility of the nest to corvids; firstly, nest type, which was classified as open or hole and secondly, nest height, which was categorised as either ground, low ($\leq 2\text{m}$) or high ($> 2\text{m}$) based on descriptions in the literature. As specific nest heights were generally not given in the studies included in this review, and the wider literature reported a range of possible nest heights for each species, this categorisation provided a solution which allowed consistency between species which have been more or less well studied. Two metres was chosen as a cut-off to distinguish species which nest low in shrub and hedgerows from those who nest higher in hedgerows and trees, due to potential differences in corvid encounter rates. Thirdly, egg size, which might affect corvids' ability to handle eggs, was given as egg length multiplied by width. Finally, the proportion of songbird species' breeding season which overlapped with magpie's breeding season was calculated. During their breeding season predators may prefer particular prey, such as eggs or chicks. If this is the case, the extent of breeding season overlap could affect the extent to which songbirds' nests are predated. Breeding seasons were defined as the period 90% of eggs or young were produced using data collected from 2000-2009 (Ferguson-Lees et al. 2011). In the case of the magpie this was early March to late June. The breeding season of the magpie was used as it was the most often cited

corvid predator in the studies found in our literature search and is the corvid most frequently controlled in predator removal studies focussing on passerine populations.

2.2.6 Study type

Studies of natural nests were distinguished from those using artificial nests. The ability of artificial nest studies to represent natural nest biology has been questioned, therefore we only included artificial nest studies if they attempted to mimic breeding biology of specific species. The factors influencing corvid predation of artificial nests may differ from those affecting the predation of natural nests. Consequently, we first analysed studies on natural nests by themselves, and then together with artificial nest studies. In the case of artificial nest studies equivalent values for the other characteristics of breeding biology were extracted directly from the papers.

2.2.7 Statistical analysis

The number of nests predated by corvids and the total number of nests were extracted from each study, and the effect of prey species biology on these nest predation rates was analysed using a generalised linear model (GLM) approach. We constructed two models; model A included studies only on natural nests and model B included all studies on natural and artificial nests.

There was high variance in the data due to the huge variation in sample sizes and nest predation rates reported by studies. To allow for this true overdispersion we assumed a quasi-binomial distribution with a logit link for the response variable. To account for non-independence of studies of the same species, species could have been fitted as random effect in a mixed model, however, the reliability of using quasi-families with mixed models has been questioned (Bolker, 2017). Therefore, the figures for number of nests predated and total number of nests extracted from papers was averaged across species (artificial nest studies were grouped by the species they aimed to mimic). These averaged values were fitted as a binomial response variable: number of nests predated by corvids (successes)/ (total nests - number of nests predated by corvids (failures)).

This essentially created a weighted average of proportion of nests predated by corvids for each species, giving greater weight to studies with larger sample

sizes. Models were also weighted by number of studies per species to account for increased confidence in predation rates based on a larger number of studies. This helped account for the much higher number of studies found for common study species such as blackbird (*Turdus merula*) and blue tit (*Cyanistes caeruleus*) compared to less well-studied species. Corvid predation rates per songbird species were therefore weighted by both sample size of studies and total number of studies.

Parameters of prey breeding biology (nest type, nest height, egg size and breeding season overlap with magpies) and category of evidence (field signs, observed, and other) were all included as explanatory variables in the GLMs. In model B, the study type (artificial or natural nests) was also included. Two-way interaction terms between the overlap with magpie breeding season term and the nest height, nest type and egg size terms were included to explicitly assess how the effect of corvid breeding biology was related to other aspects of songbird breeding biology. Further interaction terms between explanatory variables were not included to avoid overfitting the model to a relatively small sample size.

To assess the significance of explanatory terms the variables were removed one at a time and F tests were used to assess the changes in the models' deviance (Crawley, 2012). First order interaction terms that were not significant were removed from the minimal adequate models (MAMs) using backwards deletion, but all main effects were retained in final models. This meant we could assess the significance of main effects involved in non-significant interactions (Crawley, 2012; Fox et al., 2013) and identify the particular aspects of songbird breeding biology that affected corvid nest predation rate (Zuur et al., 2009; Crawley, 2012; Murtaugh, 2009). In addition, reducing model complexity generally reduces the uncertainty in model parameter estimates as the ratio of model parameters to independent data increases. This reduced uncertainty may mean that simpler models are preferred when models are used to predict values using new data (Fox et al., 2013). As we wished to use our model to predict corvid nest predation rates for songbird species for which we did not find empirical data, this method of model simplification was favoured.

Model predictions on the scale of response variable (proportion of nests predated by corvids) were extracted from both minimal models (A and B), and the

predictive ability of both minimal models (A and B) was assessed using the balanced accuracy metric. The predicted number of nest predated by corvids and the actual number of nests predated by corvids for each species was compared. The predicted numbers of nests predated was calculated by multiplying the predicted proportion of nests predated by the total number of nests given as the denominator in the original response variable. The balanced accuracy of models was calculated as $[(\text{specificity} + \text{sensitivity})/2]$. Sensitivity is the proportion of true positives (positives correctly predicted as such) as opposed to false positives (negatives incorrectly predicted as positives). Specificity is the proportion of true negatives (negatives correctly predicted as such) as opposed to false negatives (positives incorrectly predicted as negatives). As per the original response variable, positives in this case were nests predated by corvids and negatives were nests that were not predated. Balanced accuracy was used, as opposed to other metrics of model performance, to take into account the large difference in probability between positive and negative results (Féret & Asner, 2013). Nests were far more likely to not be predated (negative) than be predated (positive), if this difference in likelihood is not considered then the ability of the model to predict the more likely outcome has a greater influence in defining total error (Graves et al., 2016; Sebastián-González et al., 2015).

We then used the minimal model which had the best predictive ability to predict nest predation rates for species included in the literature search for which nest predation data was not found. Predictions on the scale of the response variable were calculated based on specified values of the explanatory variables: the attributes of breeding biology of the specific species (nest type, nest height, egg size, breeding season overlap with magpie), study type was defined as natural and evidence category as other (the most common result).

All analyses were carried out in R ver. 3.1.2 (R Core Team, 2017). Models were constructed using the lme4 package (Bates et al., 2014) and model accuracy was calculated using the confusion matrix function in the caret package (Kuhn, 2017). All mean averages are presented ± 1 SE.

2.3 RESULTS

2.3.1 Factors affecting rates of predation

Predation of songbird eggs and chicks attributed to corvids varied widely across the studies included in this review (ranging from 0 to 75% of breeding effort lost to corvid predation), with a mean of $10.29 \pm 1.48\%$ of nests lost to corvid predation. Across all species an average of $22.66 \pm 2.86\%$ of all nest predation was attributed to corvids.

Table 2.1: Generalised Linear Models showing parameter estimates for the fixed effects for the minimal adequate models (MAMs) of the rate of corvid predation of songbird nests including artificial nest studies (A) and excluding artificial nest studies (B). Non-significant interaction terms are not shown.

Fixed effects	Estimate (β)	SE	Test statistic (F)	df	P value
A					
Intercept (Nest height - Ground, Nest type - Hole, Evidence category - Field signs)	-10.57	2.12			
Nest height (Low)	4.05	1.43	10.68	2,29	<0.001*
Nest height (High)	2.27	1.34			
Overlap with MG breeding season	3.64	0.99	15.45	1,29	<0.001*
Nest type (Open)	4.12	1.25	26.98	1,29	<0.001*
Egg size	0.00	0.00	0.24	1,29	0.628
Evidence category (Observed)	1.32	1.30	7.60	2,29	0.002*
Evidence category (Other)	-1.39	0.42			
B					
Intercept (Nest height - Ground, Nest type - Hole, Evidence category - Field signs, Study type - Artificial nests)	-8.06	1.72			
Nest height (Low)	0.90	0.39	17.87	2,34	<0.001*
Nest height (Other)	1.00	0.52			
Overlap with MG breeding season	3.43	0.95	45.66	1,35	<0.001*
Nest type (Open)	5.50	1.45	37.96	1,34	<0.001*
Egg size	0.00	0.00	8.85	1,35	0.005*
Evidence category (Observed)	-2.22	0.77	8.53	2,34	<0.001*
Evidence category (Other)	1.00	1.26			
Study type (Natural nests)	0.70	0.46	8.53	1,34	0.006*
Overlap with MG breeding season*					
Egg size	0.02	0.01	8.83	1,34	0.005*

The rate of corvid predation experienced by a species was strongly predicted by aspects of its breeding biology [GLM: $F(7,29) = 16.39$; $P < 0.001$] (*Table 2.1A*).

Nest height was important, songbird species that nested off the ground but low in the canopy had a higher average corvid predation rate ($16.68 \pm 3.55\%$) than either ground nests ($7.76 \pm 3.55\%$) or nest located above 2m ($14.26 \pm 2.07\%$). This effect could be related to the significant main effect of nest type on predation rates, open nesting species experienced levels of corvid predation approximately 30 times higher than those of hole nesting species (open nesting species; $17.02 \pm 2.35\%$, hole nesting species; $0.66 \pm 0.42\%$). Hole nesting species that suffered low nest predation also tended to nest at heights above 2m whereas, open nesting species tended to nest below 2m (*Figure 2.1*).

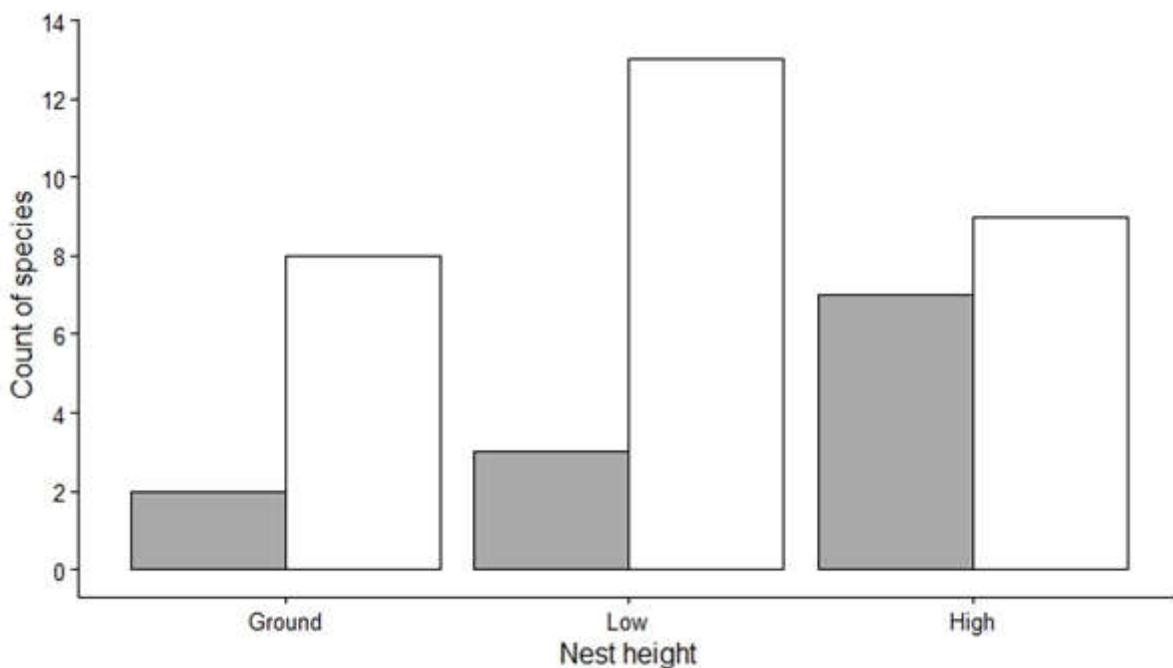


Figure 2.1: How nest height (ground/low/other) varies with nest type (open (white bars) /hole (grey bars)) in the species included in this literature review.

The degree of overlap between the breeding seasons of songbird species and magpies also predicted predation rates. Species which had breeding seasons that overlapped more with the breeding season of magpies suffered higher predation by corvids (*Figure 2.2*).

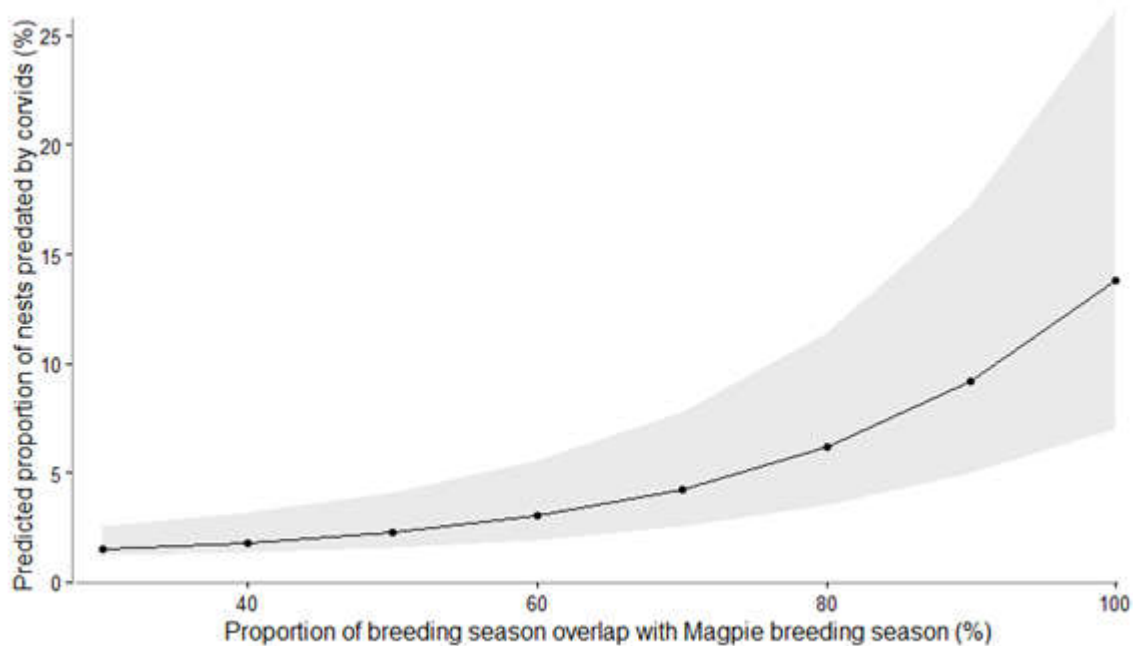


Figure 2.2: Predicted values of corvid nest predation rate relative to breeding season overlap with magpie. The probability is adjusted relative to the effects of the other variables in the MAM A. A 95% confidence interval is displayed around the estimated effect

Rates of reported corvid nest predation were influenced by the type of evidence used to identify predator type. Studies that used indirect evidence (for example observations of predators in the general vicinity of the field site) classed as 'other', were more likely to report lower rates of corvid predation than studies that used physical evidence of damage to nest and eggs (field signs) or directly observed predators at the nest (observed).

When studies which used artificial nests were included in the analysis they were found to exhibit higher nest predation by corvids when compared to studies of natural nests. Their average corvid nest predation rate was $17.12 \pm 5.11\%$ compared to $10.29 \pm 1.63\%$ for natural nests (*Table 2.1B*). The influence of some attributes of breeding biology, specifically nest height, nest type and evidence type were found to have the same effect on the corvid predation rate when artificial nests were included as when only natural nests were considered [GLM: $F(9,34) = 19.68$; $P < 0.001$] (*Table 2.1B*). Corvid predation rate was again greater when breeding season overlap with magpies was higher, but when artificial nests were included this effect was moderated by egg size. Greater breeding season overlap led to particularly high corvid predation rates when egg size was larger (*Figure 2.3*). This maybe because

artificial nest studies, with higher corvid predation rates, have generally larger egg sizes; the smallest egg used in artificial nest studies was three times larger than the smallest natural egg. Artificial nest studies that used larger eggs tended to have higher breeding season overlap. This was because nests in artificial nest studies were sometime exposed for a short amount of time, therefore had a relatively short 'breeding season', which could more easily fall entirely in the range of magpie breeding season. This means that studies with both large egg size and high breeding season overlap may be more likely to be artificial nest studies which generally have higher predation rates.

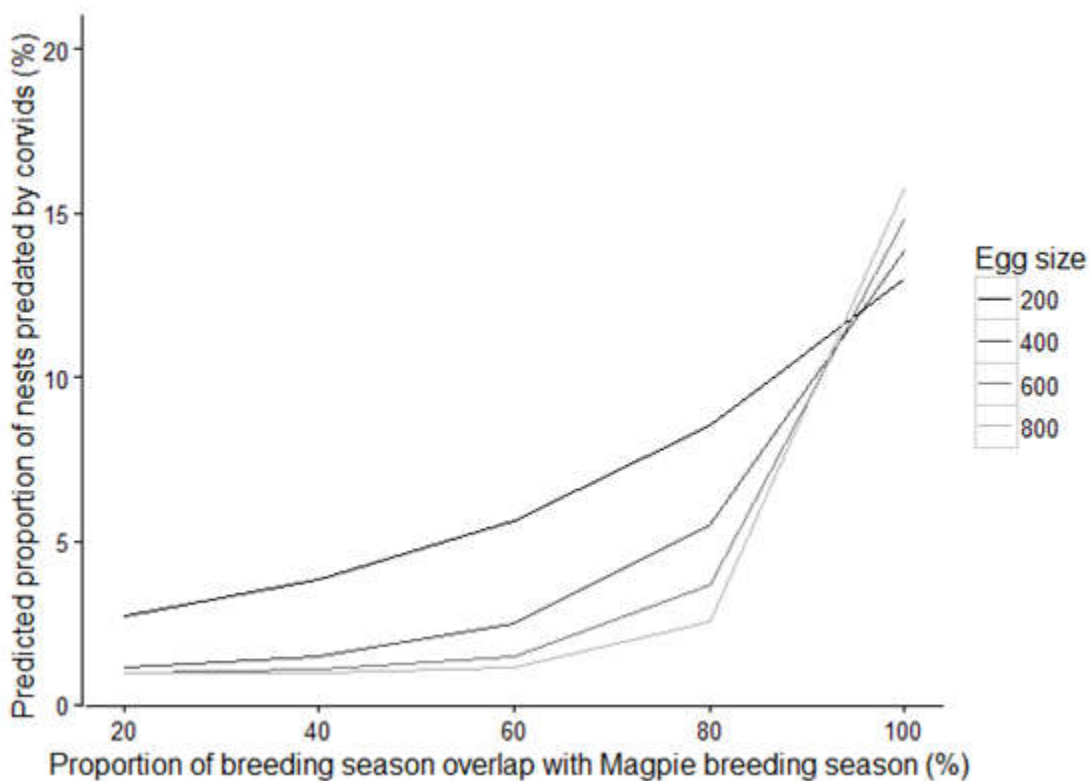


Figure 2.3: Predicted values of corvid nest predation rate relative to breeding season overlap with magpie displayed for fixed egg sizes (a relative measure of egg size was taken as egg height x egg width (mm)). The probability is adjusted relative to the effects of the other variables in the MAM B.

2.3.2 Model predictions

Both the minimal model A, which only included studies containing natural nests, and the minimal model B, which also included artificial nest, were found to have good predictive performance (balanced accuracy values of 87.7% and 89.0% respectively). As the latter model had a slightly higher predictive performance it was used to predict values on the scale of the response for the 31 UK breeding songbird

species for which reliable data on rates of corvid nest predation was not found in the literature (Table 2.2). All model predictions fell within the range of reported natural predation rates for other songbird species collected in the literature search.

Table 2.2: Predicted proportion of songbird species' nesting effort predated by corvids and count of studies from which values were taken. Where count of studies is 0, only model predictions on the scale of the response variable are shown (bold), for other studies averages from the literature included in this review are also shown.

Species	Count of cases included	Proportion of nests predated by corvids (%)	
		Prediction of the scale of the response	Average taken from the literature (data used to fit model)
Bearded tit (<i>Panurus biarmicus</i>)	0	40	
Blackbird (<i>Turdus merula</i>)	10	19	23
Blackcap (<i>Sylvia atricapilla</i>)	3	23	32
Blue tit (<i>Cyanistes caeruleus</i>)	7	0	0
Bullfinch (<i>Pyrrhula pyrrhula</i>)	0	9	
Cetti's warbler (<i>Cettia cetti</i>)	0	25	
Chaffinch (<i>Fringilla coelebs</i>)	1	5	28
Chiffchaff (<i>Phylloscopus collybita</i>)	2	74	6
Cirl bunting (<i>Emberiza cirlus</i>)	1	30	20
Coal tit (<i>Periparus ater</i>)	1	0	0
Common crossbill (<i>Loxia curvirostra</i>)	0	2	
Corn bunting (<i>Emberiza calandra</i>)	1	0	1
Crested tit (<i>Lophophanes cristatus</i>)	1	0	0
Dartford warbler (<i>Sylvia undata</i>)	0	24	
Dipper (<i>Cinclus cinclus</i>)	1	11	2
Dunnock (<i>Prunella modularis</i>)	1	23	32
Firecrest (<i>Regulus ignicapilla</i>)	0	7	
Garden warbler (<i>Sylvia borin</i>)	1	15	14
Goldcrest (<i>Regulus regulus</i>)	0	6	
Goldfinch (<i>Carduelis carduelis</i>)	0	3	
Grasshopper warbler (<i>Locustella naevia</i>)	0	4	
Great tit (<i>Parus major</i>)	5	0	0
Greenfinch (<i>Chloris chloris</i>)	2	3	1
Grey wagtail (<i>Motacilla cinerea</i>)	0	17	
Hawfinch (<i>Coccothraustes coccothraustes</i>)	0	3	
House martin (<i>Delichon urbicum</i>)	0	1	

House sparrow (<i>Passer domesticus</i>)	2	0	0
Lesser redpoll (<i>Carduelis cabaret</i>)	0	2	
Lesser whitethroat (<i>Sylvia curruca</i>)	2	21	20
Linnet (<i>Carduelis cannabina</i>)	3	18	28
Longtailed tit (<i>Aegithalos caudatus</i>)	2	41	45
Marsh tit (<i>Poecile palustris</i>)	1	1	14
Meadow pipit (<i>Anthus pratensis</i>)	0	2	
Mistle thrush (<i>Turdus viscivorus</i>)	0	6	
Nuthatch (<i>Sitta europea</i>)	5	0	0
Pied flycatcher (<i>Ficedula hypoleuca</i>)	6	0	0
Pied wagtail (<i>Motacilla alba</i>)	0	11	
Redstart (<i>Phoenicurus phoenicurus</i>)	1	1	0
Redwing (<i>Turdus iliacus</i>)	1	22	16
Reed bunting (<i>Emberiza schoeniclus</i>)	0	17	
Reed warbler (<i>Acrocephalus scirpaceus</i>)	2	11	5
Ring ouzel (<i>Turdus torquatus</i>)	1	1	0
Robin (<i>Erithacus rubecula</i>)	0	28	
Rock pipit (<i>Anthus petrosus</i>)	0	3	
Sand martin (<i>Riparia riparia</i>)	0	0	
Scottish crossbill (<i>Loxia scotica</i>)	0	2	
Sedge warbler (<i>Acrocephalus schoenbaenus</i>)	0	14	
Siskin (<i>Carduelis spinus</i>)	0	3	
Skylark (<i>Alauda arvensis</i>)	3	2	3
Song thrush (<i>Turdus philomelos</i>)	2	21	26
Spotted flycatcher (<i>Muscicapa striata</i>)	1	3	20
Starling (<i>Sturnus vulgaris</i>)	0	0	
Stonechat (<i>Saxicola rubicola</i>)	0	6	
Swallow (<i>Hirundo rustica</i>)	2	6	0
Tree pipit (<i>Anthus trivialis</i>)	0	2	
Tree sparrow (<i>Passer montanus</i>)	0	0	
Treecreeper (<i>Certhia familiaris</i>)	3	0	0
Twite (<i>Carduelis flavirostris</i>)	1	2	14
Wheatear (<i>Oenanthe oenanthe</i>)	2	0	1
Whinchat (<i>Saxicola rubetra</i>)	0	12	
Whitethroat (<i>Sylvia communis</i>)	1	16	15
Willow tit (<i>Poecile montax</i>)	1	1	0
Willow warbler (<i>Phylloscopus trochilus</i>)	0	4	
Wood warbler (<i>Phylloscopus sibilatrix</i>)	2	7	8
Woodlark (<i>Lullula arborea</i>)	2	17	4
Wren (<i>Troglodytes troglodytes</i>)	0	18	

Yellow wagtail (<i>Motacilla flava</i>)	1	3	5
Yellowhammer (<i>Emberiza citrinella</i>)	2	5	18

2.4 DISCUSSION

Corvids were found to be significant predators of UK songbirds, with approximately 10% of all nests reportedly lost to corvid predation, but the level of nest predation by corvids varied markedly across species. Such variation could be predicted by aspects of the songbird species' breeding biology. Species which nest in holes suffered far lower rates of nest predation by corvids. Conversely, species with open cup nests, situated off the ground but in low foliage, and with a high degree of overlap with the magpie's breeding season, suffered from 10% to over 60% of their nests being predated by corvids. These findings suggest that species may not respond in the same way to either population changes in corvids, or experimental removal of corvids. Such changes in corvid numbers are unlikely to directly affect hole nesting species such as great tit (predicted corvid predation rate 0%), but other species such as the open nesting blackcap may be very sensitive to corvid prevalence during the breeding season (predicted corvid predation rate 19%) (*Table 2.2*).

2.4.1 Factors influencing nest predation by corvids

The attributes of nest site, which we found to predict susceptibility to nest predation by corvids, were in accordance with those found to be influential in previous studies. The nests of hole nesting species have been shown to be inaccessible to most predators, although smaller predators such as rodents and snakes offer exceptions (Atienzar et al., 2010). Open nests are found to be more accessible to predators generally (Martin & Li, 1992) and to corvids in particular (Møller, 1987). This trend is shown clearly our results; hole nesting species had much lower rates of nest predation by corvids. We included studies using nest boxes, which are generally designed to reduce predation rates (Skwarska et al., 2009) and may have lower predation rates than nests in natural holes (Kuitunen & Makinen, 1993) but we do not believe this affected this trend. Approximately half of the studies on hole nesting species included in this review were on populations nesting in natural holes and although they reported higher predation rates ($2.72\% \pm 2.12$) than nest box studies

(0.37%±0.36), the reported predation rates were still much lower than the rates of nest predation suffered by open nesting species.

This difference in predation between open and hole nesting species may have also influenced the effect of nest height on corvid nest predation rate. The reduced rate of predation found for higher nests may have been partly driven by the increased proportion of hole nesting species, such as blue tit (predicted corvid predation rate 0%), which typically nest higher in the canopy. Species that nested low in the canopy ($\leq 2\text{m}$) experienced the highest rates of predation by corvids. This mirrors findings in other work. Corvids carry out an increasing proportion of nest predation as nest sites increase in height from ground to nests low in the shrub (Weidinger, 2002). Chiffchaff (*Phylloscopus collybita*) nests which were low in vegetation suffered higher predation in the nestling stage than those nearer the ground and this was attributed to greater visibility of higher nests to visually oriented predators such as corvids (Rodrigues & Crick, 1997). Nests placed higher in shrub may have less cover and concealment from vegetation than those near the ground. During the breeding season corvids spend more time in cover near their own nests (Vines, 1981; Birkhead, 1991), such as hedgerows and shrubs, rather than in more open habitats, such as crop fields, where ground nests are more likely to be located.

Although variation in attributes of nest site have often been related to differences in songbird nest predation risk, the effect of the timing of songbird breeding, and how it may interact with the phenology of predatory species, has been less frequently examined. The extent of overlap between the breeding season of the songbird and magpies' breeding season provided a strong predictor of a nest's likelihood of being predated. Magpies, and other corvids, may switch prey during their breeding season to meet the nutritional needs of their own young. A concentration on protein-rich vertebrate prey, specifically blue tits, is seen in tawny owls (*Strix aluco*) when they are feeding nestlings (Sasvari & Hegyi, 1998). Nest predation could also be a response to availability; the magpie breeding season may correspond to a general peak in nesting. It has been proposed that corvids are capable of forming a search image following repeated encounters of the same prey (Croze cited in Montevicchi 1976). Therefore, it may be that a sudden increase in

nest availability triggers the formation such an image, facilitating subsequent predation of this prey (Isaksson et al., 2007).

The timing of the breeding seasons of some bird species has been shown to shift in response to changes in climate. This may lead to differences in the timing of the breeding season between locations and through time, for example magpie median egg laying date in the UK has become earlier since 1939 (Crick & Sparks, 1999). Our analysis was unable to take into account any potential shift in breeding seasons through time and/or between locations. However, previous analysis of long-term data suggests that early breeders, such as magpies, are not more likely to have shifted breeding season than other later breeding species, and species from different taxonomic groups are equally likely to show a shift in breeding season (Crick, 2004). It seems unlikely that there would be a great discrepancy between songbird and corvid species' response to changes in climate over the period the studies included in this review were carried out. However, it may be that in the longer term, the extent of breeding season overlap between prey and different nest predators could change, influencing rates of nest predation experienced by prey species.

The results of our analysis also provide some insight into the methods used to examine the effects of variation in breeding biology on nest predation. Studies using artificial nests vary in methodology, and can differ from natural nests in numerous ways which might facilitate the higher rates of predation we observed in these studies. Artificial nest studies often use eggs that are larger than small songbird eggs, such as quails eggs and plasticine eggs (Ludwig et al., 2012; Erdos et al., 2011), and these may be more easily detected by predators. Man-made nest structures, for example grass lined wire baskets (Söderström et al., 1998), are unlikely to be as well constructed and concealed as natural nests and increased human activity around the nest may attract predators (Zanette, 2002). The exposure period of artificial nest studies can also be shorter than natural nesting periods, this could lead to particularly high magpie breeding season overlap that our results suggest leads to elevated nest predation rates. The inclusion of these artificial nest studies, which have unnatural nest site attributes and phenology, could affect the interpretation of the effect of attributes of breeding biology on corvid nest predation rates. When artificial nests were included in the analysis there was some evidence

that the effect of breeding season overlap on corvid nest predation was exaggerated when egg size was larger. This maybe because the studies with the largest eggs, which also had high breeding season overlap, were artificial nests studies that may already have elevated predation rates. We did not find an effect of egg size when only natural nests were considered. In this case, the relationship between breeding biology and corvid nest predation rates did differ when artificial nests were included alongside natural nests in the analysis. The ability of some artificial nests to represent natural patterns of predation, and composition of predator fauna, has been widely questioned (Zanette, 2002; Moore & Robinson, 2004; Pärt & Wretenberg, 2002). However, the effects of nest type, nest height and breeding season overlap with magpies on corvid nest predation rate were maintained when artificial nests were included in the analysis. It may be that artificial nests may be used, with caution, to assess how some attributes of breeding biology influence predation risk.

Accurate identification of nest predators is essential for our, and others, analysis (Ibáñez-Álamo et al., 2015). Comparisons of physical evidence at the nest and nest monitoring by camera has suggested that indirect methods of predator identification can be inaccurate (Schaefer, 2004). The results of our analysis suggest studies using these indirect methods (those which did not observe predators at the nest) did differ in the nest predators they identified; these studies were likely to attribute a lower proportion of predation to corvids. The increasing use of video technology, and consequent increase in predator identification accuracy, may facilitate more detailed understanding of how differences in nest predator fauna relate to prey breeding biology (Ibáñez-Álamo et al., 2015).

Although our analysis examined the effect of some the variation in methods used in the studies included in this review, we did not account for variation in predator abundance or ecology between studies, which could have influenced nest predation by specific predators. The data extracted from these studies were collected from several countries (twenty-two; mainly Western Europe) and over a relatively broad time scale (1954 – 2014; >80% from 1990 onwards). This made it very difficult to account for variation in predator population density in either time or space, which may explain differences in the relative contribution of different predator species across studies. However, analysis of European wide trends does suggests

that, for corvids at least, there has been geographically widespread long-term population growth (Voříšek et al., 2008).

2.4.2 Implications of findings

Our models indicate that particular songbird species are especially susceptible to nest predation by corvids, and this susceptibility arises from their breeding biology. Consequently, when correlational studies search for corresponding changes between corvid and songbird populations, or when corvids are experimentally removed from areas, it is perhaps not surprising that effects may be detected for some songbird species but not others. This may partly explain why previous work looking for relationships between corvids and songbirds has produced ambiguous results. These previous studies have included more resilient species, such as hole nesting species in their analysis (Thomson et al., 1998; Bolton et al., 2007a). However, these studies tended not to find population level correlations between changes in corvids and other songbirds, even amongst species that our study suggests should be especially vulnerable such as dunnock (*Prunella modularis*) (predicted corvid predation rate 23%) (Table 2.2) (Newson et al., 2010b; Thomson et al., 1998; Gooch et al., 1991). Given the high predation rates predicted for these species it seems that corvid predation could cause the loss of a large proportion of breeding effort. Therefore, it is perhaps surprising that increases in corvid populations, which might be expected to cause increase corvid nest predation rates, do not have discernible effects on these vulnerable songbird populations.

It may be that studies exploring the relationship between corvids and songbird populations are themselves not equally likely to detect an effect of corvids if present. Experimental studies may be more likely to show an effect of corvids on species that we predict to be vulnerable. The cases classed as experimental studies in Madden et al's (2015) review demonstrate the paucity of controlled experimental studies looking at the impact of corvids on songbirds. The cases are sourced from just five papers, the majority (60%) from Chiron & Julliard (2007). Some of these papers do report a negative effect of corvids on songbirds we consider susceptible. A significant negative relationship was found between corvid density and blackbird and song thrush (*Turdus philomelos*) nest survival rate (Stoate & Szczur, 2001b; White et al., 2008); both are open nesting species which nest above the ground and have

high overlap with magpie breeding season and we predicted that they would suffer high predation (predicted corvid predation rate of 19% and 21% respectively (*Table 2.2*)).

There are also cases where species we predict should be susceptible to corvid nest predation did not benefit from experimental corvid removal. When magpies were removed from an urban area, no overall effect was found for 14 songbird species (Chiron & Julliard, 2007). This lack of effect may be because of the specific location where the removal study occurred. For example, magpie removal in a suburban environment may have different consequences for songbird populations compared to those in rural environments, where most of our data came from, and where much of the population may live. Different factors affect predator-prey interaction in urban/suburban areas, for example, alternative anthropogenic food sources may facilitate prey-switching in predators (Stracey, 2011). Other habitat factors may also moderate the effect of corvid removal on species that are vulnerable to nest predation. The interactions between habitat and predator control maybe more important than either factor separately (Evans, 2004; van Oers et al., 2004). It may be that one of the reasons why White et al. (2014) did not find an improvement in daily nest survival of whitethroats (*Sylvia communis*) following systematic predator reduction, unlike in five other farmland songbird species, was because whitethroats are migratory and so did not benefit from the overwinter provision of grain that may have reduced starvation, or loss of condition, in other species. These removal studies also used population measures (as oppose to direct observations of nesting success) as indicators of responses to corvid removal which may mask variation in corvid nest predation.

Finally, there may be some cases when breeding populations of vulnerable species do not benefit from experimental corvid removal even in poor habitat. In these cases, it may be that nest predation by corvids does not cause additive mortality. In the absence of corvids, or following their removal, these individuals would simply be lost to other predators such as mammals (Côté & Sutherland, 1997; Holt et al., 2008; Bodey et al., 2009). This is supported by Parker (1984) who suggested that increased predation of nests by ermine (*Mustela erminea*) occurred in the absence of corvids. Bird breeding success might not be limited by nest

predation at all, it may be that other factors, such as ability to re-nest, have a greater influence in determining reproductive output (Nagy & Holmes, 2004). It may even be that breeding losses in general, are not a population limiting source of mortality. Overwinter losses have been found to be important in determining overall population trends in songbird species (Siriwardena et al., 2000a). Fletcher et al. (2010) did not find an increase of breeding numbers of meadow pipit and skylark following predator control, despite an increase in breeding success in meadow pipit the previous year. Our analysis has focused particularly on nesting losses, whereas other factors such as mortality at other life history stages or habitat change can also influence long-term population trends (Baillie & Peach 1992) and may also partly explain the lack of predation effect seen in these population level studies of species we expect to be vulnerable (*Chapter Three*).

Populations are unlikely to be limited by a single factor and developing a better understanding of the mechanisms which limit songbird populations will be critical in halting further population decline (Newton, 2004). There are examples of species, which we predict to be vulnerable to nest predation by corvids, showing some improvements in breeding success in response to general predator removal, whereas there are very few cases of species we predict to be less susceptible to corvid nest predation responding to corvid removal specifically (blue tit; Chiron & Julliard 2007). Consequently, it does not seem that the benefits of corvid predator removal can be entirely discounted for UK songbirds. Instead results from our analysis, which help predict vulnerability of songbird species to corvid nest predation, may help refine the application of corvid control to focus on songbird species that are most likely to benefit from reductions in nest predation by corvids

2.5 APPENDICES

2.5.1 Literature search method

Searches of multiple databases were carried out (see *Table A1*). In all databases two search perspectives were taken; one to identify reports of predation in studies of songbird reproduction and one to identify papers looking at corvid predation behaviour, which may also report corvid predation rates. The main search of scientific literature was carried out using Web of Science (apps.webof-knowledge.com). This search only included results from the Science and Technology research domain and there was no time limit. Irrelevant topics were excluded as were entirely non-English language papers. However, these searches still yielded nearly 5000 results (see *Table A1*).

As the type of studies that report this kind of ecological data may not always be in the published academic literature (Roodbergen et al., 2012), a number of other sources were also searched using similar criteria. These sources included UK and European thesis databases (EThOS (Electronic Thesis Online Service), DART-Europe (E-theses Portal)) and a grey literature database (Open Grey (System for Information on Grey Literature in Europe)). The literature of the Game and Wildlife Conservation Trust was searched as their research is likely to include work that specialises in the effect of predation on songbird populations; predator control is often an important part of land management for game. Finally, we included breeding success figures reported in Handbook of the birds of Europe, the Middle East and North Africa; the Birds of the Western Palearctic, Volumes V - IV (Cramp et al. 1994; Cramp 1988; Cramp 1992; Cramp 1993) (see *Table A1*). The results of searches from different sources were cross-referenced to avoid duplication.

Table A1: Literature sources searched

Source	Search criteria	Dates of search	No of results
Web of Science (apps.webof-knowledge.com)	("Songbird species name") AND ("nest predation" OR breeding OR productivity)	October 2014 - January 2015	4462
EThOS (Electronic Thesis Online Service)	"Songbird species name" OR Common name AND productivity OR breeding OR nest OR "nest predat*"	December 2014 - January 2015	72
GWCT (Game and Wildlife Trust Scientific Publications)	Keyword searches e.g. (Songbird species name) or (Predation)	December 2014 and January 2015	33
Open Grey (System for Information on Grey Literature in Europe)	(Songbird species name) AND (Nest predation)	December 2014 and January 2015	38
DART-Europe (E-theses Portal)	(Songbird species name) AND (Nest predation)	December 2014 and January 2015	6
Handbook of the birds of Europe, the Middle East and North Africa; the Birds of the Western Palearctic, Volumes V - IV	Songbird species name > Breeding	December 2014 and January 2015	38
Web of Science (apps.webof-knowledge.com)	(corvid OR crow OR rook OR jackdaw OR corvus OR magpie OR pica OR jay OR garrulus) AND (predat*) AND (songbird OR passerine OR wader OR artificial nest* OR dummy nest)	October 2014	309
EThOS (Electronic Thesis Online Service)		October 2014	55
GWCT (Game and Wildlife Trust Scientific Publication)	Keyword search e.g. (Corvid species name) or (Predation)	October 2014	246
Open Grey (System for Information on Grey Literature in Europe)	Keyword search e.g. (Corvid species name) or (Predation)	October 2014	46
DART-Europe (E-theses Portal)	Keyword search e.g. (Corvid species name) or (Predation)	October 2014	2
Total			5307

2.5.2 Inclusion criteria

Based on title, and in some cases abstract, papers produced by these searches were manually checked to see if they were related to the breeding biology of prey species specified in the initial search. Studies based outside of the range of the UK corvid species were excluded at this point. Artificial nest studies were included based on the identity of the species they were aiming to mimic. This meant studies based on non-UK songbirds (see Roos & Part 2004) were excluded. In total 606 accessible studies were analysed further.

Table A2: Summary of 83 papers which provided the 103 nest predation rates (cases) included in the analysis, ordered by source paper (ANSpecies name refers to artificial nest studies and the species they aimed to mimic)

Prey Species	Study	Case	Country	Reference
ANBlackbird	9	1	UK	Chamberlain, D., 1994. <i>The factors affecting reproductive success and breeding density in a rural population of blackbirds, Turdus merula L.</i> Thesis. University of Oxford.
ANBlackbird	11	1	UK	Cresswell, W., 1997. Nest predation rates and nest detectability in different stages of breeding in Blackbirds <i>Turdus merula</i> . <i>J. Avian Biol.</i> , 28(4), pp.296–302.
ANBlackbird	22	1	France	Grégoire, A. et al., 2003. Nest predation in Blackbirds (<i>Turdus merula</i>) and the influence of nest characteristics. <i>Ornis Fenn.</i> , 80(1), pp.1–10.
ANBlackbird	39	1	Hungary	Kurucz, K. et al., 2010. Survival probabilities of first and second clutches of Blackbird (<i>Turdus merula</i>) in an urban environment. <i>Arch. Biol. Sci.</i> , 62(2), pp.489–493.
ANBlackbird	40	1	Hungary	Kurucz, K., Bertalan, L. & Purger, J.J., 2012. Survival of blackbird (<i>Turdus merula</i>) clutches in an urban environment: experiment with real and artificial nests. <i>North.</i>

				<i>West. J. Zool.</i> , 8(2), pp.362–364.
ANBlackbird	51	1	Denmark	Møller, A.P., 1988. Nest predation and nest site choice in passerine birds in habitat patches of difference size; A study of Magpies and Blackbirds. <i>Oikos</i> , 53(2), pp.215–221.
ANBlackbird	52	1	Denmark	Møller, A.P., 1990. Nest predation selects for small nest size in the blackbird. <i>Oikos</i> , 57(2), pp.237–240.
ANPiedflycatcher	37	1	Latvia	Krams, I. et al., 2007. Long-lasting mobbing of the pied flycatcher increases the risk of nest predation. <i>Behav. Ecol.</i> , 18(6), pp.1082–1084.
ANReedwarbler	76	1	Slovakia	Trnka, A. et al., 2014. Management of reedbeds: mosaic reed cutting does not affect prey abundance and nest predation rate of reed passerine birds. <i>Wetl. Ecol. Manag.</i> , 22(3), pp.227–234.
ANReedwarbler	77	1	Slovakia	Trnka, A., Peterkova, V. & Grujbarova, Z., 2011. Does Reed Bunting (<i>Emberiza schoeniclus</i>) predict the risk of nest predation when choosing a breeding territory? An experimental study. <i>Ornis Fenn.</i> , 88(3), pp.179–184.
ANSkylark	50	1	Denmark	Møller, A.P., 1989. Nest site selection across Field-Woodland ecotones – The effect of nest predation. <i>Oikos</i> , 56(2), pp.240–246.
ANSongthrush	21	1	Sweden	Götmark, F., 1992. Blue eggs do not reduce nest predation in the Song thrush, <i>Turdus philomelos</i> . <i>Behav. Ecol. Sociobiol.</i> , 30(3–4), pp.245–252.
ANWheatear	58	1	Sweden	Pärt, T. & Wretenberg, J., 2002. Do artificial nests reveal relative nest predation risk for real

				<p>nests? <i>J. Avian Biol.</i>, 33(1), pp.39–46.</p>
ANYellowhammer	14	1	Poland	<p>Ejsmond, M.J., 2008. The effect of mowing on next-year predation of grassland bird nests: experimental study. <i>Polish J. Ecol.</i>, 56(2), pp.299–307.</p>
ANYellowhammer	45	1	Germany	<p>Ludwig, M. et al., 2012. Landscape-moderated bird nest predation in hedges and forest edges. <i>Acta Oecologica-International J. Ecol.</i>, 45, pp.50–56.</p>
ANYellowhammer	46	1	UK	<p>MacLeod, C.J., 2001. <i>Breeding ecology of the farmland yellowhammer (Emberiza citrinella): a Scottish case study</i>. Thesis. University of Dundee.</p>
ANYellowhammer	73	1	Sweden	<p>Söderström, B. et al., 1998. Different nest predator faunas and nest predation risk on ground and shrub nests at forest ecotones: an experiment and a review. <i>Oecologia</i>, 117(1–2), pp.108–118.</p>
Blackbird	4	1	Germany	<p>Barkow, A., 2005. Predation on passerine nests in hedges: the impact of nest placement, hedge structure, season and predators. <i>Vogelwelt</i>, 126(4), pp.346–352.</p>
Blackbird	6	1	UK	<p>Bonnington, C., Gaston, K.J. & Evans, K.L., 2013. Fearing the feline: domestic cats reduce avian fecundity through trait-mediated indirect effects that increase nest predation by other species. <i>J. Appl. Ecol.</i>, 50(1), pp.15–24.</p>
Blackbird	9	2	UK	<p>Chamberlain, D., 1994. <i>The factors affecting reproductive success and breeding density in a rural population of blackbirds, Turdus merula L.</i> Thesis. University of Oxford.</p>
Blackbird	11	2	UK	<p>Cresswell, W., 1997. Nest predation rates and nest</p>

				detectability in different stages of breeding in Blackbirds <i>Turdus merula</i> . <i>J. Avian Biol.</i> , 28(4), pp.296–302.
Blackbird	23	1	UK	Groom, D.W., 1993. Magpie <i>Pica-pica</i> predation on Blackbird <i>Turdus-merula</i> nests in urban areas. <i>Bird Study</i> , 40(1), pp.55–62.
Blackbird	26	1	UK	Hatchwell, B.J., Chamberlain, D.E. & Perrins, C.M., 1996. The reproductive success of blackbirds <i>Turdus merula</i> in relation to habitat structure and choice of nest site. <i>Ibis</i> , 138(2), pp.256–262.
Blackbird	30	1	Spain (Guejar)	Ibáñez-Álamo, J.D. & Soler, M., 2010. Investigator activities reduce nest predation in blackbirds <i>Turdus merula</i> . <i>J. Avian Biol.</i> , 41(2), pp.208–212.
Blackbird	30	2	Spain (Lecrin)	Ibáñez-Álamo, J.D. & Soler, M., 2010. Investigator activities reduce nest predation in blackbirds <i>Turdus merula</i> . <i>J. Avian Biol.</i> , 41(2), pp.208–212.
Blackbird	31	1	Spain	Ibáñez-Álamo, J.D. et al., 2014. Is nest predation an important selective pressure determining fecal sac removal? The effect of olfactory cues. <i>J. Ornithol.</i> , 155(2), pp.491–496.
Blackbird	75	1	Poland	Tomiałojć, L., 1995. Breeding ecology of the blackbird <i>Turdus merula</i> studied in the primaeval forest of Białowieża (Poland): Part 2. Reproduction and mortality. <i>Acta Ornithol.</i> , 29(2), pp.101–121.
Blackcap	4	2	Germany	Barkow, A., 2005. Predation on passerine nests in hedges: the impact of nest placement, hedge structure, season and predators. <i>Vogelwelt</i> , 126(4), pp.346–352.
Blackcap	66	1	Germany	Schaefer, T., 2004. Video monitoring of shrub-nests

				reveals nest predators. <i>Bird Study</i> , 51(2), pp.170–177.
Blackcap	80	1	Poland	Węgrzyn, E. & Leniowski, K., 2011. Nest site preferences and nest success in Blackcaps <i>Sylvia atricapilla</i> in Poland. <i>Ardeola</i> , 58(1), pp.113–124.
Blue tit	20	1	Spain	García-Navas, V. & Jose Sanz, J., 2011. Seasonal decline in provisioning effort and nestling mass of Blue Tits <i>Cyanistes caeruleus</i> : experimental support for the parent quality hypothesis. <i>Ibis</i> , 153(1), pp.59–69.
Blue tit	28	1	UK	Hinsley, S.A., Rothery, P. & Bellamy, P.E., 1999. Influence of woodland area on breeding success in Great Tits <i>Parus major</i> and Blue Tits <i>Parus caeruleus</i> . <i>J. Avian Biol.</i> , 30(3), pp.271–281.
Blue tit	32	1	Austria	Jacot, A., Valcu, M. & Kempenaers, B., 2010. Within-season divorce in Blue Tits (<i>Cyanistes caeruleus</i>). <i>J. Ornithol.</i> , 151(2), pp.477–482.
Blue tit	33	1	Poland	Kaliński, A. et al., 2014. Does the threat of European Pine Marten (<i>Martes martes</i>) predation influence the height of nests built by Blue Tits (<i>Cyanistes caeruleus</i>) and Great Tits (<i>Parus major</i>)? <i>Avian Biol. Res.</i> , 7(2), pp.83–90.
Blue tit	63	1	Spain	Robles, H., Ciudad, C. & Matthysen, E., 2011. Tree-cavity occurrence, cavity occupation and reproductive performance of secondary cavity-nesting birds in oak forests: The role of traditional management practices. <i>For. Ecol. Manage.</i> , 261(8), pp.1428–1435.
Blue tit	68	1	Sweden	Scholin, K.-G. & Kallander, H., 2013. The breeding biology of the Coal Tit <i>Pariparus ater</i> in

				South Central Sweden. <i>Ornis Svecica</i> , 23(3–4), pp.151–158.
Blue tit	82	1	Poland	Wesołowski, T. & Rowiński, P., 2012. The breeding performance of Blue Tits <i>Cyanistes caeruleus</i> in relation to the attributes of natural holes in a primeval forest. <i>Bird Study</i> , 59(4), pp.437–448.
Chaffinch	24	1	Finland	Hanski, I.K. & Laurila, A., 1993. High nest predation rate in the Chaffinch. <i>Ornis Fenn.</i> , 70(2), pp.65–70.
Chiffchaff	4	3	Germany	Barkow, A., 2005. Predation on passerine nests in hedges: the impact of nest placement, hedge structure, season and predators. <i>Vogelwelt</i> , 126(4), pp.346–352.
Chiffchaff	65	1	UK	Rodrigues, M. & Crick, H.Q.P., 1997. The breeding biology of the Chiffchaff <i>Phylloscopus collybita</i> in Britain: a comparison of an intensive study with records of the BTO Nest Record Scheme. <i>Bird Study</i> , 44(3), pp.374–383.
Cirl bunting	17	1	UK	Evans, A.D. et al., 1997. Seasonal variation in breeding performance and nestling diet of Cirl Buntings <i>Emberiza cirlus</i> in England. <i>Bird Study</i> , 44(1), pp.66–79.
Coal tit	67	1	Sweden	Scholin, K.-G. & Kallander, H., 2012. A Blue Tit <i>Cyanistes caeruleus</i> population: its recent increase and breeding data. <i>Ornis Svecica</i> , 22(1–2), pp.19–24.
Corn bunting	7	1	UK	Brickle, N.W. et al., 2000. Effects of agricultural intensification on the breeding success of corn buntings <i>Miliaria calandra</i> . <i>J. Appl. Ecol.</i> , 37(5), pp.742–755.
Crested tit	3	1	Russia	Bardin 1986 cited in Cramp, S; Perrins, C.M., 1993. <i>Handbook of the Birds of Europe, the</i>

				<i>Middle East and North Africa: The Birds of the Western Palearctic: Vol 7, Flycatchers to Shrikes</i> , Oxford University Press.
Dipper	71	1	Ireland	Smiddy, P. & O'Halloran, J., 2010. Breeding biology of Barn Swallows <i>Hirundo rustica</i> in Counties Cork and Waterford, Ireland. <i>Bird Study</i> , 57(2), pp.256–260.
Dunnock	4	4	Germany	Barkow, A., 2005. Predation on passerine nests in hedges: the impact of nest placement, hedge structure, season and predators. <i>Vogelwelt</i> , 126(4), pp.346–352.
Garden warbler	4	5	Germany	Barkow, A., 2005. Predation on passerine nests in hedges: the impact of nest placement, hedge structure, season and predators. <i>Vogelwelt</i> , 126(4), pp.346–352.
Great tit	28	2	UK	Hinsley, S.A., Rothery, P. & Bellamy, P.E., 1999. Influence of woodland area on breeding success in Great Tits <i>Parus major</i> and Blue Tits <i>Parus caeruleus</i> . <i>J. Avian Biol.</i> , 30(3), pp.271–281.
Great tit	33	2	Poland	Kaliński, A. et al., 2014. Does the threat of European Pine Marten (<i>Martes martes</i>) predation influence the height of nests built by Blue Tits (<i>Cyanistes caeruleus</i>) and Great Tits (<i>Parus major</i>)? <i>Avian Biol. Res.</i> , 7(2), pp.83–90.
Great tit	64	2	Spain	Robles, H., Ciudad, C. & Matthysen, E., 2011. Tree-cavity occurrence, cavity occupation and reproductive performance of secondary cavity-nesting birds in oak forests: The role of traditional management practices. <i>For. Ecol. Manage.</i> , 261(8), pp.1428–1435.
Great tit	69	1	UK	Shuttleworth, C.M., 2001. Interactions between the red

				squirrel (<i>Sciurus vulgaris</i>), great tit (<i>Parus major</i>) and jackdaw (<i>Corvus monedula</i>) whilst using nest boxes. <i>J. Zool.</i> , 255, pp.269–272.
Great tit	70	1	Poland	Skwarska, J.A. et al., 2009. Opportunity makes a predator: Great Spotted Woodpecker predation on Tit broods depends on nest box design. <i>Ornis Fenn.</i> , 86(3), pp.109–112.
Greenfinch	36	1	Poland	Kosiński, Z., 2001. The breeding ecology of the Greenfinch <i>Carduelis chloris</i> in urban conditions (study in Krotoszyn, W Poland). <i>Acta Ornithol.</i> , 36(2), pp.111–121.
Greenfinch	53	1	UK	Monk, J.F., 1954. The Breeding Biology of the Greenfinch. <i>Bird Study</i> , 1(1), pp.2–14.
House sparrow	10	1	Spain	Cordero 1999 cited in Cramp, S; Perrins, C.M., 1994. <i>Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic Vol 9: Buntings and New World Warblers.</i> , Oxford University Press.
House sparrow	59	1	UK	Peach, W.J. et al., 2008. Reproductive success of house sparrows along an urban gradient. <i>Anim. Conserv.</i> , 11(6), pp.493–503.
Lesser whitethroat	4	6	Germany	Barkow, A., 2005. Predation on passerine nests in hedges: the impact of nest placement, hedge structure, season and predators. <i>Vogelwelt</i> , 126(4), pp.346–352.
Lesser whitethroat	41	1	Kazakstan	Levin and Gubin 1985 cited in Cramp, S., 1992. <i>Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palearctic: Vol 6, Warblers</i> , Oxford University Press.
Linnet	13	1	Denmark (Sjællemosegaard)	Drachmann, J., Broberg, M.M. & Søggaard, P., 2002. Nest

				predation and semicolonial breeding in Linnets <i>Carduelis cannabina</i> . <i>Bird Study</i> , 49(1), pp.35–41.
Linnet	13	2	Denmark (Langholm)	Drachmann, J., Broberg, M.M. & Søgaaard, P., 2002. Nest predation and semicolonial breeding in Linnets <i>Carduelis cannabina</i> . <i>Bird Study</i> , 49(1), pp.35–41.
Linnet	54	1	UK	Moorcroft, D. & Wilson, J.D., 2000. The ecology of Linnets <i>Carduelis cannabina</i> on lowland farmland N. J. Aebischer et al., eds.,
Long-tailed tit	25	1	UK	Hatchwell, B.J. et al., 1999. Reproductive success and nest-site selection in a cooperative breeder: Effect of experience and a direct benefit of helping. <i>Auk</i> , 116(2), pp.355–363.
Long-tailed tit	27	1	Spain	Hernández, A., 2010. Breeding ecology of Long-tailed tit <i>Aegithalos caudatus</i> in northwestern Spain: phenology, nest-site selection, nest success and helping behaviour. <i>Ardeola</i> , 57(2), pp.267–284.
Marsh tit	44	1	Germany	Ludescher 1973 Cramp, S; Perrins, C.M., 1993. <i>Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palearctic: Vol 7, Flycatchers to Shrikes</i> , Oxford University Press.
Nuthatch	15	1	Sweden	Enoksson, B., 1993. Effects of female age on reproductive success in European Nuthatches breeding in natural cavities. <i>Auk</i> , 110(2), pp.215–221.
Nuthatch	42	1	Germany	Lohrl 1967 cited in Cramp, S; Perrins, C.M., 1993. <i>Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western</i>

				<i>Palaearctic: Vol 7, Flycatchers to Shrikes</i> , Oxford University Press.
Nuthatch	57	1	Sweden	Nilsson, S.G. (1987). Limitation and Regulation of Population Density in the Nuthatch <i>Sitta europaea</i> (Aves) Breeding in Natural Cavities. <i>Journal of Animal Ecology</i> . 56(3). pp. 921–937.
Nuthatch	62	1	Siberia	Pravosudov, V. V, 1993. Breeding biology of the Eurasian Nuthatch in Northeastern Siberia. <i>Wilson Bull.</i> , 105(3), pp.475–482.
Nuthatch	81	1	Poland	Wesołowski, T. & Rowiński, P., 2004. Breeding behaviour of Nuthatch <i>Sitta europaea</i> in relation to natural hole attributes in a primeval forest. <i>Bird Study</i> , 51(2), pp.143–155.
Pied flycatcher	1	1	Sweden	Alatalo, R. V & Lundberg, A., 1984. Density-dependence in breeding success of the Pied flycatcher (<i>Ficedula-hypoleuca</i>) <i>J. Anim. Ecol.</i> , 53(3), pp.969–977.
Pied flycatcher	5	1	Netherlands	Bauchau, V., 1997. Do parasitic mites decrease growth of nestling Pied Flycatchers <i>Ficedula hypoleuca</i> ? <i>Ardea</i> , 85(2), pp.243–247.
Pied flycatcher	12	1	Poland	Czeczewik, D., 2004. Breeding success and timing of the Pied Flycatcher <i>Ficedula hypoleuca</i> nesting in natural holes and nest-boxes in the Białowieża Forest, Poland. <i>Acta Ornithol.</i> , 39(1), pp.15–20.
Pied flycatcher	16	1	Switzerland	Epprecht 1985 cited in Cramp, S; Perrins, C.M., 1993. <i>Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palaearctic: Vol 7, Flycatchers to Shrikes</i> , Oxford University Press.

Pied flycatcher	55	1	Finland	Morosinotto, C. et al., 2012. Higher nest predation risk in association with a top predator: mesopredator attraction? <i>Oecologia</i> , 170(2), pp.507–515.
Pied flycatcher	79	1	Finland	Veistola, S., Lehikoinen, E. & Eeva, T., 1997. Weather and breeding success at high latitudes - The pied flycatcher <i>Ficedula hypoleuca</i> and the Siberian tit <i>Parus cinctus</i> . <i>Ornis Fenn.</i> , 74(2), pp.89–98.
Redstart	78	1	Finland	Veistola, S. et al., 1996. The breeding biology of the Redstart <i>Phoenicurus</i> in a marginal area of Finland. <i>Bird Study</i> , 43(3), pp.351–355.
Redwing	2	1	Sweden	Arheimer 1973 cited in Cramp, S., 1988. <i>Handbook of the birds of Europe, the Middle East, and North Africa: the birds of the western Palearctic. Vol. 5, Tyrant flycatchers to thrushes</i> , Oxford University Press.
Reed warbler	8	1	UK	Catchpole, C.K., 1974. Habitat selection and breeding success in reed warbler (<i>Acrocephalus scirpaceus</i>). <i>J. Anim. Ecol.</i> , 43(2), p.363-.
Reed warbler	29	1	Czech Republic	Honza, M. et al., 1998. Survival of Reed Warbler <i>Acrocephalus scirpaceus</i> clutches in relation to nest position. <i>Bird Study</i> , 45(1), pp.104–108.
Reed warbler	43	1	Spain	Lopez-Iborra, G.M., Pinheiro, R.T., Sancho, C. & Martinez, A. (2004). Nest size influences nest predation risk in two coexisting <i>Acrocephalus</i> Warblers. <i>Ardea</i> . 92(1). pp. 85–91.
Ring ouzel	35	1	Rumania	Korodi Gal 1970 cited in Cramp, S., 1988. <i>Handbook of the birds of Europe, the Middle East, and North Africa: the birds of the western Palearctic. Vol. 5, Tyrant flycatchers to thrushes</i> , Oxford University Press.

Skylark	56	1	UK (Video)	Morris, A.J. & Gilroy, J.J., 2008. Close to the edge: predation risks for two declining farmland songbirds. <i>Ibis.</i> , 150(s1), pp.168–177.
Skylark	60	1	Czech Republic	Praus, L. & Weidinger, K., 2010. Predators and nest success of Sky Larks <i>Alauda arvensis</i> in large arable fields in the Czech Republic. <i>Bird Study</i> , 57(4), pp.525–530.
Skylark	61	1	Netherland	Praus, L. et al., 2014. Predators and predation rates of Skylark <i>Alauda arvensis</i> and Woodlark <i>Lullula arborea</i> nests in a semi-natural area in The Netherlands. <i>Ardea</i> , 102(1), pp.87–94.
Song thrush	4	7	Germany	Barkow, A., 2005. Predation on passerine nests in hedges: the impact of nest placement, hedge structure, season and predators. <i>Vogelwelt</i> , 126(4), pp.346–352.
Song thrush	34	1	Ireland	Kelleher, K.M. & O'Halloran, J., 2006. Breeding biology of the Song Thrush <i>Turdus philomelos</i> in an island population. <i>Bird Study</i> , 53(2), pp.142–155.
Spotted flycatcher	74	1	UK	Stevens, D.K. et al., 2008. Predators of Spotted Flycatcher <i>Muscicapa striata</i> nests in southern England as determined by digital nest cameras. <i>Bird Study</i> , 55(2), pp.179–187.
Swallow	48	1	UK	McGinn, D.B. & Clark, H., 1978. Some Measurements of Swallow Breeding Biology in Lowland Scotland. <i>Bird Study</i> , 25(2), pp.109–118.
Swallow	72	1	Ireland	Smiddy, P. et al., 1995. The breeding biology of the Dipper <i>Cinclus-cinclus</i> in south-west Ireland. <i>Bird Study</i> , 42(1), pp.76–81.
Treecreeper	19	1	UK	Flegg 1973 cited in Cramp, S; Perrins, C.M., 1993. <i>Handbook of the Birds of Europe, the Middle East and North Africa:</i>

				<i>The Birds of the Western Palearctic: Vol 7, Flycatchers to Shrikes</i> , Oxford University Press.
Treecreeper	38	1	Finland	Kuitunen, M. & Aleknonis, A., 1992. Nest predation and breeding success in common Treecreepers nesting in boxes and natural cavities. <i>Ornis Fenn.</i> , 69(1), pp.7–12.
Treecreeper	38	2	Lithuania	Kuitunen, M. & Aleknonis, A., 1992. Nest predation and breeding success in common Treecreepers nesting in boxes and natural cavities. <i>Ornis Fenn.</i> , 69(1), pp.7–12.
Wheatear	49	1	Germany	Meffert, P.J., Marzluff, J.M. & Dziock, F. (2012). Unintentional habitats: Value of a city for the wheatear (<i>Oenanthe oenanthe</i>). <i>Landscape and Urban Planning</i> . 108 (1). p.pp. 49–56.
Wheatear	58	2	Sweden	Pärt, T. & Wretenberg, J., 2002. Do artificial nests reveal relative nest predation risk for real nests? <i>J. Avian Biol.</i> , 33(1), pp.39–46.
Whitethroat	4	8	Germany	Barkow, A., 2005. Predation on passerine nests in hedges: the impact of nest placement, hedge structure, season and predators. <i>Vogelwelt</i> , 126(4), pp.346–352.
Willow tit	3	2	Russia	Bardin 1986 cited in Cramp, S; Perrins, C.M., 1993. Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palearctic: Vol 7, Flycatchers to Shrikes, Oxford University Press.
Wood warbler	47	1	UK	Mallord, J.W. et al., 2012. Mortality of Wood Warbler <i>Phylloscopus sibilatrix</i> nests in Welsh Oakwoods: predation rates and the identification of nest predators using miniature

				nest cameras. <i>Bird Study</i> , 59(3), pp.286–295.
Wood warbler	83	1	Poland	Wesołowski, T., 1985. The breeding ecology of the Wood Warbler <i>Phylloscopus-sibilatrix</i> in primeval forest. <i>Ornis Scand.</i> , 16(1), pp.49–60.
Woodlark	18	1	UK	Eyre, J. & Baldwin, J., 2014. Nest productivity of Woodlarks: a case study on the Thames Basin Heaths. <i>Br. Birds</i> , 107(2), pp.92–102.
Woodlark	61	2	Netherland	Praus, L. et al., 2014. Predators and predation rates of Skylark <i>Alauda arvensis</i> and Woodlark <i>Lullula arborea</i> nests in a semi-natural area in The Netherlands. <i>Ardea</i> , 102(1), pp.87–94.
Yellow wagtail	56	2	UK	Morris, A.J. & Gilroy, J.J., 2008. Close to the edge: predation risks for two declining farmland songbirds. <i>Ibis.</i> , 150(s1), pp.168–177.
Yellowhammer	4	9	Germany	Barkow, A., 2005. Predation on passerine nests in hedges: the impact of nest placement, hedge structure, season and predators. <i>Vogelwelt</i> , 126(4), pp.346–352.
Yellowhammer	46	2	UK	MacLeod, C.J., 2001. <i>Breeding ecology of the farmland yellowhammer (Emberiza citrinella): a Scottish case study</i> . Thesis. University of Dundee.

Chapter Three

Variation in the effect of corvid predation on songbird population numbers



ABSTRACT

Predation is a major cause of mortality of the eggs and chicks of songbirds in the nest. Corvids are presumed to be significant predators of eggs and chicks in the nest (nest predators), therefore we might expect songbird species' population numbers to increase following corvid removal. However, previous studies have shown that this is sometimes, but not always, the case. Such effects may be species-specific because variation in life history patterns may mean some species are more (or less) susceptible to mortality during the nesting period. Differences in breeding biology may mean that species differ in their susceptibility to corvid nest predation. If the nesting mortality (mortality of eggs and chicks), caused by this corvid predation, is additive to the nesting mortality caused by other predators and/or other sources of mortality, such as starvation, then variation in susceptibility to corvid predation could be a significant cause of overall variation in nesting mortality. Species that are more susceptible to corvid nest predation could have higher nesting mortality. For these species, corvid removal may reduce nesting mortality and increase productivity. Although, this would cause an increase in post-breeding population numbers (essentially the population numbers in autumn), it may not affect the population numbers in subsequent breeding seasons. Mortality at other life history stages may be more important in limiting overall breeding population size. Therefore, we might only expect corvid removal/decline to cause increases in songbird species' breeding populations when corvid predation causes additive mortality during the nesting period, and when mortality during the nesting period has the strongest determining effect on population growth patterns. We used data from the literature to estimate mortality rates during the nesting period (egg and chick stage) as well as at other life history stages (juvenile and annual adult mortality). We asked: i) Whether nesting mortality of songbirds was affected by higher susceptibility to corvid predation (*Chapter Two*). ii) If songbird species' nesting mortality was related to their response to predator removal in previous studies. iii) How mortality during the nesting period, and at other life history stages (juvenile and adult mortality), related to long-term population trends of songbirds during a period of corvid population growth. Although songbirds that had high nesting mortality were more susceptible to corvid predation, and were more likely to respond positively to corvid removal, they were not more likely to be in long-term population decline. Corvid predation may limit productivity of

some songbirds, but mortality at other life history stages seems to be more important in limiting breeding population numbers. This may explain why corvid removal does not always lead to an increase in songbird population numbers.

3.1 INTRODUCTION

Predation can be a significant source of mortality for songbirds, particularly of songbird eggs or chicks in the nest (hereafter referred to as nesting mortality) (Remeš et al., 2012). Corvids are known to predate the eggs and chicks of songbirds (Hanmer et al., 2017; Mallord et al., 2012) and the decline of many songbird species in recent decades has, at least partially, coincided with the population growth of corvids (Newson et al., 2010b). Carrion crow (*Carrion corone*) population numbers increased by approximately 130% between 1970 and 2013 in the UK and, although magpie population numbers have been steady since the around 1990, prior to this date magpie populations increased dramatically; by approximately 99% between 1970 and 1990 (BTO, 2016). However, correlative studies using data from nationwide surveys have not found a causal relationship between the growth in corvid populations and the decline of songbird populations (Thomson et al., 1998; Newson et al., 2010b).

Experimental predator removal studies, in which predators are removed and the subsequent change in populations of their prey are monitored, are more likely to reveal a possible effect of corvid predation on prey species than correlative studies. The variation in predator numbers caused by deliberate predator control is likely to be greater than the natural variation considered in correlative studies (Aebischer et al., 2015). Yet, meta-analyses of these experimental predator removal studies, including a recent analysis specifically examining the effect of corvids on passerine populations (Madden et al., 2015), find that in most cases predators do not limit breeding populations numbers of songbird species (Gibbons et al., 2007). When predator removal does have an effect, it is more likely to increase productivity, and therefore post-breeding populations (essentially autumn population numbers), than increase the breeding population in subsequent years (Côté & Sutherland, 1997; Holt et al., 2008).

Although there is little evidence that the effect of corvids on songbirds is uniformly negative, there are some specific examples of corvid removal positively

affecting particular songbird species and/or populations (White et al., 2014; Stoate & Szczur, 2006). Such species-specific responses may be because songbird species differ in their susceptibility to nest predation by corvids. For example, differences in nest site (open/hole), in nest height, or egg size, may cause some species to be more susceptible than others (*Chapter Two*). Vulnerability to corvid predation will affect productivity if this predation is a significant determinate of mortality during the nesting period. However, predation by corvids is just one cause of egg and chick mortality. Other factors such as predation by other predators, like mammals or reptiles (Ellis-Felege et al., 2012), poor weather conditions (Chase et al., 2005), brood parasitism (Payne & Payne, 1997; Hoover & Brittingham, 1993), and food limitation (Martin, 1987), may also influence overall nesting mortality. The relative effect of these factors varies across species (Smith et al., 2007) and habitats (Bowman & Donnelly, 2001). Different causes of mortality also interact and their relative contribution to total losses varies accordingly (Dunn et al., 2010; Schmidt & Whelan, 1999; Etersson et al., 2007). For example, predators may be more likely to take young already weakened by food shortages (Newton, 1998). If nest predation by corvids is compensatory (taking individuals that would otherwise be lost due to other causes), rather than additive (taking individuals that would otherwise have survived), then susceptibility to predation by corvids will not drive overall variation in mortality rates during the nesting period (Errington, 1946b), and corvid removal will not reduce nesting mortality.

Alternatively, if corvid predation is a determinate of disproportionately high nesting mortality, we might expect that species with higher nesting mortality would be more likely to respond positively to corvid removal. Corvid removal could reduce nesting mortality, increasing productivity. This would cause population numbers in the autumn (the post-breeding population) to be higher. However, an increase in post-breeding population numbers does not always correspond to an increase in breeding population numbers in subsequent years.

Population growth rates can be sensitive to changes in mortality at particular developmental stages of the life cycle (life history stages) (Sim et al., 2010; Krebs, 1970). Methods which correlate mortality rates at different life history stages to total annual mortality are commonly used to understand population dynamics (Baillie & Peach, 1992). If changes in mortality at a given life history stage strongly correlate

with overall population trends, this could indicate that mortality at this life history stage may be population limiting (Newton, 1998). It makes biological sense to compare mortality of stages that are developmentally distinct, rather than the same length of time, because individuals at different developmental stages are likely to be susceptible to different causes of mortality (Cornell & Hawkins, 1995). Although, initially limited to species with annual generations, these methods have been modified for species which live for multiple years. In such species losses of adults can be compared to losses of individuals at earlier life history stages in order to understand change in numbers at a population level (Baillie & Peach, 1992). In the case of songbirds, changes in mortality of juvenile or adult birds, rather than in mortality of eggs or chicks, may be more likely to cause overall variation in population numbers (Järvinen, 1987). This might explain why removal of nest predators often leads to an increase in post-breeding numbers but does not increase subsequent breeding populations (Holt et al., 2008). However, for some species, such as linnet (*Carduelis cannabina*), increased mortality during the nesting period has been linked to breeding population decline (Siriwardena et al., 2000a). If these species are vulnerable to corvid predation then their breeding populations may be expected to increase following corvid removal (Fletcher et al. 2006).

The aims of this Chapter were to understand how corvid predation is related to variation in nesting mortality in songbird species, and how differences in nesting mortality related to variation in songbird species' overall population trends. We used published data to estimate average mortality rates during the nesting period for 41 songbird species. We considered egg mortality (the failure to survive to hatching) and chick mortality (failure to survive to fledgling). We asked whether variation in mortality at these life history stages was related to songbirds' susceptibility to corvid predation. If so, we might expect this variation in mortality to affect the likelihood of a species responding positively to predator removal. Therefore, we compared inter-species' variation in nesting mortality to variation in population changes observed in response to predator removal. Finally, whether this variation in nesting mortality and susceptibility to corvid predation was linked to nationwide long-term songbird population trends over a period during which corvid populations have increased. Using this method, we could make an inference about the effect of corvid predation on population numbers without having a measure of changes in nesting mortality

rates through time. We hypothesised that if corvid predation drove higher nesting mortality, then an increase in corvid numbers would cause additional nesting mortality for species susceptible to corvid predation. In this case, populations of species which have higher nesting mortality might have declined over a time period when corvid population numbers have increased. For comparative purposes, we also compared nationwide long-term population trends to juvenile mortality (first year overwinter survival from fledging), and adult survival (annual survival) to determine whether nesting mortality was a better predictor of population trends than mortality at other life history stages.

3.2 METHODS

3.2.1 Literature search

Mortality rates of songbirds at different life history stages were extracted from the literature. An initial search was carried out in Web of Science (apps.webof-knowledge.com) using the search terms (“Species name”) AND (“mortality” OR “key factor analysis” OR “annual survival” or “clutch size” or “fledgling mortality” or “hatching mortality”). The species named included all resident or migrant passerines with more than 100 pairs breeding in the UK; 68 in total (Harrop et al., 2013). Only studies carried out in the British Isles were included; this reduced variation in external factors which may affect the mortality rates of populations of species being compared. The search yielded 411 papers (excluding duplicates) in December 2015.

Data reported in Birds of the Western Palearctic (Cramp et al. 1977-1994) which met the above criteria were also included. This source provided access to additional information including older literature or less widely available journals. Finally, figures from nationwide survey schemes were extracted. Data taken from the British Trust for Ornithology (BTO) online datasets (BirdFacts and BirdTrends) provided egg and chick mortality summary data from the Nest Record Scheme. BTO BirdFacts was used to obtain data on juvenile and adult mortality from inaccessible literature (Robinson et al., 2015; Robinson, 2005).

Data from the different sources were cross referenced to avoid duplicate inclusion of data from the same study population. Results from experimental studies were averaged across treatments/habitats (weighted by sample size). Studies which

directly manipulated population demography, by altering clutch size for example, were excluded.

Average mortality rates (weighted by study sample size) were produced for each life history stage: egg mortality (the percentage of eggs laid that did not hatch), chick mortality (the percentage of nestlings that did not fledge), juvenile mortality (the percentage of fledged young that did not reach the following breeding season) and annual adult mortality (the percentage of adults that did not survive from one year to next). Species were excluded from further analysis if either egg or chick mortality data were unavailable. These data were found for 41 species.

3.2.2 Susceptibility to corvid predation

Our measure of susceptibility to corvid predation was taken from the results of a previous analysis (*Chapter Two*) which used a Generalised Linear Model (GLM) approach to analyse how parameters of species' breeding biology predicted reported levels of nest predation by corvids. The predicted values of corvid nest predation rate derived from our model were obtained for each species based on the values of the explanatory variables (parameters of the species breeding biology). To avoid duplication, studies which were used as sources of corvid nest predation rates for that analysis were excluded from the calculation of mortality rates in this analysis.

3.2.3 Response to corvid removal

We extracted the summary data from Madden et al. (2015) to get a measure of species response to corvid removal. This literature review summarised the impact of corvids on passerine species, measured by the passerine species response in terms of population productivity (post-breeding numbers) or abundance (subsequent breeding population change) following corvid removal experiments or natural population changes. We converted the results of this analysis into a binary variable. We compared songbird species that have either not responded to corvid removal/decline or have responded negatively to corvid removal or population decline (0) to species that have responded positively to corvid removal or population decline (1).

3.2.4 Long-term population trends

To analyse long-term population change (1970-2013), we used smoothed population trends (in which short term variation caused by anomalous events, such as extreme weather or measurement error has been removed) produced by the DEFRA based on data provided by the BTO, the RSPB and the JNCC (DEFRA, 2015). Population trends were reported as percentage population change based on this smoothed data.

3.2.5 Statistical analysis

Mortality rates were expressed as the percentage of the population which entered a life history stage but did not survive to the next life history stage (see 3.2.1). Survival was the proportion of the population surviving to a life history stage given cumulative loss in previous life stages (the chance of surviving to a given life history stage).

We first asked whether songbird species' susceptibility to nest predation by corvids was related to their mortality rates during the nesting period (mortality in the egg and chick stage). Egg or chick mortality rates were used as a binomial response (percentage of eggs/chicks which did not survive to the next life history stage (successes)/ percentage of eggs/chicks which did survive to the next life history stage (failures)) in a Generalised Linear Model (GLM). Due to overdispersion in the response variable a quasi-binomial model with a logit function was used. The explanatory variable was susceptibility to corvid predation (expressed as the predicted proportion of nests lost due to corvid predation, see 3.2.2).

T-tests were used to see whether egg and chick stage mortality differed between species which had been found to be positively impacted by corvid removal or population change, and those which had not. All songbird species that were not included in Madden et al. (2015) were excluded from this analysis (15 species in total) as, to the best of our knowledge, the effect of corvid removal or corvid population change on their populations has not been assessed.

The relationship between mortality at different life history stages (egg stage, chick stage, juvenile and adult) and long-term population trends (1970-2013) was analysed using Pearson correlation coefficients. We compared mortality at each stage with a single value for population change for each species, for example

between 1970 and 2013 blue tit numbers increased by 24%. The p values were adjusted for multiple comparisons using the conservative Bonferroni method.

3.3 RESULTS

Mortality rates at all life history stages varied between species and average mortality was relatively lower during the nesting period (egg stage mortality: $23.65 \pm 1.76\%$ and chick stage mortality: $24.26 \pm 2.14\%$) compared to later life history stages (juvenile mortality: $61.65 \pm 2.02\%$, annual adult mortality: $53.95 \pm 1.68\%$). However, the variation in mortality rates between species was higher in the egg stage (5.9%-50.8%) and chick stage (3.7%-54.7%) than at other stages (*Figure 3.1*).

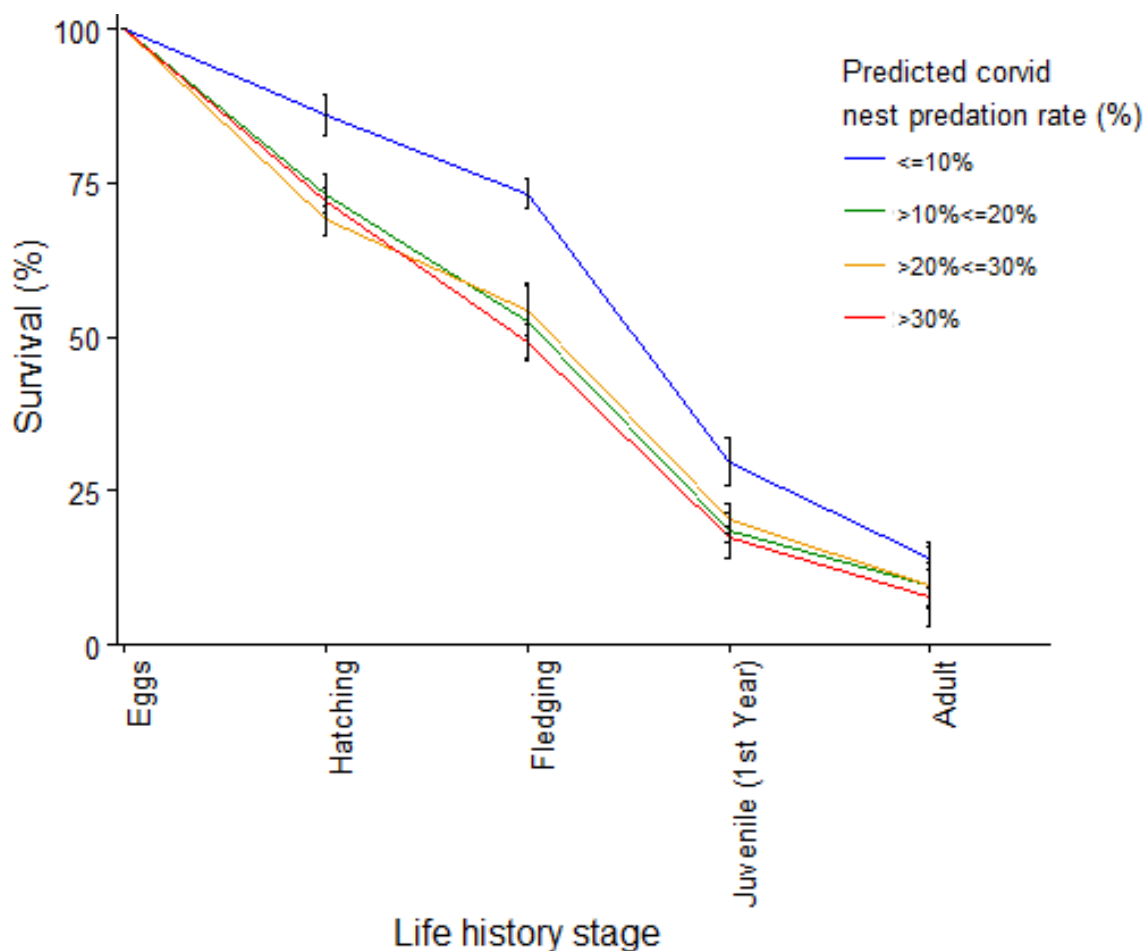


Figure 3.1: Mean average (\pm SE) relative survival to different life history stages of species displayed relative to species' susceptibility to covid predation (measured as predicted covid nest predation rates (see 3.2.2)).

3.3.1 Nesting mortality and susceptibility to corvid predation

Variation in susceptibility to corvid nest predation significantly predicted variation in nesting mortality. Species with higher mortality in the egg stage ($F_{1,39} = 7.56$ $p < 0.001$) and chick stage ($F_{1,39} = 8.60$ $p = 0.005$) also had higher susceptibility to corvid nest predation (Figure 3.1).

3.3.2 Nesting mortality and response to corvid removal

Species previously reported to respond positively to corvid removal or natural declines were more likely to exhibit higher nesting mortality, than those which were reported to either not respond or respond negatively to corvid removal or decline. Egg stage mortality was ~45% higher in species which were reported to respond positively to corvid removal or decline ($t = -2.13$, $df = 16.19$, $p = 0.04$), and chick stage mortality was ~60% higher ($t = -2.25$, $df = 11.79$, $p = 0.04$) (Figure 3.2)

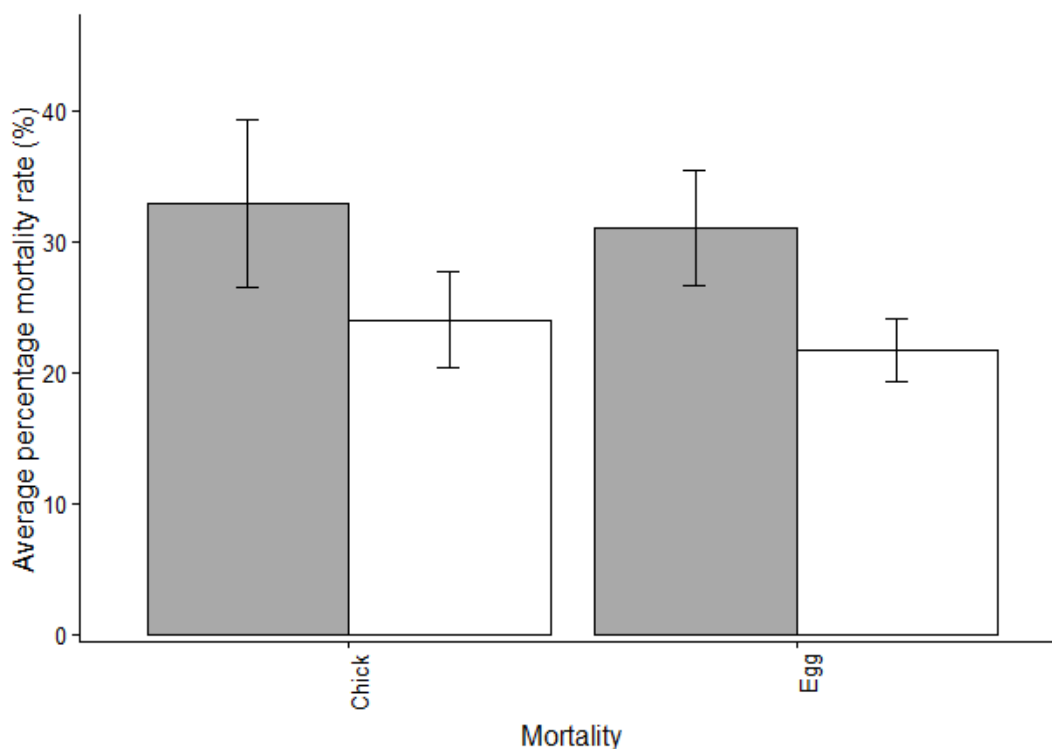


Figure 3.2: Difference in egg and chick mortality rates between species that have not responded or responded negatively to corvid removal/decline (black bars) and those that have responded positively to corvid removal/decline (white bars)

3.3.3 Mortality at different life history stages and long-term population trends

Variation in species' egg stage or chick stage mortality did not significantly predict species' long-term population change over a period where corvid population

numbers naturally increased (egg mortality: $r = -0.075$, $p > 0.99$, $n = 39$, $r^2 = -0.0049$; chick mortality: $r = 0.037$, $p > 0.99$, $n = 39$, $r^2 = 0.001$). Annual adult mortality also did not significantly relate to long-term populations trends (adult mortality: $r = 0.30$, $p = 0.31$, $n = 35$, $r^2 = 0.09$). However, juvenile mortality was positively related to long-term population increase (juvenile mortality: $r = 0.49$, $p = 0.04$, $n = 25$, $r^2 = 0.24$) (Figure 3.3). Species with higher juvenile mortality (first year overwinter survival) were more likely to have undergone population growth between 1970 and 2013.

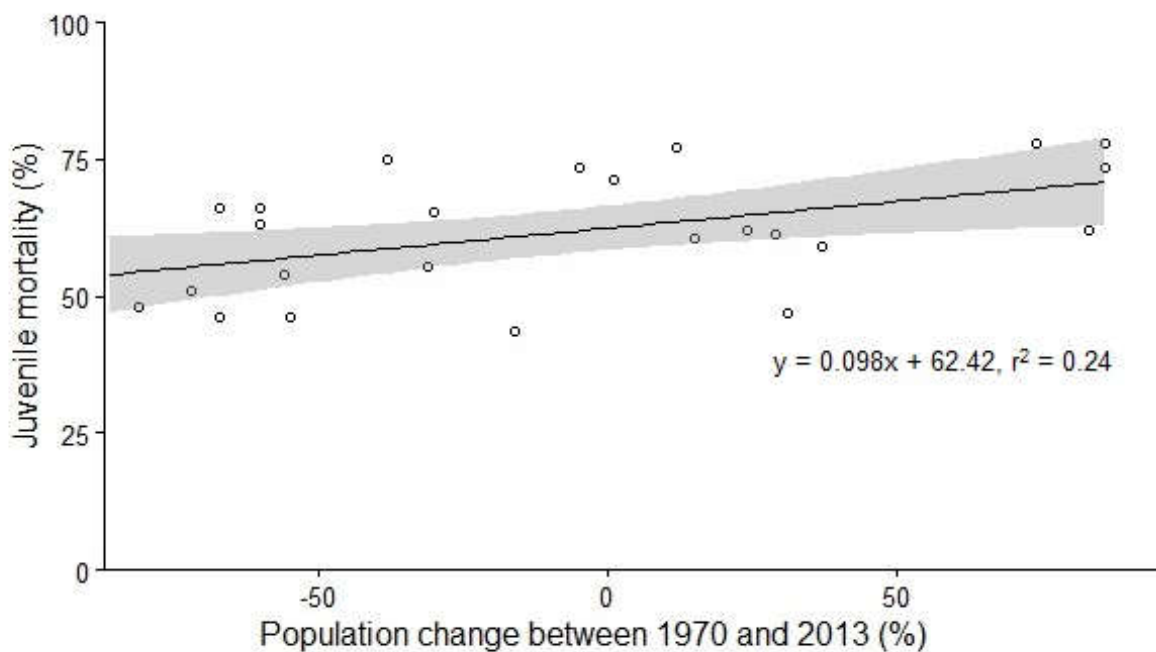


Figure 3.3: Relationship between songbird species' juvenile mortality (%) and their population change between 1970 and 2013 (%)

3.4 DISCUSSION

Species with high levels of reported nesting mortality (mortality at the egg and chick stage) were also those independently identified as being particularly susceptible to corvid predation. This suggests that predation by corvids could be an important determinate of mortality at these life stages. This vulnerability to predation may explain why these species were more likely to respond positively to corvid removal and natural declines. We might therefore expect that these species with higher nesting mortality would have been especially negatively influenced by a period of long-term population increase of corvid predators. However, high mortality during the nesting period did not predict a population decline in a songbird species in the UK over the period of corvid population increase.

Our meta-analysis of mortality rates identified similar rates of loss at different life history stages as those reported in previous studies. Lack (1954) estimated that between 45% and 67% of passerine eggs laid survive to fledging and Lack (1954) and Perrins et al. (1987) estimated that between 8% and 18% of eggs laid produced individuals that survived the first year (Lack, 1954; Perrins et al., 1987). We found that on average 59% of eggs laid produced individuals that survived to fledging and that approximately 22% of eggs laid survived the first year. The slightly higher estimate of first year survival we obtained compared to that of Lack (1954) or Perrins et al. (1987) may be because the juvenile mortality estimates that we used were largely obtained using indirect methods such as the recovery of ringed birds. Overestimation of juvenile survival can occur when using ringing recoveries as juvenile birds tend to be ringed later in the year (Siriwardena et al., 1998).

3.4.1 Nesting mortality and susceptibility to corvid predation

Predation has previously been found to be the most significant cause of egg and nestling loss, accounting for an average of 80% of mortality at this stage (Martin, 1993; Lima, 2009). It might be expected that differences in vulnerability to the biggest source of mortality would drive overall variation in mortality at this life history stage. We found that susceptibility to corvid predation specifically predicted variation in nest mortality between songbird species. This suggests that predation by corvids presents a particularly significant cause of inter-specific variation in nesting mortality. Although nest predation risk can vary over the course of the nesting period (Cresswell, 1997b) we found that, egg and chick stage mortality were strongly correlated with each other within a species and species with higher susceptibility to corvid predation suffered increased mortality in both periods.

3.4.2 Nesting mortality and response to corvid removal

Higher mortality during the nesting period does not always reduce post-breeding numbers. Species with higher predation rates may be able to compensate by increasing their fecundity by having repeat broods (Martin, 1995). However, data on the nest success of repeat broods is limited, and not available for a wide range of species (Freeman & Crick, 2003). As we did not have the ability to detect this effect in our data, any variation in mortality between first and second broods was not considered in our coarse analysis. In any case, our results suggest that species were

unable to compensate entirely for high nesting mortality by having repeat broods. Species with higher nesting mortality were more likely to respond positively to corvid removal/decline, in terms of increased post-breeding numbers or population abundance (Chiron & Julliard, 2007; Madden et al., 2015). This suggests that, at least for some species, susceptibility to corvid predation can determine high nesting mortality, and that species which suffer this high nesting mortality cannot compensate for these losses and maintain their post-breeding numbers unless corvids are removed or decline.

3.4.3 Mortality at different life history stages and long-term population trends

For some species with particularly high nesting loss, a reduction in mortality at this period can be achieved through corvid removal, and this can increase post-breeding populations. For these susceptible species, the increase in corvid numbers seen between the 1960s and the 1990s (Marchant & Gregory, 1999) might have had a detrimental effect at a population level. The growth in the density of predators could have increased nest predation rates (Evans, 2004), potentially causing an increase in nesting mortality. However, we did not find any relationship between a species' nesting mortality and its population trend between 1970 and 2013, despite the increase in corvid numbers over this period (DEFRA, 2015). This lack of relationship matches both previous correlative studies, which have analysed changes in UK breeding population numbers and failed to find an effect of nest predator population change on songbird numbers (Gooch et al., 1991; Thomson et al., 1998; Newson et al., 2010b), and a recent meta-analysis of correlative or experimental studies which found that corvid removal does not positively impact bird breeding populations internationally (Madden et al., 2015). It may be that variation in nesting mortality does not influence breeding population numbers in subsequent years (Newton, 1998). 94% of the positive effects of corvid removal or decline on songbird species, found by Madden et al. (2015), were increases in songbird productivity (post-breeding numbers) rather than increases abundance (breeding populations in subsequent years). For example, the removal of a suite of predators from a moorland habitat increased meadow pipit (*Anthus pratensis*) productivity, but not subsequent breeding populations (Fletcher et al., 2010). Other literature reviews have also suggested that predator control generally is likely to increase post-

breeding numbers rather than increase breeding population numbers (Côté & Sutherland 1997).

These results suggest that reducing nesting mortality does not always increase breeding songbird population numbers. Changes in mortality at particular life history stages do not always influence overall population trends (Newton, 1988). Several studies have used key factor analysis to identify mortalities which have a limiting effect on populations; it might be that mortality during the nesting period is not a key factor (one that correlates strongly with changes in population numbers). Variation in nest survival has been found to be unrelated to population change for marsh tits (*Poecile palustris*) (Siriwardena, 2006), reed bunting (*Emberiza schoeniclus*) (Peach et al., 1999), skylark (*Alauda arvensis*), tree sparrow (*Passer montanus*), yellowhammer (*Emberiza citronella*) and corn bunting (*Miliaria calandra*) (Siriwardena et al., 2000a). Nesting mortality could represent the loss of a doomed surplus: if the eggs or nestlings had survived then they (or an equivalent number) would have died at other life history stages before entering the breeding population (Newton, 1994a). Indeed, for many of these species, overwinter mortality has been shown to be more important in limiting the number of individuals entering the breeding population (Peach et al., 1999). This is particularly true for migratory species such as sedge warbler (*Acrocephalus schoenobaenus*) and whitethroat (*Sylvia communis*) where factors driving their decline are primarily related to mortality in their wintering grounds (Baillie & Peach, 1992).

One result from our analysis was counter intuitive: species with higher juvenile mortality rates were more likely to have undergone long-term population increases. The strength of the relationship was relatively low, explaining 24% of the variation, and was based on a small sample of species (n= 25) so, may have been driven by a few out-lying results (Figure 3.3). Chiffchaff (*Phylloscopus collybita*), for example, had a very high juvenile mortality rate but the population has undergone an increase in recent decades, possibly due to climate change facilitated improvement in overwinter survival (Hewson & Noble 2009). It may simply be that changes in juvenile mortality do not limit the population numbers of this species, improved adult overwinter survival may be sufficient to increase population numbers even if juvenile mortality is high. Alternatively, it could be that the mortality rates we extracted from the literature were not representative of the national population. It may be that

mortality rates were taken from local populations which were not typical of the national trend, perhaps these populations had particularly high juvenile mortality. There may also have been a temporal disconnect between the juvenile mortality rates we extracted and the population trend data. The studies which we drew mortality data from were unlikely to cover the entire period of population change examined (1970 – 2013). In the case of the chiffchaff, it may be that high juvenile mortality rates were recorded over a shorter time period, when population numbers were not increasing. As our data does not demonstrate how mortality rates change through time, we cannot directly assess how changes in mortality rates at different life history stages relate to changes in population numbers.

3.4.4 Conclusions

We found that, across species, high susceptibility to corvid predation appeared to be positively related to high mortality in the egg and chick stage (nesting mortality). This suggests that, in species suffering high nesting mortality, we might expect to observe long-term population declines during a period of corvid population growth. However, generally this was not the case, it appears that mortality at other life history stages, such as their first-year overwinter survival may be more likely to limit UK songbird populations. Nevertheless, previous studies have suggested that for a small number of species, such as linnet (*Carduelis cannabina*) (Siriwardena et al., 2000a) or yellow wagtail (*Motacilla flava*) (Shitikov et al., 2013), an increase in nesting mortality may have contributed to a decline in their overall population numbers. For these songbird species reducing nest predation, by removing predators or improving habitat (increasing nest cover for example) could have positive effects on breeding population numbers. In addition, the detailed life history analysis required to identify the life history stage at which mortality is likely to have population limiting effects, has only been carried out for a limited number of songbird species. Further research may indicate that the population numbers of other species can also be limited by mortality during the nesting period, and thus may have been detrimentally affected by the population increases of nest predators such as corvids.

Chapter Four

Variation in magpie predation of artificial nests



Bushnell

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ABSTRACT

Predation is an important cause of mortality of the eggs and chicks of songbirds in the nest. The recent decline in farmland songbirds in the UK has, at least partially, coincided with increases in populations of many predators of eggs and chicks (nest predators). Experimental removal of nest predators, including corvids, has sometimes led to increased breeding success of songbird populations. However, meta-analyses of these predator removal experiments have suggested that nest predation does not always limit the productivity of songbird populations. A possible explanation for this confused picture is that predators vary in how likely they are to predate nests. We would therefore only expect the breeding success of the prey population to improve, when the individuals who are most likely to predate nests are removed. Predators may vary in their likelihood to predate nests for several reasons. Variation in the external environment may affect the extent to which predators take nests. Internal variation within the predator population, such as differences in breeding status, can also cause predators to differ in their foraging behaviour. The behaviour of predators may also vary at an individual scale: certain individuals may specialise on particular prey types. We used 460 artificial nests placed in a typical farmland environment, in a systematically balanced design, to analyse the effect of these sources of variation in predation. Magpies were the most common predators of our artificial nests (70% of predation events identified using marks in wax-filled eggs were attributed to medium-sized birds, and magpies were the only medium-sized birds seen predated nests on camera). The vulnerability of songbird nests to magpie predation varied according to magpie breeding status (predation was higher inside breeding magpie territories), but this effect depended on the time in the magpie breeding season. More nests were predated inside of magpie territories late in the season, when magpies had young in the nest. However, specific nest locations were repeatedly highly predated independent of both magpie breeding status and time in magpie breeding season. Camera observations indicated that specific territorial magpies predated these specific locations (birds were individually identifiable, as a large proportion of the magpie population were colour-ringed). At these locations, the territory owners differed in other behaviour; they were also more likely to engage in aggressive territory defence when presented with a dummy territorial intrusion. Behavioural differences could be used to identify predatory individuals, and predator

removal could be more effective if management is targeted towards these particularly predatory individuals, or locations at which predation rates are high.

4.1 INTRODUCTION

Corvids, particularly magpies (*Pica pica*), have often been directly observed (Hanmer et al., 2017; Praus et al., 2014) or identified from physical evidence (Groom, 1993; Chamberlain, 1994) predated the eggs and chicks of UK songbirds in the nest (hereafter referred to as nest predation). However, investigation at the regional and national population level has found little evidence of a causal link between an increase in corvid populations and a decline in songbird populations (Newson et al., 2010a; Thomson et al., 1998). Meta-analyses of predator removal studies have not found a uniformly positive effect of corvid removal on songbird productivity or abundance (Madden et al., 2015; Holt et al., 2008). Nevertheless, some localised experimental studies have found increases in nest survival (Stoate & Szczur, 2006), and subsequent growth in some songbird breeding populations (White et al., 2008; Fletcher et al., 2010), following corvid removal. There are several possible explanations for this confused picture.

Firstly, corvids may attract undeserved blame for predation. Their large size, conspicuous behaviour, and diurnal activity, may make them appear disproportionately responsible compared to more inconspicuous nocturnal predators such as rodents (Birkhead, 1991). In reality corvids may not be common nest predators. Secondly, the eggs and chicks predated by corvids may simple be part of the population that would otherwise be lost due to different causes (compensatory mortality) (Errington, 1946a; Holt et al., 2008). In this case, higher corvid numbers will not limit songbird populations. Thirdly, the location and structure of some songbird species' nests, and the timing of their breeding attempts, may render them more or less likely to be predated by corvids (Martin, 1993). If not all songbird species are affected by corvid predation, the effects of increased corvid numbers on susceptible species may be masked by more general population trends across species. Finally, it may be that some individual corvids predate a disproportionate number of nests. In this case, we would not expect to see an increase songbird breeding success or population numbers, unless these more predatory individuals are removed. Understanding the reasons why particular individuals are more

predatory, could help identify individuals which are more likely to affect the local songbird population.

Corvids may differ in how likely they are to predate nests for several reasons, including variation in the external environment. If the habitat provides less concealment and protection for nests, for example if hedges are more severely cut and thinner (Lack, 1987), predators may be more likely to take nests (Kelleher & O'Halloran, 2007). It may also be that predators are attracted to specific habitat features, for example food sources such as roadkill (Pescador & Peris, 2007), or garden bird feeders (Hanmer et al., 2017), and nests near these features are more likely to be predated.

Predators may also vary in their predation behaviour due to variation in internal factors. For example, predators which differ in their age, sex, or breeding status may take different prey types (Dickman, 1988; Odden et al., 2002; Sacks et al., 1999). Populations of corvids such as magpies and crows (*Corvus corone*) are comprised of territorial breeding individuals as well as non-breeding itinerant individuals (Cramp & Perrins, 1994). It may be that this variation in breeding status affects foraging behaviour; territorial individuals may be more likely to predate nests. Breeding individuals regularly defend a territory around the nest from intrusions by conspecifics or predators during the breeding season. They also restrict their foraging to within these territories (Birkhead, 1991), possibly to facilitate this territorial defence (Martindale, 1982; Marzluff, 1985). Previous research has shown that nests inside these corvid territories can suffer higher predation rates (Sullivan & Dinsmore, 1990; Erikstad et al., 1982). This may be because territorial individuals who restrict their foraging to a smaller area may simply be more likely to encounter nests by chance. However, they are also likely to have more experience of the local habitat and this may also facilitate nest finding (Møller, 1988).

In addition, to causing spatial variation in nest predation risk, these external and internal factors could also cause nest predation risk to vary temporally. External variation in habitat is likely to change through the year. For example, as vegetation grows, the concealment it provides may increase and this may reduce predation. Internal variation, in breeding status for example, may have a temporal effect on predators' likelihood to take particular prey types. It may be that breeding individuals

switch their prey preference in response to the nutritional needs of their young (Annett & Pierotti, 1989). In this case, predation of nests by corvids could be higher during the corvids' own breeding season.

Alternatively, or in addition to these external and internal factors, predators may differ at an individual level in their propensity to predate nests (Woo et al., 2008). Species have often been shown to differ in the extent to which their diet is specialised. For example, a population of pallid harriers (*Circus macrourus*) specialised on voles whereas the sympatric and closely related Montagu's harrier (*Circus pygargus*) had a generalist diet which included a wider breadth of prey items, such as other small mammals and birds (Terraube et al., 2011). However, in some cases species appear to have a generalist diet at a population level, but within the population particular individuals may specialise on specific prey (Dickman & Newsome, 2015). For example, Brünnich's guillemots (*Uria lomvia*) displayed consistent individual differences in the prey types they feed their chicks (Woo et al., 2008). Therefore, although corvids are considered to be dietary generalists (Holyoak, 1968), individuals within populations may specialise on particular prey, such as eggs and chicks in the nest.

Individuals may differ in their predation behaviour for a variety of reasons. It may be that prey require specific handling strategies and, if predators are limited in the number of strategies that they can learn, individuals may specialise on different prey (Woo et al., 2008; Slagsvold & Wiebe, 2011). Differences in foraging behaviour between individuals may also be related to variation in other behaviours. Individuals demonstrate consistent behavioural characteristics across contexts, which is sometime referred to as 'personality' (Bolnick et al., 2003). Differences in personality may affect foraging behaviour and prey preferences, for example boldness may affect an individual's tendency to explore particular habitats (Patrick et al., 2013; Wolf & Weissing, 2012). Particular corvids may be more likely to predate songbird nests due to differences in personality (Blackwell et al., 2016). For example, more aggressive individuals may be more likely to engage in territorial defence, and therefore to spend more time moving through their territory and encountering songbird nests within it.

Farmland songbirds are a group of species in long-term population decline (DEFRA, 2016). Identifying factors which cause corvids to differ in their predation of songbird nests in farmland therefore has useful management implications. If predators differ in their predation behaviour independently of variation in external environment, it may be possible to remove only these particularly predatory individuals. Alternatively, if external factors such as habitat variation drive differences in predation rates, creating habitat that provides protection from predators, such as denser hedgerows, could be particularly beneficial.

We aimed to identify factors which caused variation in predation rates, using artificial songbird nests placed in an English farmland environment. Specifically, we asked whether corvids were disproportionately responsible for nest predation by monitoring the identity of nest predators using trail cameras and wax-filled eggs, which retain the beak or gnaw marks of the predators attempting to eat them (Bodey et al., 2009). We then explored whether spatial and temporal patterns of variation in predation could be explained by factors pertaining to the behaviour of local corvid predators. By presenting sets of artificial nests at different locations repeatedly throughout the breeding season, we could assess: i) whether there was variation in predation levels within or between particular locations; ii) whether variation in predation was moderated by habitat factors, specifically hedge structure iii) whether variation between locations was explained by the breeding status of predators, in this case whether predation was higher inside of the territories of breeding magpies compared to outside; iv) whether predation at a specific location varied temporally over the magpie breeding season; v) whether variation between locations corresponded to variation in other behavioural traits of the local magpies.

4.2 METHODS

4.2.1 Field site

The study was carried out over 15km² of farmland in rural Warwickshire, England (52°15'53.1"N 1°40'01.1"W). The landscape was dominated by mixed arable and pastoral farms.

4.2.2 Identification of nest predators

We constructed artificial nests from chicken wire lined and woven with hay and grass. These nests mimicked blackbird (*Turdus merula*) nests found on site in size,

shape, and use of hay and grass. Nests were baited with one real quail's egg and one wax-filled quail's egg. The wax-filled egg had light gauge wire embedded within it. This was used to attach the egg to the hedge to prevent egg removal by predators.

We placed a total of 460 artificial nests in hedgerows in selected locations (see 4.2.4). Each nest was exposed for 5 days and, to avoid alerting predators, nests were not visited during this time. Nests were considered predated if either egg was missing or damaged within the nest. Impressions on the wax-filled eggs were used to identify predators. Approximately one third of artificial nests ($n = 151$) were also monitored using trail cameras (Bushnell Trophy Camera HD) to allow more detailed identification of predators. There were no discrepancies in predator identification when both impressions on wax-filled eggs and trail camera images were used to identify predators at the nest.

A randomly selected subset ($n=30$) of the 460 artificial nests deployed were old, natural thrush nests, collected from the field site over winter, as oppose to wire nests constructed by us. This meant any effect of our manmade nests on nest predation rates could be assessed.

4.2.3 Determining magpie territories

We identified active magpie territories and territory owners in 2016, using a combination of methods. First, old magpie nest sites were located over the winter and early spring (before bud burst). This provided a likely territory centre, as nest sites were frequently reused. Second, we confirmed nest site use by observing and recording locations of birds around the nest site during the breeding season. Finally, over three years (2014-2016) we trapped, and marked with colour rings, 101 individual members of the local magpie population. We could identify territory owners as those that were repeatedly re-trapped in specific locations near active nests in 2016 (Diaz-Ruiz et al., 2010).

Active magpie nests were found less than 100m apart on this field site. It therefore seems unlikely that magpies would defend and utilise areas over 200m from their nest. Sites over 200m from known magpie nest sites (even those believed to be inactive) were therefore defined as outside the magpies' territory. Blocks of woodland over approx. 0.5 ha., and urban areas including gardens, could not be

extensively visually searched for magpie nests and these areas were therefore excluded from this experiment.

4.2.4 Measurement of nest predation

We presented artificial nests at 24 hedgerow locations. At each location, five artificial nests each separated by ~10m were placed in feasible natural nest positions on a transect along the hedgerow (*Figure 4.1*).

Twelve locations had active magpie nests (magpie-present) and at twelve locations territorial magpies were deemed to be absent (magpie-absent). In the magpie-present locations the first artificial nest was placed ~10m from the magpie nest if the nest was in a hedgerow, or at the closest point on the nearest hedgerow (<25m away) if the magpie nest was in a lone tree or copse. In the magpie-absent locations the first artificial nest was placed at a random point on the hedgerow.

Nests were presented in 6 blocks of 4 locations (2 in magpie-present, 2 in magpie-absent locations). Each block hosted presentations 4 times (in April, May, June and July 2016), except 1 block which was repeated 3 times due to logistical constraints.



Figure 4.1: Aerial Image of our field site displaying magpie-present nest transects (red), magpie-absent nest transects (blue) and magpie nest sites (yellow). Aerial imagery is taken from the ESRI World Imagery Basemap at 0.3m resolution (GB Birmingham-E) using ESRI ArcGIS 10.2.2 (ESRI, 2014).

4.2.5 Measurement of habitat variation

Hedgerows at each location were crudely categorised as either open/tall (above 2m, with an open structure, generally unmanaged and composed of a mix of tree and shrub species) or closed/short (below 2m in height, narrow and dense such that the inside of the hedgerow could not be easily accessed by humans, and composed of hawthorn (*Crataegus spp.*) and blackthorn (*Prunus spinosa*)).

4.2.6 Measurement of variation in magpie behaviour

We collected two measures of individual variation in magpie behaviour. Firstly, we compared recorded predation rates at each location. Individuals preying nests were identified by their colour rings from trail camera photos. Secondly, we quantified the intensity of the territorial defensive behaviour displayed by the territory holders in each territory in which a magpie-present transect was placed ($n = 12$). During the breeding season (15/04/2016-09/06/2016) we used a plastic dummy magpie mounted on a stick to simulate a territorial intrusion. The dummy was placed 6m from the magpie's nest to the North, South, East and West in a random order. We recorded the number of responses that a focal magpie (a member of the territorial pair) made to the dummy. A response was categorised as focal individual making a vocalisation (alarm calls), visual display (tree-topping, parallel walking) or mobbing (Birkhead, 1991; Pinkham, 2016). If there was no response after 40 minutes the dummy was removed and, to avoid habituation to the dummy, it was also removed 15 minutes after the start of a response. This was converted into a simple response rate for each territory (number of responses/number of times the dummy magpie was placed in the territory as a simulated territorial intrusion).

4.2.7 Statistical analysis

Firstly, we assessed the effect of aspects of the experimental design on predation rate. This was captured by three measures: the presence of cameras; the type of nest (artificial or natural nest); and the position of the nests along a transect (proximity to magpie nest). We assessed the effect of these measures on nest predation using chi-squared tests, and found that predation did not significantly differ between nests with and without cameras ($\chi^2_1, N = 460 = 2.54, p = 0.11$), between artificial or real nests ($\chi^2_1, N = 460 = 0.94, p = 0.33$), or with nest position within a transect ($\chi^2_1, N = 460 = 0.91, p = 0.92$).

We used a generalised linear mixed modelling (GLMM) approach to assess the effect of the factors of interest (magpie presence, time in breeding season and habitat variation) on artificial nest transect predation. Inclusion of additional factors in these models led to model over-parametrisation and reduced model fit (Thomas et al., 2015; Grueber et al., 2011). Therefore, the factors related to experimental design (camera presence, natural/artificial nest, transect position), which were shown to have no effect on artificial nest predation, were excluded from these analyses.

Nest outcome (success/failure) was used as a binomial response, and magpie territory presence (magpie-present vs. magpie-absent), time of nest transect presentation (date as a numeric variable), and hedge type (open/dense) were used as explanatory variables. To account for changes in habitat and magpie activity throughout the breeding season, the interaction terms date*magpie presence and date*hedge type were included. Nest transect location was fitted as a random effect. Twenty-four transect locations were used in total (see 4.2.4). We included location as a random effect in order to account for potential spatial autocorrelation between nests exposed at the same transect location and to explicitly examine differences in predation rates between transect locations, not accounted for by the fixed effects.

To examine if factors predicting predation rates differed depending on predator identity we initially fitted two maximal models; the first included all instances of predation (A) and the second included only predation attributed to medium-sized bird predators (B), effectively magpies (see 4.4.1).

The significance of explanatory terms was evaluated by removing the variables one at a time from the maximal model, and using chi-squared tests to assess the change in model deviance (Crawley, 2005). If the removal of interaction terms did not significantly increase the model deviance, these terms were excluded from minimal adequate models. This reduced model complexity and meant the significance of the fixed effects involved in these non-significant interactions could be assessed (Crawley, 2012; Fox et al., 2013). We were also able to identify the particular explanatory variables that influenced the response variable, in this case artificial nest predation rate (Zuur et al., 2009; Fox et al., 2013; Crawley, 2012; Murtaugh, 2009). All fixed effects were retained in the minimal model (Thomas et al., 2015). The random effect (nest transect location) was tested using a likelihood ratio

test of the maximal model, with and without the random effect (Westneat et al., 2014).

Data about individual magpie predation behaviour was collected from a subset of transect locations (only magpie-present locations). We therefore carried out a separate analysis looking specifically at the relationship between individual differences in magpie behaviour and magpie nest predation at these locations. However, we could not assess temporal effects in this analysis as, although the territorial intrusions were carried out over the same time period as the artificial nest experiments, the timings did not precisely match up at each location. It was not possible to relate specific territorial intrusions to specific nest transect exposures and specific nest predation events. We therefore summed the number of nests predated by medium-sized birds (predominantly magpies, see 4.4.1) across nests placed at a specific location over the entire experimental period, and used this measure as proxy for magpie predation rate at that location. Response rate of the territory holder to simulated territorial intrusions at a given location was used as a measure of magpie defence behaviour. We used a quasi-binomial generalised linear model (GLM) with total nests predated by medium-sized birds/ (total nests – total nests predated by medium-sized birds) and response rate (number of responses to simulated territorial intrusions/number of simulated territorial intrusions) as the explanatory variable. The significance of the fixed explanatory variable was assessed using chi-squared tests comparing the model with or without the term (Crawley, 2005).

All analyses were carried out in R ver. 3.1.2 (R Core Team, 2017) and GLMs and GLMMs were constructed using the *lme4* package (Bates et al., 2014).

4.3 ETHICAL STATEMENT

Between May 2014 and July 2016, 101 magpies were trapped and ringed with colour rings. Magpies were re-trapped on 205 occasions. All magpie trapping, and colour ringing followed best practice guidelines of Natural England and the Game and Wildlife Conservation Trust, and was carried out under Natural England licence 2016-19794-SCI-SCI.

4.4 RESULTS

4.4.1 Predator identity

Across all exposures of all artificial nest transects, 133 of the total 460 nests (28.9%) were predated. Medium-sized birds were identified as predators in 70.3% of cases where predators could be identified ($n=81$) (*Figure 4.2*). Corvids were the only medium-sized birds observed predated nests on camera (48.5% of the 33 nests monitored by cameras). Of these corvids, 87.5% were magpies. There was 1 instance of jackdaw predation (*Corvus monedula*) and 1 of jay (*Garrulus glandarius*). It follows that the majority of nests identified as predated by medium-sized birds were likely predated by magpies, therefore we assume they were the major predators of our artificial nests.

In cases where the wax-filled egg was removed from artificial nest or untouched, and there were no camera observations, we could not determine predator identity (*Table 4.1*). Camera observations suggested that neither mammals nor birds were more likely to leave eggs untouched or to remove them.

Table 4.1: Count of the fate of predated artificial nests in magpie-absent ($n=60$) and magpie-present ($n=73$) transects (expressed percentage of total predated nests in parenthesis)

Nest Outcome		Magpie-absent	Magpie-present	Total
Predator	Small mammal	8 (6%)	11 (8%)	19 (14%)
	Small bird	1 (1%)	4 (3%)	5 (4%)
	Medium bird	21 (16%)	36 (27%)	57 (43%)
Predator unknown	Unknown	4 (3%)	6 (5%)	10 (8%)
	Wax-filled egg gone	8 (6%)	7 (5%)	15 (11%)
	Wax-filled egg untouched	18 (14%)	9 (7%)	27 (20%)
	Total	60 (45%)	73 (55%)	133 (100%)

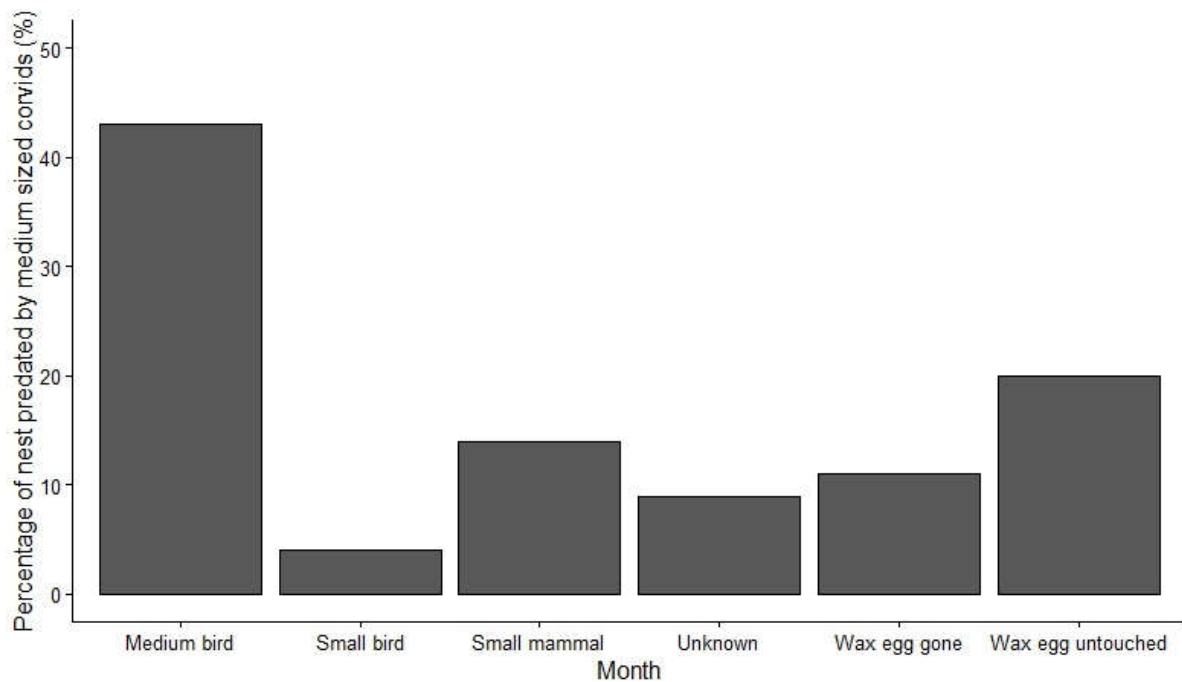


Figure 4.2: Nest outcome for all predated artificial nests (n=133)

4.4.2 Factors affecting artificial nest predation

When predation by all predators was considered (model A) neither magpie presence, nor hedge type influenced predation rate. Time in breeding season was significant, with predation rates generally declining over the breeding season [$X^2_{1,87} = 5.12$; $P = 0.02$] (Table 4.2A), Figure 4.2). However, when we examined factors that predicted only predation by medium-sized birds, the results differed (model B). This suggested that the factors which caused variation in nest predation rates differed depending on the identity of the predators. The effect of magpie presence on the proportion of nests predated by medium-sized birds varied temporally. Although approximately 75% more nests were predated in magpie-present locations overall, the disparity in predation rates between magpie-present and magpie-absent transects was much greater later in the breeding season. In the last month of the breeding season (July), 20% of nests were predated by medium-sized birds in magpie-present locations, whereas none were predated in magpie-absent transects [$X^2_{1,86} = 4.84$; $P = 0.03$] (Figure 4.4).

Table 4.2: Summary of test statistics from Generalised Linear Mixed Models (GLMMs) of rate of artificial nest predation by A) all predators and B) medium-sized birds.

A)					
Maximal model					
Fixed effects	Estimate (β)	SE	Test statistic (χ^2)	df	P value
Intercept (Magpie presence – absent, Hedge - open)	-0.31	0.97			
Magpie presence	-0.21	0.8	0.31	1	0.58
Hedge type	-0.3	0.89	3.25	1	0.07
Date	0	0.01	5.18	1	0.02*
Magpie presence * date	0	0.01	0.05	1	0.82
Hedge type * date	-0.01	0.01	2.13	1	0.14
Random effects	Estimate (σ^2)	SE	Test statistic (χ^2)	df	P value
Location	1.29	0.23	51.89	1	<0.001*
Minimal model					
Fixed effects	Estimate (β)	SE	Test statistic (χ^2)	df	P value
Intercept (Magpie presence - absence, Hedge - open)	0.75	0.55			
Magpie presence	0.6	0.57	0.32	1	0.57
Hedge type	0.66	1.83	3.24	1	0.07
Date	0	2.29	5.18	1	0.02*
Random effects	Estimate (σ^2)	SE	Test statistic (χ^2)	df	P value
Location	1.3	0.23	53.46	1	<0.001*

B)					
Maximal model					
Fixed effects	Estimate (β)	SE	Test statistic (χ^2)	df	P value
Intercept (Magpie presence - absence, Hedge - open)	-1.64	1.35			
Magpie presence	-1.24	1.17	0	1	0.97
Hedge type	-0.84	1.24	2.33	1	0.13
Date	0	0.01	0.87	1	0.35
Magpie presence * date	0.02	0.01	2.18	1	0.14
Hedge type * date	-0.01	0.01	0.18	1	0.67
Random effects	Estimate (σ^2)	SE	Test statistic (χ^2)	df	P value
Location	1.67	0.26	28.29	1	<0.001*
Minimal model					
Fixed effects	Estimate (β)	SE	Test statistic (χ^2)	df	P value
Intercept (Magpie presence - absence, Hedge - open)	-1.25	0.99			
Magpie presence	-1.49	1.03	0	1	0.98
Hedge type	-1.25	0.8	2.33	1	0.13
Date	-0.01	0.01	0.87	1	0.35
Magpie presence * date	0.02	0.01	4.84	1	0.03*
Random effects	Estimate (σ^2)	SE	Test statistic (χ^2)	df	P value
Location	1.67	0.26	28.42	1	<0.001*

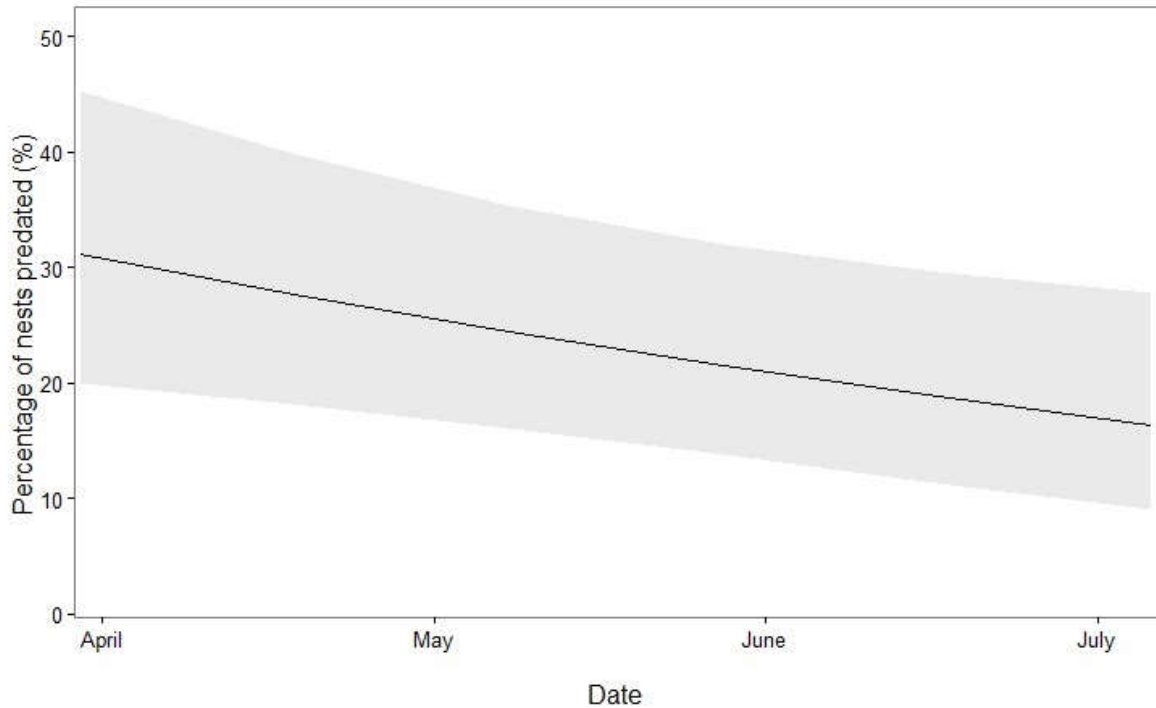


Figure 4.3: Predicted values for percentage of artificial nests predated by medium-sized birds relative to time in the breeding season. The predicted values are displayed with 95% confidence interval.

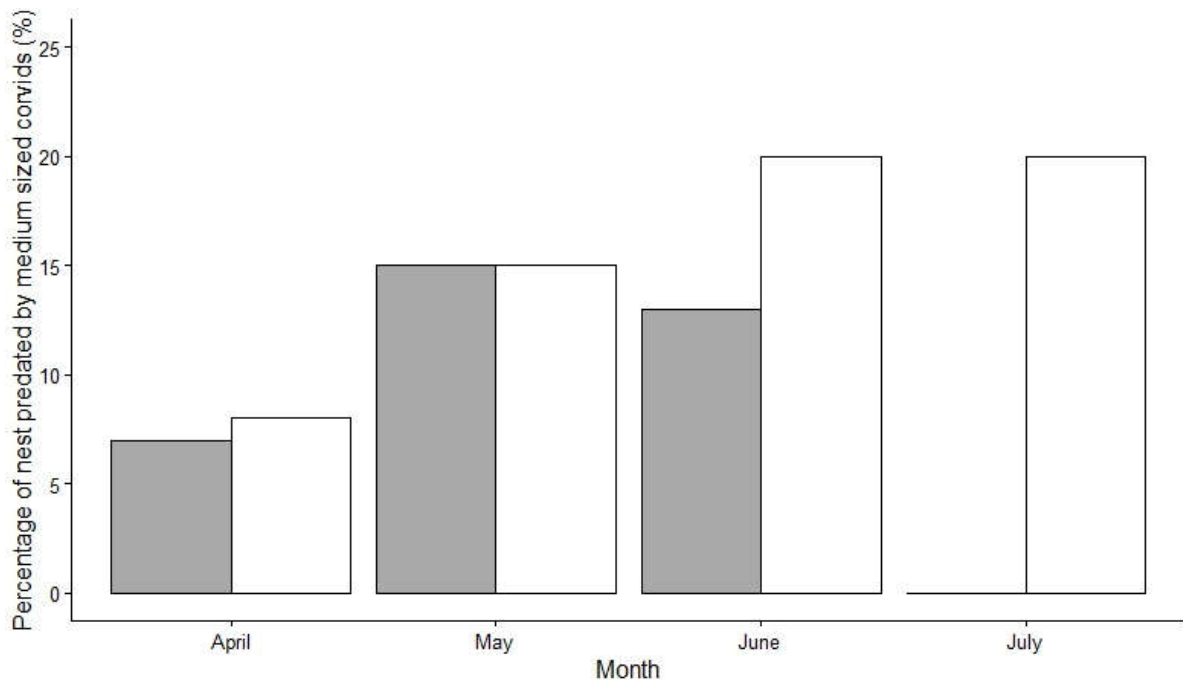


Figure 4.4: Percentage of nests predated by medium-sized birds in magpie-present (white bars) and magpie-absent (black bars) locations for each month in 2016.

In both models (A and B) the specific location of nest transects, which was fitted as a random effect, was also highly significant (Table 4.2). Predation rates, by all predators and by medium-sized birds only, differed between transect locations

beyond the effect of the fixed factors (magpie presence and time in the breeding season) on nest predation rates (*Figure 4.5*). We examined the identity of individual magpies predated at particular transect locations, and evidence indicated that higher predation at specific locations was driven by increased predation by local magpies. The individual colour-ringed magpies that were identified predated nest transects were only observed predated magpie-present transects within their own territories, or in magpie-absent areas immediately adjacent to their territories. On the two occasions when unringed birds were seen predated nests, the transects were located in territories where the territory holders were not ringed

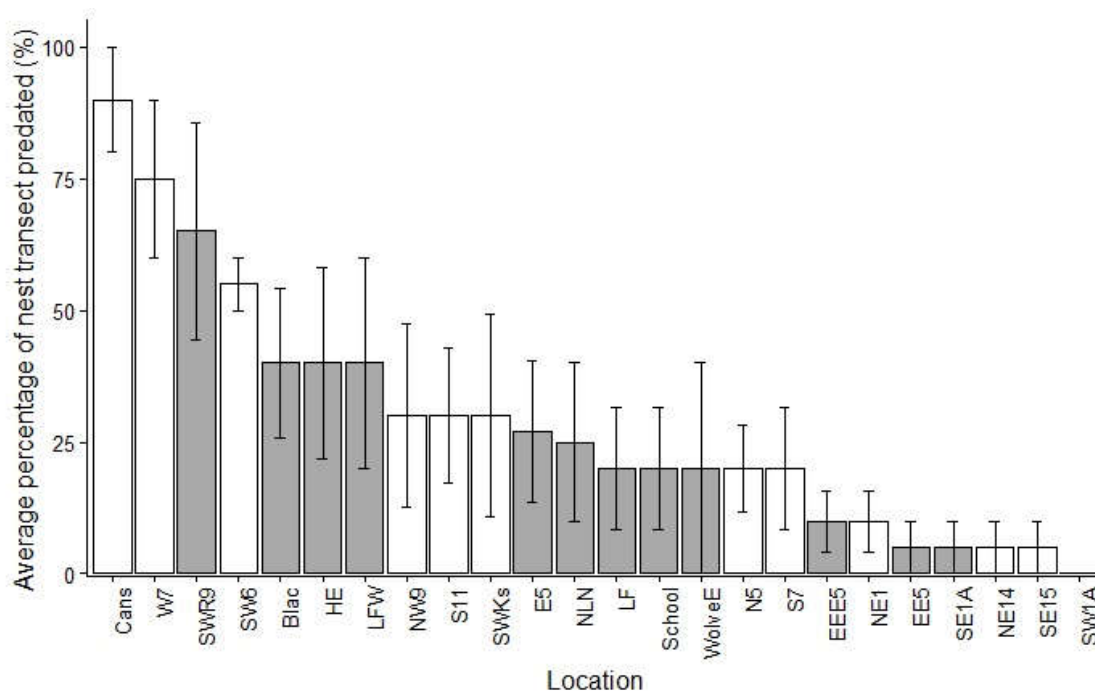


Figure 4.5: Average percentage of nest transects predated per exposure ± 1 SE at magpie-present (white bars) and magpie-absent (dark grey bars) sites

This variation in nest predation by local magpies may have related to differences in the territorial defence behaviour of these magpies. Magpie-present sites where the owners exhibited stronger territorial defence behaviour tended to suffer slightly higher levels of predation by medium-sized birds [GLM: ($X^2_{1,9} = 3.54$; $P = 0.058$)] (*Figure 4.6*).

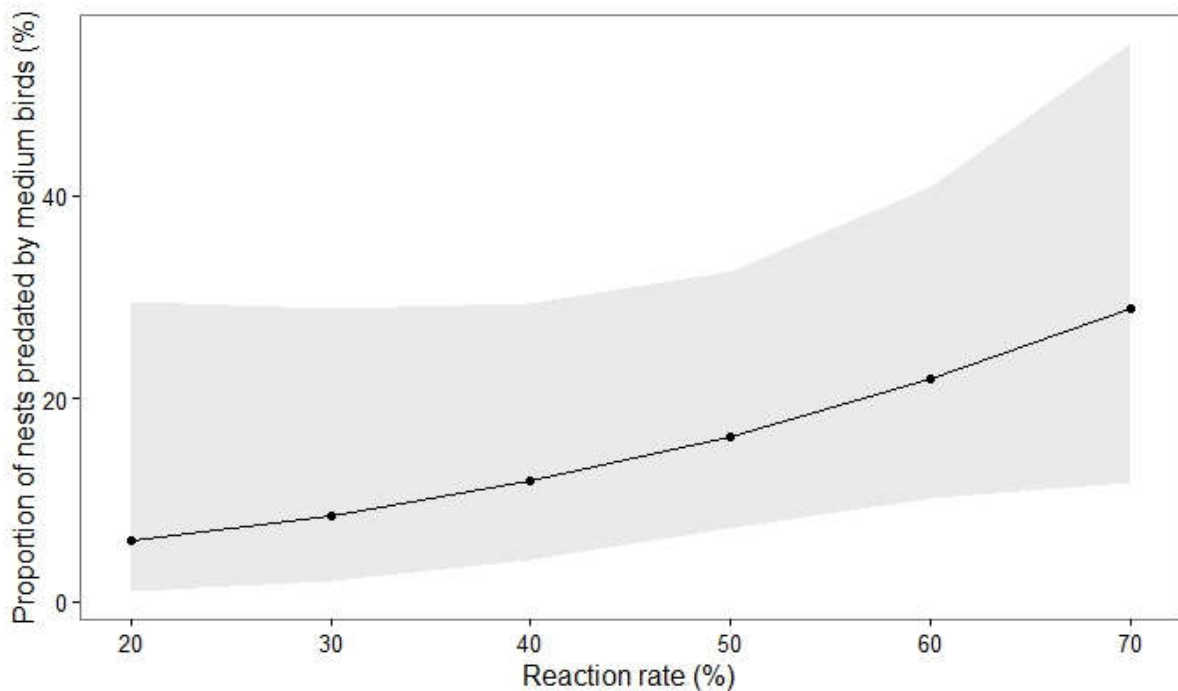


Figure 4.6: Predicted values for proportion of artificial nests, placed in magpie-present transects, predated by medium-sized birds relative to response rate of the territory holding magpies to a model intruder placed 20m from the nest to North, South, East and West. The response rate is presented as percentages of intrusions that magpies responded to. The predicted values are displayed with 95% confidence interval.

4.5 DISCUSSION

Predation of artificial nests by all predators decreased over the course of the breeding season, independent of magpie presence. This is probably due to variation in external habitat, specifically growth in the vegetation that provided nest cover. However, at certain times during the breeding season, nests placed within active magpie territories were more frequently predated, by medium-sized birds only, compared to those placed outside magpie territories. Given that the vast majority of medium-sized birds identified predated nests were magpies, we suggest that this higher level of predation in magpie territories, late in the breeding season, was driven by predation by the territorial magpies during the period they were provisioning dependent young.

Predation of artificial nests was also predicted by the identity (location) of the nest transect itself. Some magpie-present transects suffered ~80% predation rates, while others suffered only ~5% predation rates. We found that, in territories in which artificial nest predation rates were high, territorial birds did differ in behavioural attributes; they were more likely to defend their territory strongly against simulated

intrusions. These differences between territorial locations could be therefore be related to the attributes of individual birds; to properties of the territories (habitat variation we did not account for could increase the likelihood of predators encountering nests); or to a combination of the two (particularly predatory birds may be more likely to hold territories with specific habitat characteristics). Consequently, we suggest that the effects specific corvid predators have on songbird nests may differ due to variation in breeding status, time in the breeding season, and possibly due to additional differences in foraging behaviour between territory holders.

4.5.1 Predators of artificial nests

The most frequently identified predators of wax-filled eggs in artificial nests were medium-sized bird predators. Medium-sized birds were three times more likely than mammals to predate nests, and camera evidence suggests that approximately 90% of these medium-sized bird predators were magpies. Therefore, throughout this discussion, nests predated by medium-sized birds were presumed to be predated by magpies. One explanation for the apparently higher predation rates by magpies is that artificial eggs are less attractive to mammals than birds. This may be because of their unnatural smell, which may reduce predation by predators which rely more on olfactory cues (Purger et al., 2012; Rangen et al., 2000), or because of their size, as smaller mammals such as mice may be unable to handle larger dummy eggs (Degraaf & Maier, 1996; Marini & Melo, 1998). If this is the case, using marks in wax-filled eggs to identify predators may have led to an underestimation of mammalian predation. However, marks in our wax-filled eggs revealed that they were attacked by various mammalian predators including small rodents, and that when real eggs were predated wax-filled eggs were generally predated as well; only 21% of all wax-filled eggs in predated nests were found untouched. In those cases where wax-filled eggs were untouched we rarely found evidence which suggested that the real eggs had been taken by mammals (shell fragments or egg contents left in the nest) (Best, 1978; Marini & Melo, 1998; Major, 1991). It therefore seems unlikely that, when compared to avian predators, mammalian predators disproportionately predated real eggs and left wax-filled eggs untouched.

Magpies were the most frequently identified predators of our artificial nests, and there is no reason to suspect that this was biased by our method of predator

identification. We were not able to directly assess how comparable the predators identified at artificial nests were to the predators of natural nests on the same site (predators could not be identified from the remains of predated natural nests), and it has been suggested that predation of artificial nests does not always represent natural nests in terms of predator fauna (Pärt & Wretenberg, 2002). However, the high proportion of nest predation attributed to avian predators in our artificial nests is comparable to studies of natural nests in similar environments. For example, Chamberlain (1994) found approximately 65% of predators identified predated the nests of a rural population of blackbirds were avian (probably magpies or jays).

The use of artificial nests has been criticised for other reasons. It has been suggested that predation of artificial nests does not represent the spatial and temporal patterns of natural nest predation (Zanette, 2002). However, studies have previously used artificial nests to analyse corvid predation of nests (Møller, 1988), and artificial nests have been shown to suffer ecologically realistic patterns of nest predation, particularly when an attempt is made to mimic natural eggs and nests. A number of studies have validated the use of artificial nests with comparisons to concurrent studies of natural nests (Roos, 2002; Pehlak & Lohmus, 2008). In this study, the artificial nests were not directly comparable with the natural nests studied on the same site for many reasons. For example, the artificial nests had a much shorter exposure time. However, natural songbird nests were monitored in hedgerows on the field site in 2015 and 2016 and were found to suffer similarly high failure rates (approx. 60%) to the artificial nests. Therefore, it does not seem that the use of artificial nests would have introduced a systematic bias in our results.

4.5.2 Effect of magpie presence on nest predation

Transects adjacent to active magpie nests suffered an increased proportion of predation attributable to magpies, specifically late in the breeding season. Predation risk for songbird nests may be higher within the territories of breeding magpies because breeding pairs restrict how far they range from the nest during the breeding season (Vines, 1981) and are therefore more likely to forage and encounter nests near their own nests (Erikstad et al., 1982; Roos & Pärt, 2004). In addition, these territorial birds spend a longer amount of time utilising a small amount of habitat. Therefore, they are more likely to have thoroughly searched the habitat area than

wider ranging non-territorial individuals. This increased local knowledge may improve their chances of finding nests within their territories (Møller, 1988). Alternatively, it may be that those birds that become breeding individuals and territory holders, are intrinsically more likely to predate songbird nests, for reasons other than the spatial restriction of foraging increasing the probability of encountering nests (Graham et al., 2011). It was not possible to separate these two possibilities in this experiment.

The effect of magpie presence on nest predation by magpies varied temporally. Nests in magpie-present transects were significantly more likely to be predated relative to nests outside of magpie territories only towards the end of the breeding season. This suggests that magpies foraging in territories (probably breeding individuals) continue to prey on nests as foliage becomes denser and they become harder to find, whereas magpies which forage further from active magpie nests (likely non-breeding individuals) do not. We observed that the exposure dates of these later artificial nest transects coincided with the period when magpies were known to have eggs and young in the nest; transects were exposed within eight days of magpies fledging young. Other bird species favour more nutrient-rich vertebrate prey when feeding young (Gotmark, 2002; Sasvari & Hegyi, 1998). A possible explanation for the higher predation of the nests exposed later in the breeding season in magpie-present transects may therefore be that breeding magpies (the territory holders) continue to seek out protein-rich prey, as this type of prey may provide particular benefits for their young, for example it may increase their growth (Annett & Pierotti, 1989).

Magpie presence did not cause increased nest predation late in the breeding season when predation by predators other than magpies was also included in the analysis. This suggests that, at least at the end of the season, other predators may be compensating for relatively lower predation rates by magpies in magpie-absent transects, compared to magpie-present transects. The absence of one predator species will not improve nest success if other predators predate the nests instead (Bodey et al., 2011). It may be that in areas where magpies are less likely to spend time, in this case outside of magpie territories, the chance of other predators encountering the nests first is greater.

Nest predation by all predators generally decreased over the breeding season, the opposite trend to nest predation by magpies in magpie territories. Predation may be higher earlier in the season due to nest conspicuousness caused by an absence or sparsity of foliage in the largely deciduous hedgerow species. In contrast later in the breeding season, when foliage is densest, nests may be better concealed (Rodewald et al., 2009; Söderström, 2001). Variation in the external habitat may have affected nest predation by all predators.

4.5.3 Effect of location on artificial nest predation

We have suggested that higher predation in magpie-present transects, late in the breeding season, is due to predation by the territorial pair. However, it might be argued that, as on average our magpie-present transects tended to be clustered in a central area whereas the magpie-absent transects were more dispersed, our findings are more indicative of an effect of a generally higher magpie density on nest predation (*Figure 4.1*). Firstly, it should be noted that a lack of magpie-present transects identified in these peripheral areas is not necessarily indicative of absence. The area the surveyor could cover in detail was limited. Therefore, although magpie territory absence could be relatively easily established by a total lack of magpie nests and/or nest sites, it was not possible to confirm whether magpie nests in this peripheral area were active. Density of active magpie nests might not in reality be lower in peripheral areas.

Secondly, although spatial association with an active magpie nest did increase nest predation rates, not all the magpie-present transects suffered high predation. When considering either all predation or only predation by magpies, there was an overall effect of transect location, independent of magpie nest presence. Some artificial nest transects directly under active magpie nests were not heavily predated, and these included transects located under magpie nests in the area where magpie territories were at high density. Further exploration of this significant effect of location does show some magpie-absent transects also have higher predation. These are not always in the areas identified as having high magpie density which, again, suggests that it is not simply being placed in an area with many active magpie nests that increases predation.

However, predation of these magpie-absent transects, away from active magpie nests, may be indicative of predation by non-territorial individual. High predation at particular locations may not always be due to territorial breeding individuals. An ongoing trapping program that revealed a number of magpies were existing in the farmland without holding territories. However, non-territorial magpies are ephemeral in any particular area, especially during the breeding season (Birkhead, 1991), and the consistency of high nest predation by magpies over four separate exposures of the artificial nests means it seems unlikely that these more transient individuals were responsible. All individuals identified on camera were known to be highly local to the transect they predated, and were believed to be part of the local breeding pair. There were no occasions where known individuals were seen predated more than one transect location, or transects outside their territories. Therefore, it seems most likely that the magpie-absent transects that had higher predation rates were within the foraging range of a local magpie pair. Territorial corvids have been shown to forage further from the nests in order to exploit particular, sparse, resources (Neatherlin & Marzluff, 2004). We also found that individual magpies ranged over a wider area (radio tracked birds had an average home range size 45.2 ha.) than the area around the nest they were observed actively defending (Capstick, Christou & Pinkham, unpublished data).

In summary, we found evidence that variation in predation of our artificial nests by magpies, can be partially explained by the presence of a breeding pair of magpies. Proximity to an active magpie nest did increase nest predation rates, late in the breeding season, and nest predation was primarily carried out by magpies which were local to transects, presumed to be territory holders. However, the effect of specific transect location on predation requires further exploration; specifically, why were some magpie-present transects not heavily predated? Some territorial magpies did not seem to repeatedly predate songbird nests around their own nest, even late in the breeding season when magpie predation in magpie-present transects was highest. Some predators within a population may specialise on specific prey, developing particular foraging skills such as nest predation, whereas others may be more generalist (Steenhof & Kochert, 1988; Dickman & Newsome, 2015). Although magpies are considered to have a broad generalist diet, this does not preclude some individuals preferentially taking particular prey (Corbett & Newsome, 1987).

Individual predators within a population have been shown to differ in their foraging behaviour, both in prey choice and foraging location (Patrick & Weimerskirch, 2014; Graham et al., 2011). One explanation for the pattern we observed is that there were differences between territorial magpies at an individual level in the extent to which they engaged in nest predation.

Consistent differences in foraging behaviour between individuals have been linked to variation in a number of factors, from sex differences (Wilkinson & Barclay, 1997) to differences in exploratory behaviour and associated habitat preferences (Wolf & Weissing, 2012). As previously reported (see Avilés et al. 2014) we found that magpies in different territories varied in their nest defence behaviour, and there was some evidence to suggest that nest predation was higher in the territories where the resident magpies exhibited more aggressive territorial behaviour. These more territorially defensive individuals may be likely to spend more time in their territory, and therefore more likely to encounter songbird nests close to their own nests. Alternatively, it may be that there are underlying differences in behaviour, with more territorially defensive individuals likely to have differences in foraging behaviour even when encounter rates with prey are similar (Linnell et al., 1999). Aggression, including nest defence behaviour, has been linked to boldness and exploratory behaviour (the 'proactive-reactive axis') in a number of species (Cole & Quinn, 2012; Hollander et al., 2008). Variation in this behavioural axis has also been associated with differences in foraging behaviour. For example, it may be that more aggressive territorial individuals are likely to forage in particular habitats (Patrick et al., 2013), or exploit novel prey (Chiarati et al., 2012).

We were only able to relate variation in magpie behaviour and nest predation by magpies at the territory scale. To avoid human disturbance of behaviour (Kenney & Knight, 1992), we observed territorial defence behaviour from a distance which precluded direct identification of individuals using their colour leg rings. This meant we could not identify the specific member of the territorial pair engaged in territorial defence. Nevertheless, it does seem that nest predation was higher in territories where at least one member of the pair engaged in more vigorous nest defence.

However, as the data included in this analysis were collected in one year only, we cannot be certain that the higher predation rates observed in certain locations

were due to particularly predatory individuals holding those territories, or whether this was because of some inherent property of those territories that we did not account for. In the latter case, the removal of particular territory owners would not reduce nest predation rates within a territory; rates of nest predation would always be higher in that territory, independent of the territory owners. Variation between transect locations, which was not included in our analysis, could further explain the predation patterns we found. For example, more complex hedge features, such as presence of intersections and corners (Lack, 1988), may reduce predator encounters with prey. However, as nest transects were placed in similar mixed arable and pastoral farms within a 15km² area, it seems unlikely there was a significant systematic variation in habitat between transect locations that has not been accounted for.

On the other hand, it could be that there is some interaction between the properties of a territory and the behaviour of the territory holders. The owners of particular territories may be more likely to predate nests within them. For example, the owners of the best quality territories may engage more frequently in territorial defence (Møller, 1982), and be more likely, for the reasons suggested above, to predate nests in their territory. Alternatively or additionally, individuals which are likely to be dominant and hold particular territories may be older birds (Birkhead, 1991), and therefore more experienced predators who are more likely to have encountered nests previously and developed a search image for that prey type, facilitating future predation (Vigallon et al., 2005; Montevecchi, 1976).

Further fine-scale multi-year analysis relating magpie territory ownership to predation rates within those territories would be necessary to disentangle the relative influence of habitat variation between territories and magpie identity. In any case, identifying either territory holders or territories that are likely to suffer increased risk of nest predation could be still be beneficial, as it may indicate where management of predators and/or habitat should be targeted (Swan et al., 2017).

4.5.4 Conclusions

Our results suggest that magpies could be major predators of songbird nests on this field site, and that spatial association with territorial magpies late in the magpies' breeding season can increase predation risk for songbird nests. Previous studies have tried to increase songbird breeding success using predator removal and/or

habitat management, and have had mixed success (Baines et al., 2008; Chiron & Julliard, 2007; White et al., 2014). This may be because all the factors which may cause variation in nest success are not always considered. Survival of nests which have a relatively high risk of predation (in this study those located in magpie territories late in the season) may be more likely to improve following predator removal or nest habitat creation. Identifying the most at-risk farmland songbird nests, possibly by using artificial nest studies, could facilitate more effective and targeted management of habitat and/or predators. Targeted management is more likely to increase the overall productivity of farmland songbird populations, which may help halt the ongoing population decline of this group of species.

Chapter Five

Effect of magpie ecology and habitat variation on farmland songbird nest site choice and nest success



ABSTRACT

The increasingly intensive management of farmland has led to the degradation and/or loss of habitats previously used by songbirds which specialise on the farmland environment. The loss of these habitats may have contributed to the population decline of these birds. For example, the removal of hedgerows has reduced the availability of suitable nesting habitat, which has led to lower breeding success of some farmland songbirds. Identifying nest site attributes which increase breeding success could facilitate the preservation/provision of favourable nest habitat. We examined how nest site attributes affected nest site choice and nest success of birds on a typical farmland field site. Predation is generally the most common cause of breeding failure, therefore we focused specifically on attributes which were likely to directly, and indirectly, influence the risk of predation of eggs and chicks in the nest (nest predation), particularly by magpies which were the most frequent nest predator on this field site. We also identified territories of breeding songbirds and subsequently surveyed these territories for fledged broods. This provided a complementary measure of songbird productivity: fledged broods produced per territory. Songbird nests were on average further than expected from magpie nest sites, but they were also more likely to be in some magpie territories than others. Songbirds were not avoiding particularly predatory magpies, instead they were choosing sites in the densest hedges. Predators on our farmland field site existed at high density and songbirds may have been choosing sites which would provide protection from predation, rather than avoiding predators specifically. Songbird nest success was generally low but, nests in denser hedges were more likely to be successful. Fledged brood monitoring provided a higher estimate of overall breeding success than the direct nest monitoring, possibly because our nest finding was biased towards nests likely to fail. Nevertheless, the territories of hole nesting species, which are less vulnerable to predation, were more likely to produce fledged broods than open nesting species. This suggests that nest predation did have a significant effect on breeding success on our field site. Provision of more hedges which comprise of denser vegetation could increase the availability preferred habitat for nesting songbirds, and potentially reduce the effect of predation on songbird breeding success.

5.1 INTRODUCTION

Availability of suitable nest sites affects the breeding success of songbirds (Newton, 1994b). Recent declines in some farmland songbirds, such as reed bunting (*Emberiza schoeniclus*), and skylarks (*Alauda arvensis*), have been attributed, at least in part, to reductions in nesting habitat caused by agricultural intensification (Brickle & Peach, 2004; Newton, 2004; Whittingham & Evans, 2004; Siriwardena et al., 2000b). Such reductions may lead to greater inter or intra-specific competition for a limited number of favourable nest sites, forcing some birds to use suboptimal locations (Hagan et al., 1996; Goodenough et al., 2008). Variation in nest site attributes can cause breeding success to be reduced at these sub-optimal sites: chick starvation may be increased in nest sites further from preferred adult foraging locations (Murray, 2004), or deaths from exposure may be greater in less sheltered sites (Thingstad, 1997) and those with less favourable thermal conditions (Rauter et al., 2002; Kim & Monaghan, 2005). However, predation of eggs and chicks in the nests, hereafter referred to as nest predation, is the most common cause of breeding failure (Martin, 1993), therefore understanding the attributes of nest site that interact to directly, and indirectly, affect a nest's risk of predation is particularly important.

The likelihood of a predator encountering a nest may be affected by the predator's ecology, behaviour, and movement patterns (Storch et al., 2005). For example, activity of predators is likely to be increased near their own breeding sites. Songbird nest sites located in close proximity to predator breeding sites may therefore be more vulnerable to predation (Tryjanowski et al., 2002; Møller, 1988). Alternatively, nesting near a predator's breeding site could have a protective effect if the breeding individuals exclude other predators (Tryjanowski et al., 2014).

The chance of a predator encountering and predating a nest is also affected by broader ecological factors. Nest sites with greater cover and concealment, such as those in thick vegetation (Hinsley & Bellamy, 2000), or those lower down in vegetation (Hatchwell et al., 1999) generally have greater breeding success (Hatchwell et al., 1996; Kelleher & O'Halloran, 2007) and species like blackcap (*Sylvia atricapilla*) have been shown to prefer such sites (Wegrzyn & Leniowski, 2011). However, sometimes nest concealment does not have the effects we predict on nest success, other attributes of nest site appear to have a greater influence on

nest success. For example, Cresswell (1997) found that independent of how detectable blackbird nests were, those that were lower down were predated more often.

The habitat around the nest site can also influence nest success. Reduced availability of habitat which provides chick food can directly increase chick starvation but may also affect nest predation risk (Murray, 2004). Poorly provisioned chicks beg more loudly making them easier to locate (Evans et al., 1997). Additionally, where chick provisioning habitat is poor and nest predator abundance is high, adult birds may be unable to make the more frequent foraging trips required to prevent chick starvation, whilst also reducing activity around the nest to avoid attracting the attention of nest predators (Dunn et al., 2010).

There are many nest site attributes, including and additional to those mentioned above, which affect the predation risk of a given nest site. Nest site choice is a trade-off between these different attributes (Cuervo, 2004), so when nest sites become limiting, birds may have to compromise more in their nest site choice. Birds using suboptimal sites may have generally lower breeding success. Alternatively, birds may be able to maintain breeding success in less preferred sites by adjusting their breeding behaviour, for example through moderating nest defence behaviour (Cresswell, 1997a; Weidinger, 2002). To investigate this trade-off, it is important to look both at factors which drive nest site choice, and at factors which drive nest site success. If factors which determine nest site choice do not relate to nest success, birds may be compensating for differences in quality between preferred and less preferred nest sites.

If attributes of nest site which affect nest site choice and nest success of farmland songbirds are identified, it may be possible to increase the availability of favourable nesting habitat. This in turn could lead to higher breeding success, and potentially population recovery, of these threatened species (Kelleher & O'Halloran, 2007; DEFRA, 2016). We therefore aimed to identify the factors that influenced nest site choice, and how they affected nest success of a community of songbirds on a typical farmland site. The main cause of nest failure on this field site was predation, and previous work using artificial nests suggested that magpies (*Pica pica*) were the most frequent nest predators (*Chapter Four*). We therefore examined how aspects of

magpie ecology and behaviour, such as nest site proximity and predatory behaviour, influenced songbird nest site choice and nest success. We also looked at habitat factors which might affect predation risk, such as the foraging opportunities available in the surrounding habitat. We assessed the effect of features of the songbird nest itself such as nest height and nesting materials. In addition to monitoring the fates of nests that we located, we also surveyed songbird territories for fledged broods, and measured the number of songbird territories that produced a fledged brood. This provided a supplementary assessment of songbird productivity independent of monitoring nest outcome, which may have been biased towards nests that are easy to find and likely to fail. Comparing the location of nest sites, and of fledged broods, allowed us to assess the relative effect of predation and habitat on nest and fledged brood site choice. This was because predation, particularly by magpies, would not be expected to have as great an effect on fledged brood site choice as on nest site choice, as magpies are not believed to be frequent predators of juvenile birds (Chiron & Julliard, 2007; Fernández-Juricic et al., 2004).

5.2 METHODS

5.2.1 Field Site

All data was collected on an arable and pastoral farmland site with a typical population of farmland songbirds. The site was in Warwickshire, central England (52°15'53.1"N 1°40'01.1"W).

5.2.2 Songbird nest searches

All 40.5km of hedgerows on the field site were systematically searched for old, and active, open songbird nests. Each hedgerow was searched three times from March to July in 2015 and 2016. Hedgerows were also searched at least once from May to July 2014. In total 518 nests were found and categorised according to the species that built them. When the species which built the nests could not be identified, for example when nests were old, they were categorised by building materials and size. These categories did provide some indication of the species which were likely to have built the nests, for example small grass and moss nests were similar to dunnock nests (*Prunella modularis*) whereas moss nests were likely to belong to finch species or wrens (*Troglodytes troglodytes*) (see *Table 5.1* for the full categories). Most nests found belonged to thrush species (blackbird (*Turdus merula*))

and song thrush (*Turdus philomelos*). This did not seem to be due to variable preservation of different species nests; a similar proportion of nests were classified as belonging to thrush species whether the nests were found newly built (46%, n=123) or old (42%, n=395)

Table 5.1: Count of nests found categorised by species or by nesting materials when species was unknown. In this table nests categorised by nesting material are grouped with species which build similar style nests.

Nest type	Count
Blackbird (<i>Turdus merula</i>)	42
Song thrush (<i>Turdus philomelos</i>)	23
Unknown thrush	167
Dunnock (<i>Prunella modularis</i>)	25
Small grass and moss nest	29
Long-tailed tit (<i>Aegithalos caudatus</i>)	10
Wren (<i>Troglodytes troglodytes</i>)	33
Chaffinch (<i>Fringilla coelebs</i>)	8
Goldfinch (<i>Carduelis carduelis</i>)	1
Moss nest	51
Linnet (<i>Carduelis cannabina</i>)	2
Robin (<i>Erithacus rubecula</i>)	1
Whitethroat (<i>Sylvia communis</i>)	3
Blackcap (<i>Sylvia atricapilla</i>)	1
Yellowhammer (<i>Emberiza citrinella</i>)	4
Medium grass nest	24
Small grass nest	40
Twig/moss nest	3
Unknown	51
Total	518

5.2.3 Fledged brood surveys

Fledged brood surveys were carried out twice a week, from mid-May to the end of June in 2015 (9 surveys in total) and 220 fledged broods of all songbird species (including hole nesters) were identified by call or direct sighting. Each survey followed the same route, which ensured the surveyor (always T. Powell) passed within earshot of all hedgerows on the site.

5.2.4 Assessing the effect of site attributes on songbird nest and fledged brood distribution

Nest site and fledged brood site preferences were assessed by comparing the attributes and distribution of songbird nest sites and fledged brood sites, to the attributes and distribution expected under a null model. In this case the null model was an equal number of randomly distributed points (hereafter random nest sites or random fledged brood sites) (Mchugh et al., 2016; Schneider et al., 2012b; Shipley et al., 2013). The random nest sites were generated within the hedgerow and scrub habitat searched for songbird nests, and the random fledged brood sites were generated in areas where fledged broods were detected, mainly hedgerows and some woodland edges. These points were produced using the Create Random Points tool in the Data Management toolbox ArcGIS 10.2.2. (ESRI, 2014). This tool produces a random number stream and then uses numbers from that stream to randomly select values on the x axis and y axis within a specified range of coordinates (in this case the areas searched for either songbird nests or fledged broods). Each value within the range has an equal chance of being selected (ESRI, 2017).

5.2.5 Predator attributes of songbird nest and fledged brood sites

We first identified predator locations, specifically magpie nest sites, by repeated visual searches of the field site between late spring 2014 and winter/early spring 2016. Magpie nests have a characteristic structure and, on our field site, could be distinguished by the universal presence of a domed roof (Tatner, 1980). Active nests were identified in each year through direct observations of adults in and around the nest site, and indirect identification of magpie activity, specifically repeated re-trapping of the same individuals near given nest sites (Diaz-Ruiz et al., 2010). Re-trapped individuals could be identified as such, because all magpies were colour ringed the first time they were trapped.

We often found several magpie nests that were clustered together (<5m apart) and were never used concurrently. Old nests were well preserved on our field site and it is likely these clustered nest sites belong to the same territory, and were used in different years. To distinguish these clustered nests, from nests that were active concurrently and belonged to separate territories each magpie nest found was

assigned to a particular magpie territory, referred to as magpie territory identity. Twenty-eight magpie territories were identified.

To assess how predator location affected songbird site choice first, we measured distance to the nearest active magpie nest for all 518 songbird nests, all 220 fledged brood sites, and to the equivalent random nest sites and random fledged brood sites. Secondly, we determined whether songbird site location was affected by differences between magpie territories. To address this question, the identity of the nearest magpie nest (which territory it belonged to) was assigned for all songbird nests, fledged brood sites, random nest sites and random fledged brood sites. Finally, to see if songbird site choice was specifically affected by differences in predation risk between magpie territories we measured variation in predation rates between magpie territories. Fourteen artificial nest transects (each consisting of 5 nests) were placed along a ~60m section of hedgerow adjacent to active magpie nests. These transects were placed in the hedgerow for 5 days and then collected and the predation rate recorded. The exposure of nest transects was repeated at least three times in each territory from May to July in 2015 and/or 2016. An overall predation rate was taken as number of nests predated divided by the total nests exposed.

5.2.6 Habitat attributes of songbird nest and fledged brood sites

A digitised habitat map of the study area was used for all habitat analysis. Habitat was sorted into categories ecologically relevant to songbirds (*Table 5.2*). A 70m circular buffer was created around each songbird nest site and each random nest site using ESRI ArcGIS 10.2.2 (ESRI, 2014). This represented an area of habitat likely to be used by breeding songbirds and was based on an approximate home range for breeding thrushes according to studies which radio-tracked these birds in farmland (Peach et al., 2004; Murray, 2004). This area was calculated based on thrush ranging behaviour as the most frequently found nests were thrush nests (*Table 5.1*). This buffer area was also created for the fledged brood and random fledged brood sites. Little is known about post-fledging movements in hedgerow passerines (Sage et al., 2015; Cox et al., 2014) so this 70m buffer area was used for consistency.

The proportion of each habitat type within these buffer areas was measured and a Shannon-Weiner index of diversity was calculated. The proportion of cover available to songbirds in these buffer areas was also measured. For nest sites, this was the proportional area of hedgerow, for fledged brood sites the proportional area woodland was also included. This was because the fledged brood surveys identified some woodland species whereas the nest search did not.

Table 5.2: Description of habitat categorisation

Category	Included habitats
Grass	Pasture, hay crops, field margins, verges and gardens
Hedge	Wide hedges (4m), narrow hedges (2m) and scrub
Woodland	All types of woodland (mainly small mixed copses and conifer woods)
Urban Crops	Houses, farm buildings, roads and water Cereals – wheat, barley and oats Break crops (crops planted between cereals in a crop rotation to reduce disease and increase soil fertility) – oil seed rape, field peas and field beans

5.2.7 Nest site attributes

At each songbird nest site, the nest height was measured using a tape. Height was defined as from the top of the nest to the ground and the average height of nests was $118\text{cm} \pm 1.93$ ($\pm\text{SE}$) ($n=444$). The species of vegetation that the nest was situated in, and the main materials that nests were made from, were also documented. These variables were specific to songbird nests and not collected for random nest sites.

To generate a quantitative measure of hedgerow density at a nest site, we photographed a white A2 piece of card through the hedgerow using a camera which was 1m high and 4m away on the opposite side of the hedge. We then calculated the proportion of white space to branches by converting the image into a binary image using manual thresholding. To account for the influence of width on this 2d measure, the proportion of white was multiplied by hedgerow width for further analysis. Photographs were taken at the sites of 84 nests with a known outcome in 2015 or 2016 and at 50 of the random nest sites (a randomly selected subset).

Image analysis was carried out using Imagej 1.51j8 (National Institutes of Health, USA;URL: <http://rsb.info.nih.gov/ij>) (Schneider et al., 2012a).

5.2.8 Breeding success

5.2.8.1 Songbird nest success

Of the 518 songbird nests found, 101 were found when active and the fate of these nests were monitored. Nests were relocated using hand-held GPS and checked every 4-8 days. Success was inferred when the nest was found empty and undamaged after the expected fledging date. Otherwise the nests were considered failed. Where possible, cause of failure was identified based on evidence at the nest site (for example, broken egg shells and/or ripped nest lining indicated predation). Evidence at the nest is not a reliable indicator of predator identity, so no attempt was made to identify predators responsible (Schaefer, 2004; Lariviere, 1999). Outcome was known for 64 nests (*Table 5.3*). Analysis of factors which predict nest success was limited to a subset of those for which hedgerow density data was also available (n=50).

Table 5.3: Count of nests with known outcome, ordered by species (n=64).

Species	Outcome				
	Abandoned	Abandoned/ Predated	Fledged	Predated	Total
Blackbird (<i>Turdus merula</i>)	0	1	5	14	20
Blackcap (<i>Sylvia atricapilla</i>)	0	0	0	1	1
Chaffinch (<i>Fringilla coelebs</i>)	1	0	0	1	2
Dunnock (<i>Prunella modularis</i>)	0	1	4	5	10
Linnet (<i>Carduelis cannabina</i>)	0	0	0	1	1
Long-tailed tit (<i>Aegithalos caudatus</i>)	0	0	6	1	7
Song Thrush (<i>Turdus philomelos</i>)	0	0	0	8	8
Unknown	0	0	0	1	1
Whitethroat (<i>Sylvia communis</i>)	0	0	0	2	2
Wren (<i>Troglodytes troglodytes</i>)	0	4	3	4	11
Yellowhammer (<i>Emberiza citrinella</i>)	0	0	1	0	1
Total	1	6	19	38	64

5.2.8.2 *Fledged brood success*

Territories belonging to 20 species were identified and surveyed for fledged broods (n=204). We used the number of territories that produced a fledged brood as an alternate measure of the productivity of hedgerow bird species following Sage et al. (2015). Territories of the breeding birds on the field site were mapped as per the BTO Common Bird Census (Marchant, 1983 cited in Sage et al., (2015)) in three surveys carried out in early May 2015. The subsequent six surveys (See 5.2.3) focused on the mapping of fledged broods.

The alternative measure of productivity ascertained from these surveys is the probability of a territory being occupied by a fledged brood. This is essentially the number of fledged broods divided by the number of territories found along the survey route and is known as the observed territory occupancy probability (Sage et al., 2011).

However, fledged broods are not always detected in surveys and if many broods are undetected, this observed occupancy probability could be an underestimate. Therefore, firstly we calculated the probability of detecting a brood on a given survey (so-called daily detection probability) using Presence software version 11.6 (<https://www.mbr-pwrc.usgs.gov/software/presence>, MacKenzie et al. 2002; MacKenzie et al. 2006). This software compares the number of times a brood was detected compared to the number of times it could have been detected. In this case the number of times a fledged brood was recorded compared to the number of times a fledged brood survey was undertaken during the fledging to maturity phase (Cramp et al. 1977-1994).

The same software was then used to calculate an adjusted territory occupancy probability. This adjusts a species observed occupancy probability according to the probability of detecting a fledged brood of that species. Species which have fledged broods which are less likely be detected have an adjusted territory occupancy much higher than the observed territory occupancy. The adjusted occupancy probability is essentially a measure of how many fledged broods would have been identified per territory if all fledged broods were located in every survey (Sage et al., 2011).

As per Sage et al. (2015), species with daily detection probabilities of less than 0.20 were excluded from overall calculations. Below this level the estimates of Presence can be biased (Mackenzie et al., 2002).

5.2.9 Statistical analysis

5.2.9.1 *Analysing songbird nest site choice*

The factors influencing songbird nest site choice were assessed by comparing songbird nest site choice to a null model of nest site choice; the random nest sites (see 5.2.4). We used a generalised linear model (GLM) with a binomial distribution and a logit function (*Table 5.4A*) with nest site type (actual vs. random) as the response variable. We only included nest attributes which were known for both songbird nest sites and random nest sites as explanatory variables. We excluded nest height, year nest was active and nest type (species/building materials) as they were not applicable to random nest sites. The maximal model therefore included habitat diversity, proportion of cover (see 5.2.6), distance to the nearest magpie nest and the identity of nearest magpie nest (magpie territory to which it belonged) (see 5.2.5) as explanatory variables. We considered fitting an interaction term to the latter two explanatory variables to assess territory specific effect of magpie presence on nest site choice. However, the identity of nearest magpie nest variable had 28 levels. Therefore, we did not have sufficient power to fit an interaction between this variable and a continuous variable with our sample size (Bolker et al., 2008)

As we wished to test the null hypothesis that none of these variables predicted nest site choice we adopted a model simplification approach. This allowed us to identify which, if any, of the specific explanatory variables were driving nest site choice (Zuur et al., 2009; Fox et al., 2013; Crawley, 2012). Although model simplification has been criticised (Whittingham et al., 2006), it has also been shown to perform as well as other methods of variable selection (Fox et al., 2013; Murtaugh, 2009). This method can allow inferences to be made about the ecological system studied and has been utilised in several other studies examining the influence of different habitat variables on songbird nest site choice and nest site success (McHugh et al., 2017; Mikula et al., 2014; Stevens et al., 2007; Dunn et al., 2016). Models were simplified using backwards stepwise deletion of the least significant terms and changes in deviance following term removal were assessed using χ^2

statistics. Terms were only retained in the final minimal adequate models if their removal caused a significant increase in deviance (Crawley, 2005).

We only had hedgerow density measures for a subset of the overall dataset; songbird nests known to be active 2015 and 2016 and a randomly selected sample of the random nest sites (2015 n=33, 2016 n = 49, Random nest sites n = 47). This hedgerow density subset represents a potentially skewed sample of the total dataset, we might not expect the explanatory variables found to be significant in the overall model to affect this subset in the same way. Therefore, to assess the effect of hedgerow density on nest site choice we fitted the minimal adequate model of songbird nest site choice to this subset but included a measure of hedgerow density (see 5.2.7) as an additional explanatory variable. We included factors found to be significant in the overall model of nest site choice to control for these potential effects, but we did not interpret them in this model. The effect of hedgerow density was tested by assessing the change in deviance following removal of the term from the model using χ^2 statistics.

To investigate whether magpie nest predation rates affected songbird nest site choice we carried out a separate analysis on the subset of magpie territories for which we had an estimate of predation rates. We used a GLM with a binomial distribution and a logit function to test whether the number of songbird nests present within 100m of magpie nest sites were related to the predation rate of artificial nests within that territory. The response variable in this analysis was count of songbird nests/ (count of songbird nest + count of random nest sites). This method allowed differences in nest count between territories due to area of available habitat to be taken into account. Random nest sites represent a null model of nest site choice, the count of random nests should be roughly proportional to the area of available habitat. If songbird nests occur at a greater frequency than random nest sites this suggests that songbirds are more likely to nest in a specific territory independent of the availability of nesting habitat.

Table 5.4: Structure of GLMs used to analyse songbird nest and fledged brood site choice and nest success

	Model distribution	n	Response	Fixed effects
Site choice				
A) Nest site choice	Binomial (logit link)	1036	Songbird nest site/ Random nest site	Proportion of cover Habitat diversity Magpie territory identity Distance to nearest magpie nest
B) Fledged brood site choice	Binomial (logit link)	440	Fledged brood site/ Random fledged brood site	Proportion of cover Proportion of woodland Habitat diversity Magpie territory identity Distance to nearest magpie nest
Breeding success				
C) Nest success	Binomial (logit link)	50	Nest success/Nest failure	Proportion of cover Habitat diversity Hedgerow density Bird nest type Distance to nearest magpie nest Nest height Year nest was active

5.2.9.2 Analysing fledged brood site choice

Location of fledged broods was analysed using a similar GLM with fledged brood sites and random fledged brood sites as the binary response variable. Habitat diversity (see 5.2.6) and proportion of cover and proportion of woodland (see 5.2.6), distance to the nearest magpie nest and the identity of nearest magpie nest was fitted as explanatory variables (Table 5.4B). As above (5.2.9.1) we used stepwise backwards deletion of non-significant terms to produce the most parsimonious model of fledged brood site choice (Crawley, 2005).

5.2.9.3 Analysing songbird nest success

Analysis of factors which predict nest success was limited to nests for which the outcome was certain and hedgerow density data was available (n=50). For comparative purposes, all habitat attributes used to assess songbird nest site choice were included as explanatory variables in this analysis with nest success as binary

response (*Table 5.4C*). Additional factors (which were only known for active songbird nest sites) were also included; year nest was active (2015 or 2016), nest height and nest type. Nests was categorised according to nesting material and size: small grass/moss (similar to dunnock or whitethroat), moss (similar to wren or finches) and thrush (blackbird or song thrush). Our small sample size meant we could not analyse each songbird species separately and using the broad categories of nest type meant we had a sufficient sample for each category (Bolker et al., 2008). Again, we used the method of model simplification described above (5.2.9.1)

5.2.9.4 Statistical and analytical methods

We checked the collinearity of all explanatory variables included in GLMs using Pearson correlation coefficients and Variance Inflation Factors (VIFs). None of the explanatory variables included in the GLMs had VIFs that exceeded the acceptable threshold >3 (Zuur et al., 2010). Model assumptions were checked using model diagnostic plots. All analysis was carried out in R ver. 3.1.2 (R Core Team 2016). GLMs were constructed using the lme4 package (Bates et al. 2014). VIFs were calculated using the car package (Fox & Weisberg, 2011).

All mapping and GIS analysis was carried out using ArcGIS 10.2.2 (ESRI, 2014). Habitat mapping was based on aerial imagery and was taken from the ESRI World Imagery Basemap at 0.3m resolution (GB Birmingham-E) using ESRI ArcGIS 10.2.2 (ESRI, 2014). All mean values are presented ± 1 standard error.

5.3 ETHICAL STATEMENT

Between May 2014 and July 2016, 101 magpies were trapped and ringed with colour rings. Magpies were re-trapped on 205 occasions. All magpie trapping, and colour ringing followed best practice guidelines of Natural England and the Game and Wildlife Conservation Trust, and was carried out under Natural England licence 2016-19794-SCI-SCI.

5.4 RESULTS

5.4.1 Songbird nest site choice

There were significant differences in how songbird nests were distributed [GLM: $X^2_{29, 1006} = 126.8$; $P < 0.001$] compared to random nest sites. Songbird nest sites were on average further away ($94.73\text{m} \pm 2.68$) from the nearest magpie nest than random

sites ($83.72\text{m}\pm 2.48$). There were also more likely to be in particular magpie territories than others (*Table 5.5*). However, this did not appear to be due to relative difference in predation risk between territories. The number of songbird nests in the vicinity of a particular magpie nest was not related to artificial nest predation rates in that magpie territory [GLM: $X^2_{1,17} = 1.42$; $p = 0.2$].

Table 5.5: GLMs showing main effects and interaction terms for the maximal (all non-significant factors included in the analysis) and minimal (all significant factors) model of the songbird nest site choice ($n = 1036$).

Explanatory variable	Test statistic (χ^2)	df	p value	Direction of effect (Songbird nest site < Random nest site)
Maximal model				
Habitat diversity	0.47	1	0.50	
Proportion of cover available	2.68	1	0.10	
Distance to nearest magpie nest	3.97	1	0.05*	
Magpie territory identity	109.42	27	<0.001*	
Minimal model				
Proportion of cover available	48	1	0.02*	Less cover < more cover
Distance to nearest magpie nest	4.59	1	0.03*	Further from magpie nest < closer to magpie nest
Magpie territory identity	109.00	27	<0.001*	

Habitat factors also influenced nest site choice. Proportion of cover in the vicinity of nest site was lower for songbird nests overall; $3.18\%\pm 0.09$ compared to $3.79\%\pm 0.12$ at random nest sites (*Table 5.5*). When this model of nest site choice was fitted to the subset of data for which hedgerow density data was available ($n=129$), hedgerow density was found to significantly predict songbird nest site location compared to random songbird sites [Hedgerow density: $\chi^2_{26, 103} = 9.36$; $p = 0.002$]. Hedgerow density was ~80% less at random nest sites compared to real songbird nest sites.

5.4.2 Fledged brood site choice

The location of fledged broods differed from that of random fledged brood sites (GLM; $X^2_{21,420} = 150.74$, $p < 0.001$) (*Table 5.6*) and the distribution pattern of fledged broods had some similarity to that of songbird nest sites. Although, fledged brood sites were not further from, or closer to magpie nests than randomly distributed sites, they were more likely to be in particular magpie territories than others. The fledged

broods and songbird nests were likely to be closer to the same magpie nests and further away from others. The distance to the nearest magpie nests was calculated for fledged broods and songbird nests. Both fledged broods and songbird nests were closer to magpie nests in some magpie territories than others. The average distance to magpie nest in each magpie territory was significantly correlated between fledged brood and songbird nest sites ($r = 0.77$, $n = 16$, $p < 0.001$).

Table 5.6: GLMs showing main effects for the maximal (all non-significant factors included in the analysis) and minimal (all significant factors) model of the fledged brood site choice including hedgerow density (n=440).

Explanatory variable	Test statistic (χ^2)	d f	p value	Direction of effect (Fledged brood site < Random fledged brood site)
Maximal model				
Habitat diversity	2.70	1	0.10	
Proportion of cover	91.70	1	<0.001*	More cover<Less cover
Proportion of wood available	123	1	<0.001*	Less woodland<More woodland
Distance from nearest magpie nest	0.57	1	0.45	
Magpie territory identity	26.62	2 8	0.06	
Minimal model				
Proportion of cover	90.42	1	<0.001*	More cover<Less cover
Proportion of wood available	22.52	1	<0.001*	Less woodland<More woodland
Magpie territory identity	60.68	2 8	0.02	

5.4.3 Breeding success

5.4.3.1 Songbird nest success

Nest success was predicted by some aspects of nest site (GLM; $X^2_{4,44} = 13.31$, $p < 0.01$). Nest success was higher when nest height was lower, hedgerow density was greater and when the nest belonged to a specific nest type (*Table 5.7*). Nests made from moss (generally belonging to long-tailed tits or wrens) were six times more likely to be successful than those belonging to thrushes.

Table: 5.7 GLMs showing main effects for the maximal (all non-significant factors included in the analysis) and minimal (all significant factors) model of the nest success.

Explanatory variable	Test statistic (χ^2)	df	p value	Direction of effect Success>Failure
Maximal model				
Distance to nearest magpie nest	0.03	1	0.86	
Hedgerow density	6.41	2	0.01*	More dense > Less dense
Nest type	11.12	2	0.004*	Moss > Small moss/grass > Thrush
Habitat diversity	0.05	1	0.84	
Proportion of cover available	0.45	1	0.50	
Year	0.01	1	0.91	
Nest height	3.48	1	0.06	
Minimal model				
Hedgerow density	90	1	0.01*	More dense > Less dense
Nest type	11.47	2	0.003*	Moss > Small grass/moss > Thrush
Nest height	07	1	0.02*	High > Low

5.4.3.2 Fledged brood success

Although the sample size was small, adjusted occupancy estimation suggested that hole nesting species (n=2) were more successful than open nesting species (n=6) (~50% more territories produced a fledged brood). However, the breeding success of open nesting species was higher when measured using adjusted occupancy probability of a territory compared to when nest success was measured. Although not directly comparable due to the possibility of re-nesting within a territory, 62% of territories produced a fledged brood whereas only 20% of nests were successful (Table 5.8).

Table 5.8: Summary of the fledged brood survey of the field site in 2015. Observed occupancy is the brood to territory ratio and adjusted occupancy is the predicted occupancy taking into account the daily detection probability (calculated in Presence) (see 3.8.2).

Species	No. of territories	No. of fledged broods	Observed occupancy	Adjusted occupancy \pm SE	Detection probability \pm SE	Nest type
Great tit (<i>Parus major</i>)	15	15	1	1 \pm 0	0.41 \pm 0.05	Hole
Blue tit (<i>Cyanistes caeruleus</i>)	17	15	0.88	0.94 \pm 0.09	0.38 \pm 0.06	Hole
Linnet (<i>Carduelis cannabina</i>)	8	2	0.25	0.27 \pm 0.17	0.46 \pm 0.20	Open
Lesser whitethroat (<i>Sylvia curruca</i>)	5	2	0.40	0.44 \pm 0.25	0.46 \pm 0.20	Open
Goldfinch (<i>Carduelis carduelis</i>)	5	4	0.60	0.64 \pm 0.24	0.36 \pm 0.13	Open
Blackcap (<i>Sylvia atricapilla</i>)	6	6	1.00	1 \pm 0	0.29 \pm 0.09	Open
Robin (<i>Erithacus rubecula</i>)	19	11	0.58	0.82 \pm 0.22	0.22 \pm 0.07	Open
Wren (<i>Troglodytes troglodytes</i>)	22	10	0.45	0.59 \pm 0.16	0.22 \pm 0.07	Open

5.5 DISCUSSION

The nest site choice of hedgerow songbirds within an agricultural environment was influenced by the ecology of predators within this habitat and by aspects of the habitat itself. Songbirds nested further from magpies than would be expected if nest sites were chosen randomly. They were also more likely to nest in some magpies' territories than others. As opposed to a more direct relationship with predation risk associated with specific magpie territories or territory holders, it appears this relationship was driven by selection of nest sites in denser hedgerows. Nest failure was high and largely attributed to predation, and nest success was positively associated with denser hedges. Songbirds appeared to be choosing to nest in sites that provided the best physical protection from predation as opposed to avoiding predators in general. Fledged broods (which would be less frequently predated by magpies than songbird eggs and chicks) were found in similar areas to songbird

nests, possibly because they had not dispersed from their nest site or because of other common habitat preferences.

5.5.1 Nest site choice

We found that songbird nests were ~13% further away from magpie nest sites than random nest sites. Previous research found that songbird nests that were located nearer to the breeding sites of corvids suffered greater rates of predation (Salek, 2004; Erikstad et al., 1982). Songbirds are also to be able to actively avoid the breeding sites of predators when choosing nest sites (Roos & Pärt, 2004; Suhonen et al., 1994; van der Vliet et al., 2008). As magpie nest site choice tended to be highly conserved on our field site, it seems feasible that the songbirds were attempting to reduce the risk of their eggs and chicks being predated by choosing nest sites away from these magpie breeding sites.

Songbirds were more likely to nest in the vicinity of some magpie nests than others. The identity of the nearest magpie nest was not random. There was a high-density of magpies on our field site and radio-tracking of territorial magpies (see *Chapter 6*) suggested that there were no gaps between territories. Thus, it seems likely that the songbird nests would be in the foraging range of the magpie pair whose nest they were nearest to. One explanation for choosing to nest in one magpie territory over another could be that songbirds recognised particular predatory magpies and avoided them. Songbird species have been shown to respond to previous predation by changing aspects of re-nesting sites, both within (Hatchwell et al., 1999; Beckmann & McDonald, 2016; Chalfoun & Martin, 2010) and between breeding seasons (Haas, 1998; Slagsvold, 1984). Using our proxy measure of predation risk, artificial nest predation rate within territories, we found no evidence that songbirds on our field site were more likely to nest in particular magpie territories because they had relatively lower predation risk.

If songbirds were not avoiding areas close to particularly predatory individuals, then other factors must drive the choice to nest in some magpie territories and not others. It may be that the availability of habitats songbirds preferred differed between magpie territories. For example, we found that songbirds preferred nesting in dense hedgerow (hedgerow density was ~80% greater at songbird nest sites compared to random nest sites). Nest sites in denser vegetation

have numerous advantages, they are better concealed from visually oriented predators like corvids (Weidinger, 2002; Wegrzyn & Leniowski, 2011), and are less physically accessible to predators (Lazo & Anabalón, 1991; Dunn et al., 2016). Additionally, dense vegetation may provide greater insulation (Burfield, 2002; Burton, 2006; Gillis et al., 2012) and improved protection from extreme weather (Rauter et al., 2002). Therefore, it may simply be that songbirds preferred to nest in some magpie territories because hedgerow density was higher in that area rather than any direct effect of the magpie territory or individual magpies.

We would need to carry out more comprehensive assessment of the distribution of denser hedges relative to magpie nest sites, to establish whether this was the case. Additional work would also allow us to validate our method of measuring hedgerow density. The hedgerow density data used in this study was collected on one sampling occasion therefore we did not assess the repeatability of our method.

The habitat surrounding the nest site also influenced nest site choice. Proportion of cover (hedgerow and scrub) within 70m of the nest site was lower at songbird nest sites than at random nest sites. This may be because, in general wider hedges, which would provide a greater amount of cover by area, were less dense they were older, unmanaged and shrubby hedgerows (DEFRA, 2007; Dunn et al., 2016). A higher proportion of cover by area may therefore relate to a less preferred old, sparse and shrubby hedge.

5.5.2 Fledged brood site choice

Like songbird nest sites, fledged brood sites were more likely to be in some magpie territories than others. Specifically, they were found in the same magpie territories as the songbird nest sites. Given that we expect fledged broods to be at less direct risk of predation from magpies (Fernández-Juricic et al., 2004), and we find that fledged broods, unlike songbirds choosing nest sites, do not seem to further from expected from magpie breeding sites generally, it seems unlikely that fledged broods are choosing sites in certain territories to avoid a particular predation threat.

As with songbird nest site choice, it could be that fledged broods choose to be in particular magpie territories because of the availability of preferred habitat. Like songbird nests, fledged broods were less likely to be in areas with a high proportion

of cover (hedges and scrub). As mentioned above, this may be because lower quantity of cover area is associated with higher cover quality (narrower, denser hedges) which would provide better shelter from extreme weather (Lack, 1988; Hinsley & Bellamy, 2000) and refuge for fledglings foraging nearby (Hinsley & Bellamy, 2000; Robinson & Sutherland, 1999; Robinson, 1997)

In any case, very little is known about dispersal in passerines during the period we monitored fledged broods (12 to 24 days after the birds left the nest but before the chicks were independent (Sage et al., 2011)). If fledgling birds do not disperse far from the nest during this time, then we should not expect fledged brood sites to differ extensively from songbird nest sites (Sage et al., 2015).

However, fledged brood site choice did differ from nest site choice in preference for some habitat attributes due to the inclusion of hole nesting species in fledged brood data. Fledged brood sites were positively associated with proportion of wood within 70m. Many hole nesting species, including the most common (great tit and blue tit) nest in woodland and are therefore likely to be detected in the woodland edges (Ferguson-Lees et al., 2011).

5.5.3 Breeding success

5.5.3.1 *Nest success*

If, as we have suggested, songbirds on this field site were choosing nest sites to minimise predation risk, we would expect nest success to be limited by predation and, songbirds which chose preferred sites to have higher breeding success rates. We find this to be the case, predation did appear to cause the majority of nest failure (84% according to analysis of physical damage at failed nests) and songbirds nesting in preferred nest sites, those in denser hedges, were also the most successful. This suggests predation in preferred sites may have been minimised by the reduced visibility and access provided by the dense vegetation (Whittingham & Evans, 2004). Conversely it did not seem that birds nesting in less preferred sites could compensate for this difference in site quality, through means such as increasing nest defence behaviour.

The other attributes collected for active nests which were found to influence nest success were also related to nest predation risk. For example, songbirds were

found to nest low in the hedgerows, which is again a likely response to predation pressure; visually oriented avian predators (like magpies) are less likely to see lower nests when looking from above (Marzluff, 1988; Remeš, 2005a).

Nest success was also influenced by nest type, this may be indicative of differing nest failure rates between species. It may be that some species were simply more likely to nest in nest sites with lower predation risk, and thus there are between species differences in nest success. For example, moss nests (which were mainly long-tailed tits') were more successful than thrush nests. However, our categorisation of nest type was relatively broad, for example the category of moss nests contained both long-tailed tit nests and chaffinch nests. These species differ in other aspects of breeding biology that might affect their nest success. A more detailed comparison between species would give better insight into how species differ in nest site choice and subsequent nest success.

5.5.3.2 Fledged brood success

On our field site, the adjusted occupancy estimate suggested that 67% of the open nesting species' territories produced a fledged brood. This result is likely to be positively biased as species that have very low detection probability (either due to their discreet behaviour or due to very poor breeding success) were not included in the analysis. Even so, for species where both nest success and fledged brood data were available, the fledged brood occupancy was still much higher than we would have predicted from our nest success data; 20% of wrens' nests were successful (*Table 5.3*) whereas the fledged brood survey suggested that 59% of wrens' territories produced a fledged brood (*Table 5.8*).

Although, the levels of nest failure detected in this study (83%) are comparable with other failure rates reported in studies of hedgerow nesting species suffering high predation rates (Garson, 1978; Cresswell, 1997c; Chamberlain, 1994). It is possible that the discrepancy we observed between breeding success estimated from fledged brood occupancy, and breeding success estimated from nest monitoring is because our sample of monitored nests was biased towards nests which were likely to fail. Most of our nests were found by visually searching the hedgerows, therefore we were more likely to locate nests early in the season when vegetation was sparser. Success is known to be lower early in the breeding season for a number of farmland

songbirds (Hatchwell et al., 1996; Evans et al., 1997), partly because early season nests are more visible and vulnerable to predation (Ferguson-Lees et al., 2011).

Our comparison of these two methods of assessing songbird productivity, indicates that studies that only look at survival of eggs and chicks in the nest (Cox et al., 2014), may not always provide a complete estimate of breeding success.

However, although the results of the fledged brood survey suggested that breeding success was not as poor as the monitoring of nest success indicated, the results of the former did not negate our supposition that predation had significant effect on the breeding success on our field site. The territories of hole nesting species, which we presumed to be less susceptible to predation (Martin & Li, 1992; Ricklefs, 1969), were more likely to produce a fledged brood.

5.5.4 Conclusions

Predation appeared to be a major cause of breeding failure on our field site and songbirds did nest further from predators (magpie nest sites) than expected. However, it did not seem that songbirds were avoiding particularly predatory individuals but, it did seem that nest site choice and subsequent nest success was linked to sites that provided protection from predation. Open nesting species were more likely to choose nest sites which provided greater physical protection and concealment, and nests in these sites were also more successful. In addition, species which nested in holes, which are likely to provide additional physical protection from predation, were more successful than open nesting species. Habitat improvements have been shown to benefit songbird breeding on farmland (Aebischer et al., 2015); farmland songbirds have been shown to make nest site choices that utilise created habitats (Mchugh et al., 2016) and these choices can improve their breeding success (Dicks et al., 2014). Our results suggest that management of hedgerows to maintain structural complexity (density) could provide particular benefits for open nesting farmland songbirds, including better protection from predation. The provision of such vegetation could improve the breeding success a group of species in long-term population decline.

Chapter Six

Factors affecting magpie (*Pica pica*) habitat use in farmland



ABSTRACT

Magpie populations have undergone rapid growth in agricultural habitats in recent decades. Understanding how magpies use this habitat may provide insight into how their population growth, and the consequent high density of magpies in agricultural habitats, may affect other species which also use these habitats. Here we examined magpie habitat preferences in a farmland environment, with a focus on how this may affect farmland songbirds, whose eggs and chicks magpies are known to predate. By analysing magpie habitat selection at multiple spatial scales, it was possible to examine scale-dependent variation in their habitat preference. We therefore analysed factors predicting magpie nest density (as a proxy for habitat preference) at a landscape scale (per 1km²). We then looked at a more local scale to assess how habitat differences, social factors and songbird presence predicted magpie nest site location. To assess which of these factors were particularly important, we examined how they differed between the most preferred nest sites (magpie nest sites used more frequently year on year) and the least preferred nests sites (magpie nest sites used less often). Finally, we used individual-based measures of habitat preference (radio-tracking and assessment of defence behaviour in different habitats) to assess habitat use around the nest site. At a landscape scale, magpie nest density was positively related to the availability of hedgerows, the main habitat in which their nests were situated. At a local scale, magpies avoided conspecifics and selected nests sites with greater areas of pasture (foraging habitat) in the vicinity. Pasture may be a particularly preferred habitat, radio-tracked magpies were more likely to be found in grassland and magpies responded more frequently to simulated territorial intrusions in grassland habitats than crop habitats. It seems therefore that the availability of suitable nest sites and foraging habitat are important drivers of magpie nest site selection. Magpies do not appear to prefer nest sites in areas where prey (in this case songbird nests) are concentrated. However, magpies and at least some songbirds are likely to overlap in their preferred nest location and in habitat use around the nest site, and we found some evidence that songbirds were less likely to nest in areas most frequently occupied by magpies. Therefore, if good quality habitat is limited, then these songbirds may be forced into using suboptimal habitats. Additional, targeted provision of suitable habitat may therefore facilitate some separation of predator and prey.

6.1 INTRODUCTION

Magpie (*Pica pica*) populations have grown across much of their geographic range in recent decades (Cramp et al., 1994; Voříšek et al., 2008), largely due to a reduction in widespread predator control following the First and Second World War (Tapper, 1992; Nicoll & Norris, 2010). This population growth is indicative of the range of habitats that this generalist species can exploit (Birkhead, 1991). In Britain populations increased by ~5%/year across farmland, in woodland, and in suburban areas between 1966 and 1986 (Gooch et al., 1991). Although this population growth slowed after the 1980s, magpie population numbers today remain at a relatively elevated level (BTO, 2016). Magpies are known predators of the eggs and chicks of farmland songbirds (Cresswell, 1997c; Baláz et al., 2007), therefore the elevated numbers of magpies could potentially have a detrimental effect on these songbird species. Although, evidence for a general impact of magpies on songbird populations remains mixed (Díaz-Ruiz et al., 2015; Thomson et al., 1998; Gooch et al., 1991)

Previous work has provided an insight into many aspects of magpie ecology and behaviour in suburban, rural and urban habitats (Birkhead, 1991; Eden, 1989; Vines, 1981; Goodburn, 1991; Tatner, 1980; Vernelli, 2013). Outside of the UK there have also been several informative long-term studies on rural populations (Møller, 1982; Buitron, 1983; Baeyens, 1979). However, more recent ecological work has tended to focus on urban populations (Mérő et al., 2010; Antonov & Atanasova, 2002; Nakahara et al., 2015; Chiron & Julliard, 2007) and there is very little current information about magpie populations in mixed arable and pastoral agricultural environments in the UK. Since, magpies have been shown to negatively affect songbird breeding success in agricultural habitats (White et al., 2014; Stoate & Szczur, 2006) it is necessary to gain a better understanding of how magpies utilise agricultural habitats, and how this relates to the use of the same habitats by farmland songbirds, a group of species in long-term decline (Fuller et al., 1995). This may help us determine circumstances when or where a high density of magpies may be likely to affect farmland songbirds.

Birds have been shown to select habitats at multiple hierarchical spatial scales (Saab, 1999; Marzluff & Withey, 2007; Johnson, 1980). They may choose

landscape areas (possibly at the scale of 10s or 100s of km²) which are likely to contain preferred habitat. They could then select home ranges or territories within this landscape area, which may contain suitable breeding sites. Finally they may utilise specific areas within these territories, such as sites where specific foraging resources are available (Becker & Beissinger, 2003; Withey & Marzluff, 2009). Factors which influence landscape scale distribution of a species may not vary sufficiently to influence local distribution of a species (Jedlikowski & Brambilla, 2017). The extent to which predator and prey species overlap may vary depending on the spatial scale considered; predators and prey may have similar habitat preferences at a landscape scale but some prey species may avoid predators within a habitat patch. For example, songbirds and Steller's jays (*Cyanocitta stelleri*) were both associated with secondary forest at a landscape scale (measured as 1km² scale this case), but songbirds avoided predators' nest sites within particular small fragments of forest (Marzluff & Withey, 2007). Alternatively, predator and prey may have similar local scale preferences, such as specific foraging habitat, but overall overlap between predators and prey may be constrained by landscape scale factors. For example, predator-prey overlap may be higher at forest-agricultural habitat boundaries but, only in fragmented landscapes with a high proportion of agricultural land as these landscapes support a higher number of predators (Chalfoun et al., 2002).

At a landscape scale magpie population growth has not been uniform; numbers have been suppressed by game management in the south-east (Gooch et al., 1991), whereas higher population densities exist in the west of England, probably due to greater availability of their preferred grassland foraging habitat (Birkhead, 1991; Goodburn, 1991; Whittingham et al., 2007). This landscape scale variation in population density may have an effect on prey populations (Baláz et al., 2007). When predators exist at higher densities, prey may have a greater chance of encountering predators (Evans, 2004). Identifying landscape scale habitat attributes that predict a higher density of magpies in a landscape may help predict areas where predators may be significantly impacting prey populations (Aebischer et al., 2015; Manzer & Hannon, 2005).

At a local scale, the chance of prey encountering predators will be affected by specific habitat use of predators. Prey which nest near areas predators use more frequently, such as near perching sites or foraging sites, may be more vulnerable

(Kenward et al., 2001; Tryjanowski et al., 2014; Dunn et al., 2016; Roos & Pärt, 2004; Pescador & Peris, 2007). Breeding sites may provide a particularly pertinent indication of habitat use for territorial species, such as magpies, which are restricted to an area around their nest (Vines, 1981; Baeyens, 1981a).

Within a local area, a more detailed understanding of how individual predators use and move through habitat may further aid our identification of areas where prey are especially susceptible to predation (Graham et al., 2005; Smith et al., 2010; Marzluff & Neatherlin, 2006). To identify habitat preferences at a fine-scale animal movements can be directly monitored, or an animal's valuation of resources can be indirectly assessed, for example, individuals may exhibit stronger defensive responses when habitat quality is higher and hence more valuable (Ewald & Bransfield, 1987; Hoi-Leitner et al., 1995).

We aimed to assess how the habitat selection of magpies in a mixed agricultural environment could affect their impact on songbird populations. At a landscape scale, we asked which factors predicted magpie nest density. This meant we could identify the type of agricultural landscape magpies preferred at a 1km² scale. Then, at a local scale we examined which factors magpies might use to select their nest sites. We specifically tested whether nest site choice was driven by habitat factors (availability of foraging habitat) and/or social factors (proximity of nearest neighbour). At this scale, we also asked how magpie habitat selection directly related to songbird nest site density. In addition, within this local scale we assessed which of these factors were especially important in nest site choice, by comparing the most preferred nest sites (magpie nest sites used more frequently year on year) and the least preferred nests sites (magpie nest sites used less often). Finally, we used individual scale measures of magpie habitat preference to examine how they utilised habitat within their territories. If magpies' habitat use is non-random, it may be that songbirds nesting within particular habitats are more likely to be encountered by magpies and thus preyed upon.

We related our understanding of magpie habitat preferences to the songbird population in two ways. Firstly, we compared the magpies' habitat preferences to known preferences of farmland songbirds to identify areas of potential overlap in habitat use, where songbird could be particularly vulnerable. Secondly, in a local

area, we compared the abundance of songbird nest sites in habitat preferred by magpies versus habitat avoided by magpies, to see if songbird habitat use was directly affected by magpie habitat preferences.

6.2 METHODS

6.2.1 Field site

This study was carried out in spring and summer of 2014-2016 over a 40km² landscape area of mixed farmland in Warwickshire, England (*Figure 6.1*). Within this landscape area a farm area of approx. 4.5km² was designated as our local area (*Figure 6.1*).

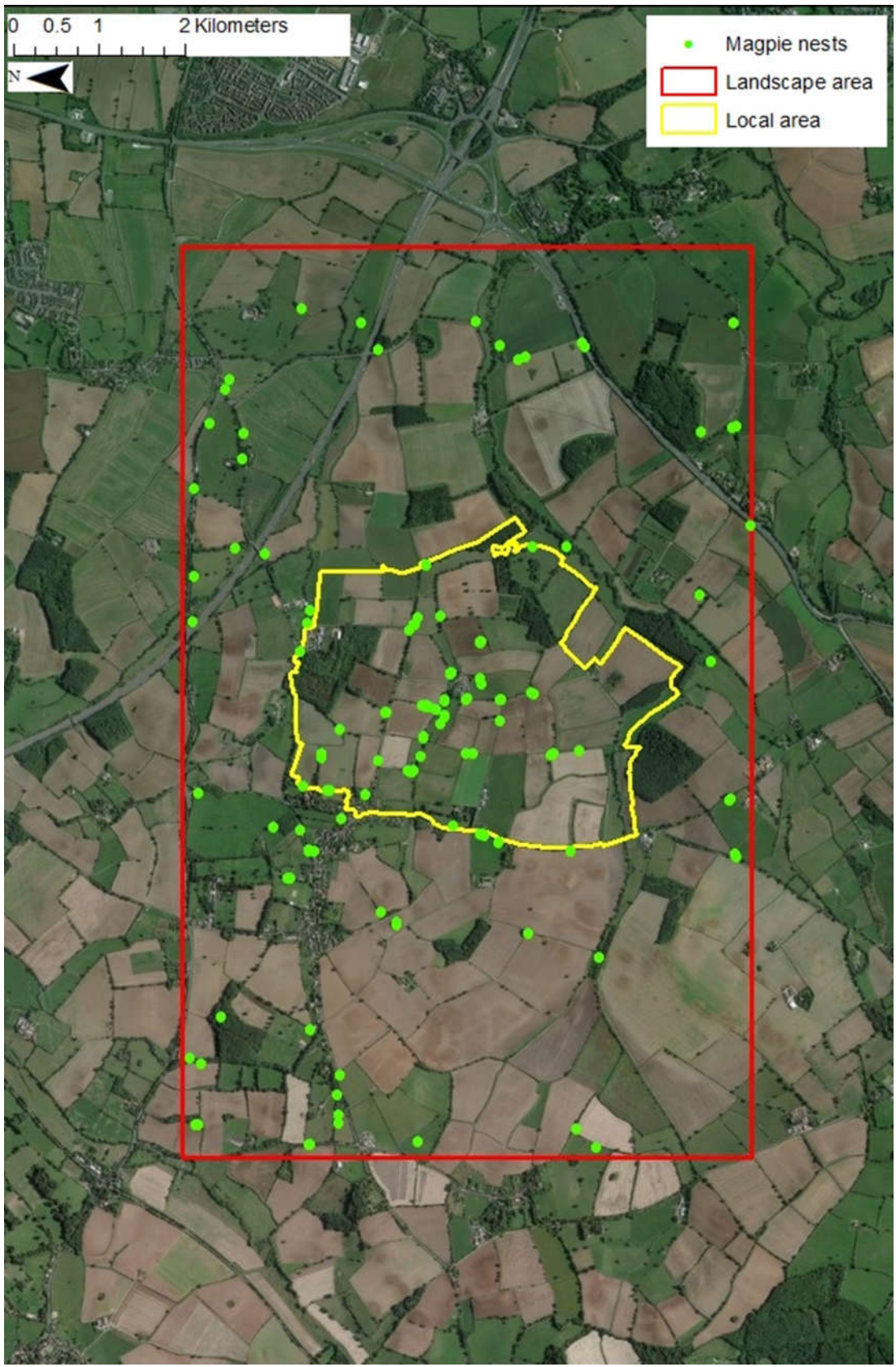


Figure 6.1: Aerial image with the landscape and local area of study superimposed. Aerial imagery is taken from the ESRI World Imagery Basemap at 0.3m resolution (GB Birmingham-E) using ESRI ArcGIS 10.2.2 (ESRI, 2014).

6.2.2 Landscape scale habitat selection

In early March 2016 (before bud burst) the landscape area was searched for magpie nests used in previous years. These were distinguished by their characteristic structure, in particular an ever-present domed roof (Tatner, 1980). Count of old magpie nest sites was used as an index of preferred magpie habitat.

The landscape area that was searched for magpie nests was divided into 1km² blocks, and magpie nest site density per 1km² block was used as a measure of habitat selection. For each 1km² block we calculated habitat attributes which might predict magpie habitat selection; i) the length of road (km), ii) the length of hedgerow (km), iii) the area of grass (km²), iv) the area of woodland (km²), v) the area of buildings/gardens (km²). Road, woodland and building data was taken from OS VectorMap District (Edina Digimap, 2017), other habitat variables were mapped from aerial imagery.

A Generalised Linear Model (GLM) was used to analyse the effect of these habitat attributes on the count of magpie nests in each 1km² (*Table 6.1A*). As most roads in this landscape were lined with hedgerows, an interaction was fitted between hedgerow length and road length. Some habitats were not searched for nests due to lack of visibility and/or limited access (woodland and buildings/gardens). The areas of these habitats were nevertheless included in the analysis, so the area within each 1km² that did not contain magpie nests but was not indicative of magpie habitat avoidance could be taken into account.

Table 6.1: Structure of GLMs used to analyse landscape habitat selection and local scale nest site choice. Following tests for collinearity between explanatory variables, proportion of cover was excluded from models B and C. Songbird nest abundance was measured as count of songbird nests/(count of songbird nests + random songbird nest sites) (see 6.2.3.1)

	Model distribution	Response	Explanatory variables
Landscape			
A) Nest site choice	Poisson (log link)	Count of magpie nests/1km ²	Area of grass/1km ² Area of buildings/km ² Area of woodland/1km ² Length of road/1km ² Length of hedge/1km ² Length of road/1km ² * Length of hedge/1km ²
Local scale			
B) Nest site choice	Binomial (logit link)	Magpie nest site/Random magpie nest	Proportion of cover Proportion of pasture Habitat diversity Songbird nest abundance Distance to urban habitat
C) Nest site preference	Binomial (logit link)	Nest observed active in > 1 year/ Nest observed active <= 1 year	Proportion of cover Proportion of pasture Habitat diversity Songbird nest abundance Distance to urban habitat Tree type

6.2.3 Local scale habitat selection

6.2.3.1 Magpie nest site choice

Within the local area of 4.5km², 62 previously used magpie nest sites were located using a visual search of hedgerows and scrub before bud burst. We wished to assess how magpie nest site choice differed from a null model, an essentially random nest site distribution. We therefore distributed an equivalent number of sites (hereafter random magpie sites) in all hedgerows searched for magpie nests. The specific points were randomly determined using the Create Random Points tool in the Data Management toolbox ArcGIS 10.2.2. (ESRI, 2014). This tool randomly selected co-ordinates on the x axis and y axis within the range of co-ordinates which defined the area of hedgerow searched for magpie nests (ESRI, 2017). Magpies on

this site did not nest below 2m (per. obs.), therefore random magpie sites were only distributed in locations with vegetation over 2m in height.

Habitat attributes which may influence nest distribution were extracted for a 125m radius area around magpie nest sites and random magpie sites. Although various magpie ranging and foraging areas have been reported in the literature (Birkhead, 1991; Vines, 1981; Jones & Hungerford, 1972), we chose a 125m radius area as, on our site, average relocation distance of radio-tracked magpies from the nest was 125m. Habitat within this area was therefore considered representative of an area utilised by nest owners. A habitat map of the local area was digitised using aerial imagery supplemented with field observations, and habitat was assigned to one of 5 broad categories (*Table 6.2*). We used this habitat map to calculate i) proportion of cover, ii) proportion of pasture (an important magpie foraging habitat (Møller, 1982)), iii) a Shannon-Weiner index of habitat diversity, for each 125m radius area around magpie nests and random magpie sites. For each magpie nest and random magpie site, distance to the nearest urban habitat (generally road or farm buildings) was also calculated.

Table 6.2: Description of habitat categorisation.

Category	Included habitats
Grass	Pasture (permanent grassland used for grazing sheep or cattle), hay crops, field margins, verges, and gardens
Hedge	Wide hedges (4m), narrow hedges (2m) and scrub
Woodland	All types of woodland (mainly small mixed copses and conifer woods)
Urban	Houses, farm buildings, roads and water
Crops	Cereals – wheat, barley and oats Break crops (crops planted between cereals in a crop rotation to reduce disease and increase soil fertility) – oil seed rape, field peas and field beans

To see if songbird habitat use was directly affected by magpie nest site choice, we also compared songbird nest abundance within a 125m radius of the magpie nest sites and random magpie sites.

In total 518 songbird nest sites were located across the local area. We distributed an equal number of random songbird nest sites in searched hedgerows, again using the Create Random Points tool in ArcGIS 10.2.2. We counted the number of songbird nest sites and the number of random songbird nest sites within the 25m radius of the magpie nest sites and random magpie sites. The number of real songbird nests was compared to the total number of nests (number of songbird nest site plus number of random songbird nest sites). By comparing real and random songbird nest sites we avoided biasing counts towards sites where songbird nest abundance was higher simply because a greater area of nest habitat was available.

To assess how magpie nest site choice differed from random we used a binomial GLM to compare the habitat attributes and songbird nest density of real magpie nest sites to random magpie sites (*Table 6.1B*).

Some magpie nest site attributes (specifically tree species and nearest neighbour distance) could only be collected for a subset of magpie nest sites and random magpie sites. Separate analyses were therefore carried out to assess how these attributes affected nest site choice. For example, we did not know the tree species random magpie sites were in, but the tree species the nest was built in was recorded at each real magpie nest site. We also identified all other trees (over 2m) within 6m of the magpie nest sites as a measure of available tree species. Nest tree choice was compared to total tree species available (taken from the 6m radius around the nests sites) using a G-test (as per Pinkham, 2016).

The analysis of the effect of presence of conspecifics on nest site choice was restricted to nests active in 2016 (the year the magpie nest sites were best characterised). We wished to see if magpies were avoiding concurrently active territories rather than just other magpie nest sites whether active or not. We compared the distance to nearest neighbour of 22 magpie nests active in 2016, to the distance to nearest neighbour of the equivalent number of random magpie sites (a random subset drawn from the total random magpie sites) using a t-test.

6.2.3.2 Magpie nest site quality

To identify habitat attributes that particularly influenced magpie nest site choice, we compared nest sites that were used more frequently (and therefore assumed to be of higher quality) to those used less frequently. We therefore used the number of years

a nest site was re-used as proxy for territory quality (Sergio & Newton, 2003). Nest sites used in subsequent years that were <5m apart were considered equivalent to the same nest site being re-used.

Our knowledge of nest site activity was incomplete in the first year of observation (2014). Nest site quality was therefore categorised as a binomial variable (seen active in one year or less out of the three years observed, or in more than one year of the three years observed). We used a GLM to assess how habitat attributes and measure of songbird nest density predicted the most frequently used nest sites (*Table 6.1C*)

6.2.4 Individual scale habitat selection

6.2.4.1 Magpie home range selection?

Magpies were trapped in their territories using Larsen traps in the spring of 2015. Sixteen of these trapped magpies had VHF radio transmitter tags (weighing 5.5g) (Predix Wildlife Solutions Ltd) fitted to their two central tail feathers. This ensured the tag would be shed as part of the moult (Cramp et al., 1994). These birds were tracked between 17/04/2016 and 02/08/2016 using a Biotrack Sika receiver with a hand-held three-element Yagi antenna (Biotrack Ltd, Wareham, Dorset, UK). To avoid disturbing the tagged birds, one location/bird was obtained per day by triangulation from a distance of 100-300m. Other relocations of individuals, such as ad hoc direct sightings of known colour-ringed birds, were included in the analysis. All birds which were relocated less than 10 times were excluded from this analysis. Eleven tracked birds were used for further analysis.

Two methods were used to calculate home range. Home range represents the area of space used by an animal, and in this case we consider it approximately equivalent to the territory of the breeding magpies (Powell & Mitchell, 2012). We used the Minimum Convex Polygon (MCP) method which is widely deployed (Yaremych et al., 2004; Coppes et al., 2017) and appropriate for our analysis due to the small relocation sample size (average of 22 relocations/bird) (Boal et al., 2003; Browne & Aebischer, 2003). However, MCP is limited; it does not take into account the variation in time that an individual spends in different areas of their home range. Instead, each relocation is weighted equally, which may mean that single relocations have undue influence. We therefore also calculated the fixed-kernel home range.

This method estimates the utilisation distribution of the location data; a probability density function of the likelihood of finding an animal in a given area (Kenward, 2001; Neatherlin & Marzluff, 2004). It allows for some uncertainty about the exact site of each relocation, taking into account radio-tracking error (Marzluff et al., 2004). This uncertainty is estimated using a smoothing parameter. We used the reference bandwidth as a smoothing parameter around the relocation points as an alternative to least square cross validation smoothing (LSCV). The reference bandwidth estimates the smoothing parameter around the relocation points assuming the utilisation distribution (the probability of relocating an animal in a specific location) is approximately normal (calculations are based on the standard deviations in x and y co-ordinates) (Kernohan et al., 2001; Calenge, 2006). LSCV estimates the smoothing parameter by minimizing the error between the estimated density and true density (Kernohan et al., 2001). However, LSCV can result in under-smoothing, when sample size is small. In this case, a home range comprised of multiple islands, rather than a complete home range, is created when the animal has specific areas of particularly high utilisation (Seaman & Millsbaugh, 1999; Kie, 2013).

We used habitat compositional analysis (Aebischer et al., 1993) to analyse how the eleven radio-tracked magpies selected the habitat of their home range compared to the habitat available in the wider environment. Using the digitised habitat map of the local area we compared the proportional area of each habitat category (see *Table 6.2*) in the used habitat (home range) to the proportional area of each habitat category available across the local area. Due to slight inaccuracy in relocations gained through radio-tracking, confidence in MCPs was lowered. Therefore, although fixed-kernel home ranges may have been an overestimation of areas used by magpies, they were conservatively used for habitat composition analysis.

To analyse habitat selection within the home range, we compared the habitat at sites where birds were relocated (either the triangulated areas obtained by radio-tracking magpies, or the point locations obtained when magpies were directly re-sighted) to that available within the home range.

For all habitat compositional analysis, Wilks' lambda was calculated to test how observed habitat selection differed from available habitat. Randomisation tests

were used to assess significance and to test differences between pairs of habitats, in order to rank habitat preferences. (Aebischer et al., 1993; Calenge, 2006).

6.2.4.2 Magpie territorial defence behaviour

We assessed magpie use of habitat around the nest by determining the area the territorial birds would actively defend. We used a simulated territorial intrusion; a plastic dummy magpie was mounted on a stick and placed at set distances from an active magpie nest site. A response to the intrusion was classified as the focal individual making a vocalisation (alarm calls), a visual display (tree-topping, parallel walking) or mobbing within 40 minutes of exposure (Birkhead, 1991; Pinkham, 2016). For the first intrusion, the dummy was placed 6m from the nest. If the bird reacted, the next intrusion was presented 12m away in the same cardinal direction and so on. Each territorial intrusion was separated by a gap of at least four hours. This continued until the maximum distance at which the bird would respond was found in each cardinal direction.

The habitat in which the dummy magpie was placed during each intrusion was recorded. To examine how birds differed in their defence behaviour depending on the habitat, response to simulated territorial intrusion was fitted as a binary response variable with habitat type in which the dummy magpie was placed and distance of the dummy magpie from the nest, and the interaction between them, as a fixed explanatory variable in a Generalised Linear Mixed Model (GLMM). Territory identity was fitted as a random effect, to account for inherent differences in territory owner behaviour and territory composition and any spatial autocorrelation between simulated territorial intrusions carried out in the same territory (*Table 6.3*).

Table 6.3: Structure of GLMM used to analyse habitat preference around the nest

	Model distribution	Response	Fixed effects	Random effect
a) Nest site choice	Binomial (logit link)	Reaction to territorial intrusion/ No reaction to territorial intrusion	Habitat type Distance of challenge from the nest (m) Habitat type*distance of challenge from the nest (m)	Territory identity

6.2.5 Statistical and analytical methods

We checked the collinearity of all explanatory variables included in GLMs and GLMMs using Pearson correlation coefficients and Variance Inflation Factors (VIFs). Pearson correlation coefficients >0.5 or < -0.5 and VIFs >3 are considered indicative of collinearity (Zuur et al., 2010). We found that there was significant pairwise positive correlation between proportion of cover and habitat diversity (used in models of local scale nest site choice and local scale nest site preference (*Table 6.1B and 6.1C*)). The proportion of cover variable was therefore removed from all models, and all VIFs were re-calculated and shown to be below the required threshold (<3) (Zuur et al., 2010).

As we wanted to identify the particular variables which predicted magpie habitat selection (specifically nest site choice and nest site use frequency), we used a backwards stepwise model selection approach for all GLMs and GLMMs (Zuur et al., 2009; Fox et al., 2013; Crawley, 2012). Changes in deviance following term removal was assessed using χ^2 statistics. If removal of terms did not cause significant increase in model deviance the terms were eliminated from the final minimal models (Crawley 2005). This allowed us to test the null hypothesis that none of the variables we included in analysis affected magpie habitat selection. This method of model selection has been criticised (Whittingham et al., 2006). However it has been shown to perform as well as other methods of variable selection (Fox et al., 2013; Murtaugh, 2009) and similar methods have been used in other studies examining habitat selection of corvids and other avian predators (Kumar et al., 2017; Moreno-Opo et al., 2012; Antonov & Atanasova, 2002). All model assumptions were checked using diagnostic plots.

All mapping and GIS analysis was carried out using ArcGIS 10.2.2 (ESRI, 2014). Aerial imagery was taken from the ESRI World Imagery Basemap at 0.3m resolution (GB Birmingham-E) using ESRI ArcGIS 10.2.2 (ESRI, 2014). All analysis was carried out in R ver. 3.1.2 (R Core Team 2016). GLMs and GLMMs were constructed using the lme4 package (Bates et al. 2014), VIFs were calculated using the car package (Fox & Weisberg, 2011), and habitat compositional analysis was done using adehabitatHS (Calenge, 2006).

6.3 ETHICAL STATEMENT

Between May 2014 and July 2016, 101 magpies were trapped and ringed with colour rings. Magpies were re-trapped on 205 occasions. All magpie trapping, and colour ringing followed best practice guidelines of Natural England and the Game and Wildlife Conservation Trust, and was carried out under Natural England licence 2016-19794-SCI-SCI.

6.4 RESULTS

6.4.1 Landscape scale habitat selection

Habitat attributes significantly predicted the density of magpie nest sites in a given 1km² [GLM: $\chi^2_{6,39} = 28.904$, $p < 0.001$]. Magpie nest sites were more frequently situated in areas where there was a greater length of hedgerow and greater length of road. The area of unsearched habitat (buildings and woodland) did not negatively affect the density of magpie nests within that 1km². In fact, unexpectedly, magpie nest density was higher in 1km² blocks containing a greater area of woodland (*Table 6.4*).

Table 6.4: GLMs showing main effects and interaction terms for the maximal (all non-significant factors included in the analysis) and minimal (significant factors only) model of landscape scale magpie nest site choice.

Explanatory variables	Estimate	Std. Error	df	χ^2	P
Maximal model					
Intercept	-2.37	0.86			
Hedgerow length (km)	0.44	0.14	1	9.17	0.002*
Woodland area (km ²)	5.03	1.78	1	7.50	0.006*
Buildings area (km ²)	1.61	3.61	1	0.20	0.66
Road length (km)	1.10	0.53	1	5.18	0.02*
Grass area (km ²)	0.36	0.61	1	0.36	0.55
Hedgerow length (km) * Road length (km)	-0.14	0.09	2	2.45	0.12
Minimal model					
Intercept	-1.33	0.52			
Hedgerow length (km)	0.29	0.08	1	12.36	<0.001*
Woodland Area (km ²)	4.19	1.65	1	5.78	0.02*
Road length (km)	0.29	0.13	1	5.25	0.02*

6.4.2 Local scale habitat selection

6.4.2.1 Magpie nest site choice

The clear majority of the 64 magpie nests found on the local area were in hedgerows adjacent to agricultural land (87%). The remainder were in small copses (8%) or lone standing trees (5%). Magpies chose some nest tree species more than predicted by their availability within the nest patch (n=40) (G-test = 201.38, df = 33, p <0.001). Magpies were significantly more likely to nest in hawthorn (*Crataegus monogyna*) (Figure 6.2).

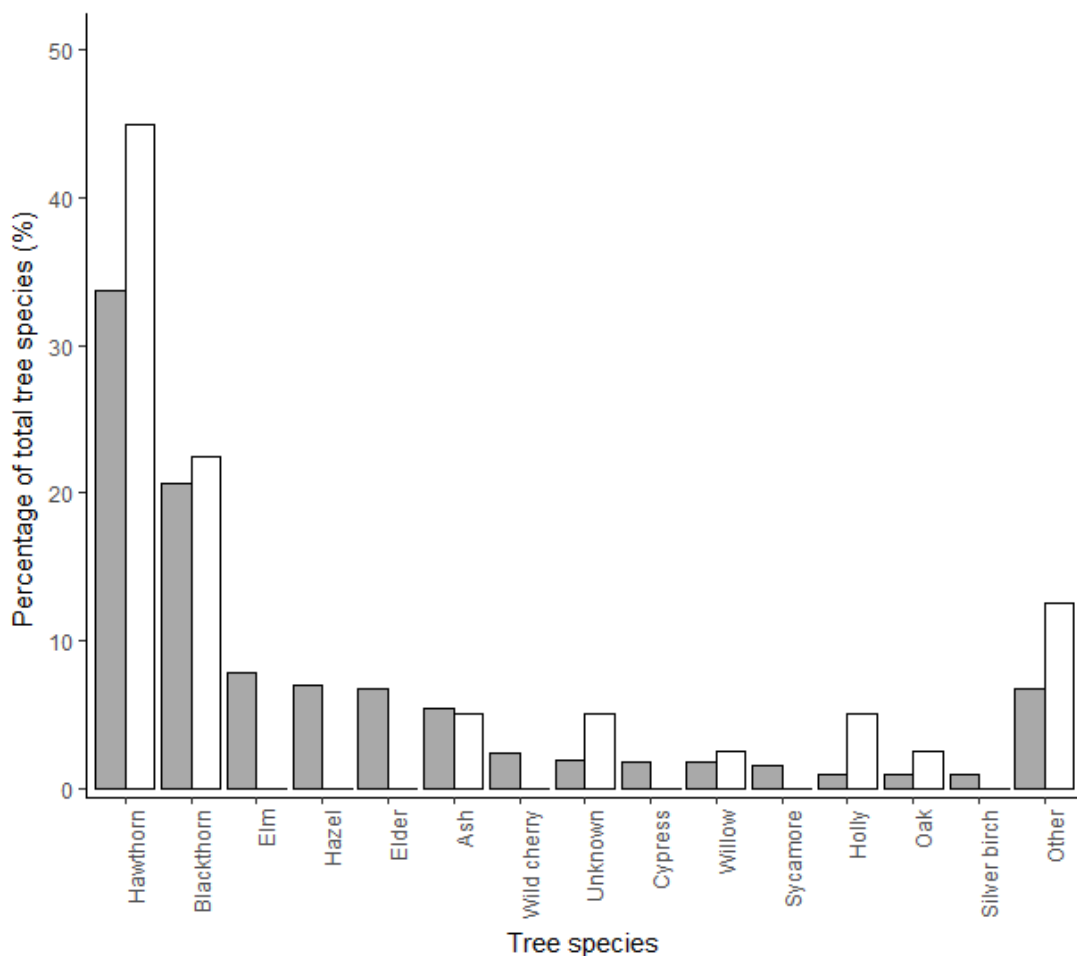


Figure 6.2: Proportion of tree species (%) available within 6m of the nest site (grey bars) compared to tree species magpies were observed using as a nest site (white bars).

Magpie nest site choice was not random (n = 62) [GLM: $\chi^2_{1,122} = 4.049$, p = 0.044]. The proportion of pasture, a foraging habitat, was ~55% greater at magpie nest sites than at random magpie sites (Table 6.5). However, magpie nest sites did not have significantly different numbers of songbird nests in the vicinity compared to random magpie sites.

Table 6.5: GLMs showing main effects for the maximal (all non-significant factors included in the analysis) and minimal (significant factors only) model of local scale magpie nest site choice

Explanatory variables	Estimate	Std. Error	df	χ^2	P
Maximal model					
Intercept	-0.04	0.89			
Habitat diversity	0.37	0.68	1	0.31	0.58
Proportion of pasture	0.02	0.01	1	3.85	0.05*
Distance to urban	0.00	0.00	1	2.24	0.13
Songbird nest abundance	-2.11	1.10	1	3.83	0.06
Minimum model					
Intercept	-0.29	0.23			
Proportion of pasture	0.02	0.01	1	4.05	0.04*

Magpie nest sites were on average ~80% further from their nearest neighbour (other magpie nest sites active at the same time) than randomly distributed nest sites (random magpie sites) were from their nearest neighbour ($t = -4.42$, $df = 41.99$, $p < 0.001$).

6.4.2.2 Magpie nest site quality

Magpie nest sites that were regularly used, and therefore considered of better quality, differed in the following ways from sites that were sporadically used and considered of poorer quality [GLM: $\chi^2_{2,21} = 9.21$, $p = 0.01$]. Regularly used magpie nest sites had fewer songbird nest sites in the vicinity than sporadically used nest sites (Table 6.6). Despite magpies' general preference for hawthorn and blackthorn (*Prunus spinosa*), nests that were regularly used were more likely to be in trees other than hawthorn or blackthorn, compared to those used only sporadically.

Table 6.6: GLMs showing main effects and interaction terms for the maximal (all non-significant factors included in the analysis) and minimal (only significant factors) model of local scale magpie nest site use frequency

Explanatory variables	Estimate	Std. Error	df	χ^2	P
Maximal model					
Intercept (Tree – Other)	6.44	4.29			
Habitat diversity	0.07	2.37	1	0.00	0.98
Proportion of pasture	-0.01	0.03	1	0.39	0.75
Distance to urban	0.01	0.01	1	1.54	0.21
Tree Thorn	-3.45	1.69	1	6.08	0.01*
Songbird nest abundance	-10.13	5.80	1	5.82	0.02*
Minimal model					
Intercept (Tree – Other)	5.48	2.34			
Tree Thorn	-2.42	1.25	1	4.99	0.03*
Songbird nest abundance	-7.16	4.14	1	4.46	0.03*

6.4.3 Individual scale habitat selection

6.4.3.1 Home range selection

Home range size did not correlate with number of times birds were relocated for either fixed-kernel home ranges ($r_{10} = 0.18$ $p = 0.57$) or MCP ($r_{10} = 0.34$ $p = 0.28$). This indicated that home range estimation was not biased by sample size. Average size of home ranges calculated using fixed-kernel was 48.33 ha \pm 9.00 whereas those calculated using MCP was 18.19 ha \pm 3.16.

Selection of home range habitat (based on fixed-kernel home ranges) within the local area did not significantly differ from random ($\Lambda = 0.351$, randomisation $p = 0.08$) (Table 6.7).

Table 6.7: Ranking matrix comparing habitat within home range to total available habitat. +++ and --- show significant differences in preference for habitat types.

	Crop	Grass	Hedge	Urban	Woodland	Rank
Crop	0	+++	+	+++	+++	4
Grass	---	0	---	+	+	2
Hedge	-	+++	0	+++	+	3
Urban	---	-	---	0	-	0
Woodland	---	-	-	+	0	1

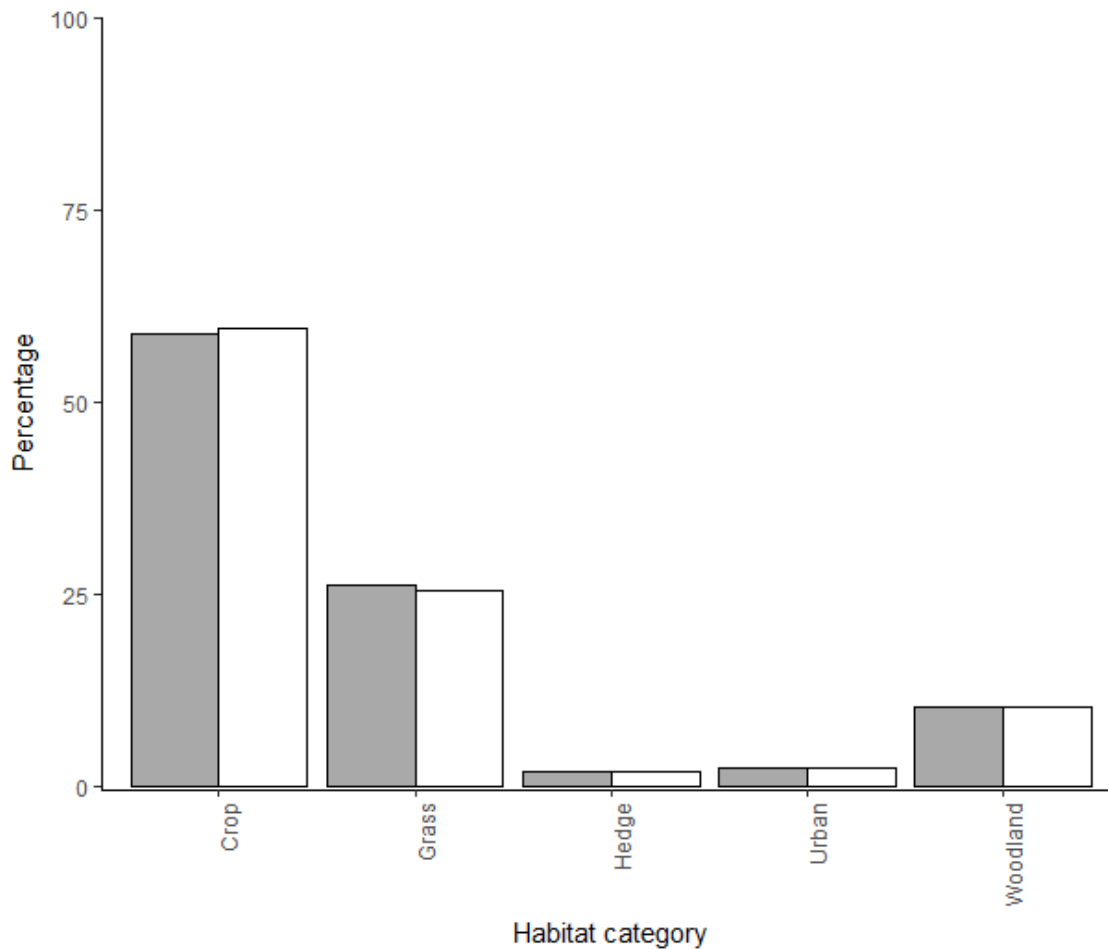


Figure 6.3: Proportional selection of habitat categories of home range (white bars) compared to the proportion area of habitat categories available in the local area (grey bars)

Habitat selection within the home range approached significantly different from random ($\Lambda = 0.252$, randomisation $p = 0.054$). Birds were relocated more frequently in grass and hedgerow than expected relative to availability (Table 6.8, Figure 6.3).

Table 6.8: Ranking matrix comparing habitat utilised within home range compared to total available habitat within home range. +++ and --- show significant differences in preference for habitat types

	Crop	Grass	Hedge	Urban	Woodland	Rank
Crop	0	-	---	+++	+	2
Grass	+	0	-	+++	+	3
Hedge	+++	+	0	+++	+	4
Urban	---	---	---	0	-	0
Woodland	-	-	-	+	0	1

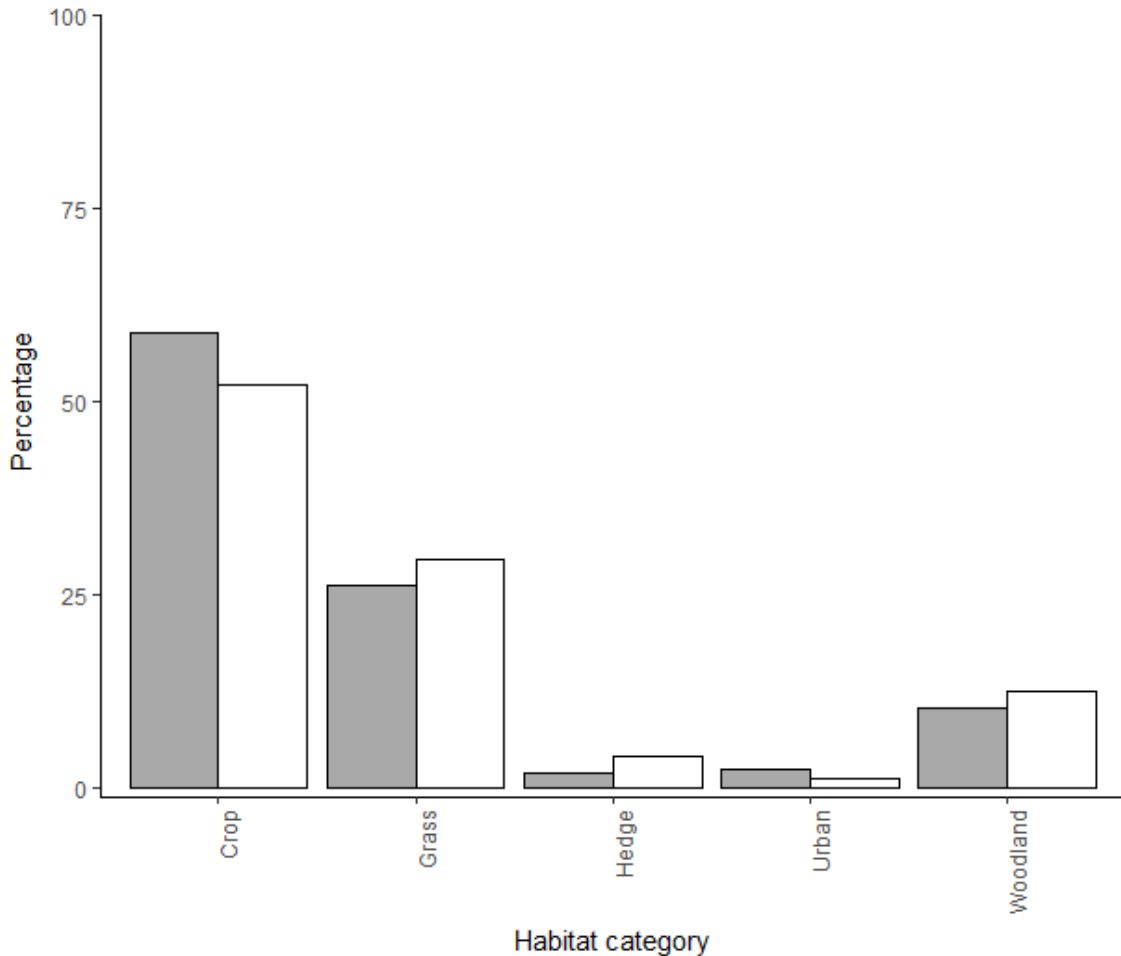


Figure 6.4: Proportional selection of habitat categories observed within the home range (white bars) compared to the proportion area of habitat categories available in the home range (grey bars)

6.4.3.2 Magpie territorial defence behaviour

The probability of response to simulated territorial intrusion was affected by both the habitat the dummy magpie was situated in and the distance the dummy was situated from the nest [GLMM: $\chi^2_{3,5} = 13.70$, $p = 0.003$] (Table 6.9). The probability of response declined with distance from the nest and was lower in crop than in field margins (grass around the edge of crop), or grassland (permanent grass fields) (Figure 6.4). Due a relatively small sample size, and a skewed response rate, which caused extremely high uncertainty in model estimates, simulated territorial intrusions in woodland were not included in the final GLM analysis. The response rate in woodland was the lowest of any habitat type (~15%), but further sampling would be required to assess exactly how magpie territorial defence behaviour is moderated in woodland.

Table 6.9: GLMs showing main effects and interaction terms for the model of territorial magpies' reaction to simulated territorial intrusions

Maximal model						
Fixed effects		Estimate	SE	Test statistic (χ^2)	df	P value
		(β)				
Intercept (Habitat type – Crop, Distance*Habitat type – Crop)		-2.74	1.22			
Distance		-2.51	1.46	9.12	1	0.003*
Habitat type	Field margin	2.60	1.26	7.21	2	0.03*
	Grass	2.57	1.24			
Distance*Habitat type	Field margin	2.16	1.49	3.35	2	0.18
	Grass	1.87	1.48			
Random effects		Estimate	SE	Test statistic (χ^2)	df	P value
		(σ^2)				
Territory identity		0.06	0.06	0.10	1	0.76
Minimal model						
Fixed effects		Estimate	SE	Test statistic (χ^2)	df	P value
		(β)				
Intercept (Habitat type – Crop)		-1.51	0.51			
Distance		-0.61	0.23	9.12	1	0.003*
Habitat type	Field margin	1.37	0.61	7.21	2	0.03*
	Grass	1.34	0.57			
Random effects		Estimate	SE	Test statistic (χ^2)	df	P value
		(σ^2)				
Territory identity		0.08	0.07	0.17	1	0.68

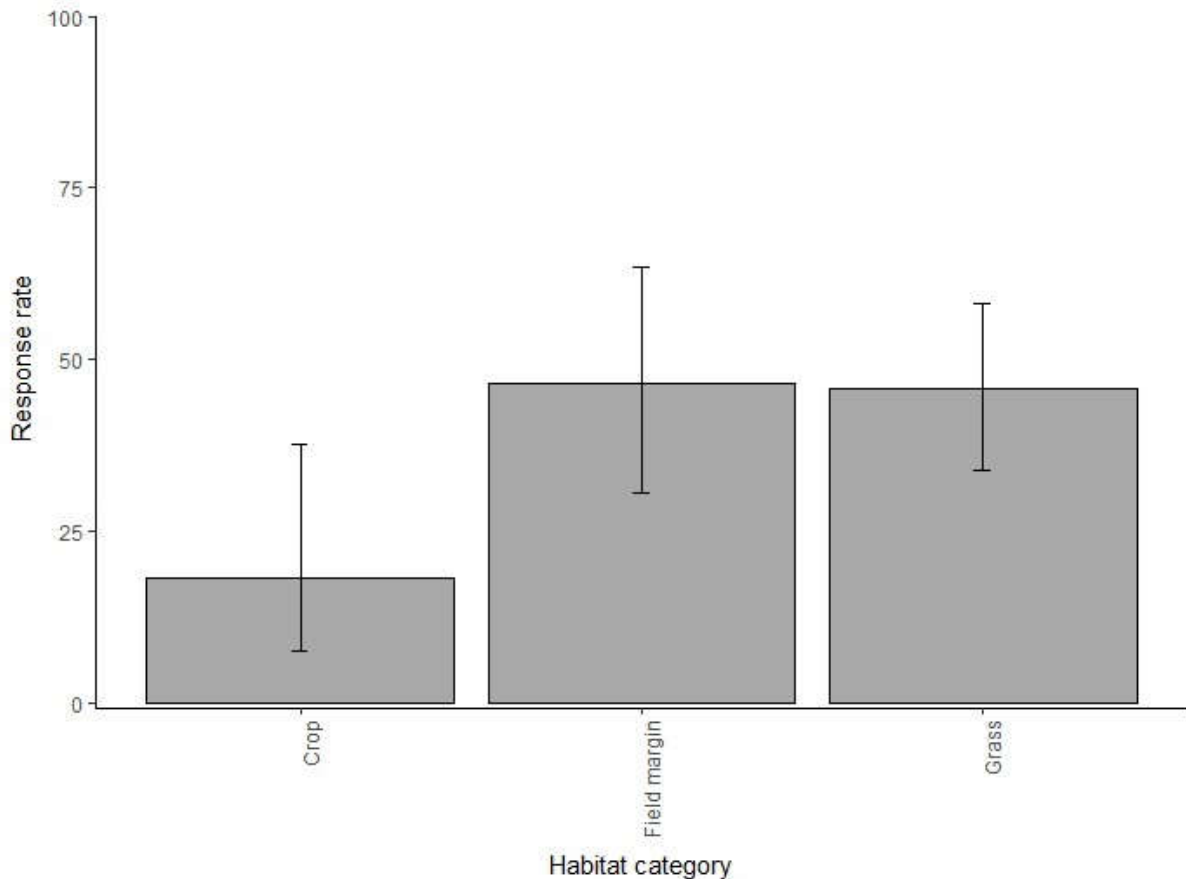


Figure 6.5: Predicted values for difference in magpie response to simulated territorial intrusion, depending on the habitat the dummy magpie was situated in. Probabilities are adjusted relative to the other variables modelled.

6.5 DISCUSSION

Habitat attributes which influenced magpie habitat use differed depending on the spatial scale of habitat variation considered. At a landscape scale, (per 1km²) magpie nest density was higher in areas with more road and hedgerow. At a local scale however, availability of pasture was the most important factor influencing nest site choice. Individual scale measures of habitat selection suggested a particular preference for the same grassland habitats which determined magpie nest site choice at a local scale. We might expect that songbirds and corvids would overlap in habitat preferences, especially of grassland and hedgerows, this could facilitate predator-prey encounters. However, we did not find evidence that songbirds were using the same areas as magpies at a local scale. Magpie nest sites did not overlap with areas of high songbird nest site occurrence. In fact, there was some evidence that songbirds avoided nesting near the most frequently used magpie nest sites. We can therefore surmise that magpies may have an indirect effect on songbirds at a

local scale. By avoiding areas frequently used by nest predators such as magpies, songbirds may be compromising on other habitat requirements such as food availability.

6.5.1 Landscape scale habitat selection

Habitat attributes were found to predict magpie density at a landscape scale; magpie nest density was reduced in areas where the length of hedgerow was shorter. Given that the vast majority of magpie nests found were situated in hedgerows, a decrease in hedgerow length is probably associated with a limitation of nest sites (Birkhead, 1991).

Roads in our landscape areas tended to be hedgerow lined meaning road length was often greater in areas with more hedgerow. However, road length affected magpie nest density independently of hedgerow availability. Magpies may favour nesting in areas with more road as they can forage on road kill (Santos et al., 2011; Chace & Walsh, 2006), and in rural areas prefer to nest close to areas of human activity generally (Møller 1978 cited in Birkhead, 1991), possibly due to reduced risk of predation, particularly by carrion crows (*Corvus corone*) (Baeyens, 1981b; Antonov & Atanasova, 2003).

In the landscape area used for this study, most woodland areas were dense conifer plantation, so were not searched for magpie nests. However, we did find a positive effect of woodland area on the density of magpie nests in the surrounding 1km². As areas of woodland were generally small patches (0.32km² max.) rather than larger blocks, there was a relatively large amount of edge habitat associated with presence of woodland areas. Magpies have been shown to prefer foraging in agricultural woodland edge habitats (Møller, 1989), and it maybe that the density of magpie nest sites was increased in areas where the availability of this preferred edge habitat was greater.

At a landscape scale, we identified several habitat factors that were associated with increased density of breeding magpies. We did not directly assess songbird distribution at the same scale, but the abundance of farmland songbird species may be affected by some, if not all, of the same factors. For example hedgerow availability, which we found to limit magpie density, will certainly also be limiting for many farmland songbirds which utilise them for nesting, shelter and

foraging (O'Connor, 1984). It follows that magpies might exist at higher densities in areas where farmland songbirds that nest in hedges are also more frequent. On the other hand, we found that increased road length led to high magpie nest density, whereas roads have been shown to adversely affect songbirds (McClure et al., 2013; Kociolek et al., 2011). If songbirds do avoid roads this may facilitate a separation of magpie and songbird populations.

6.5.2 Local scale habitat selection

Factors which determined landscape scale magpie density differed from those which affected magpie habitat choice at a local scale. This may have been because factors which drove differences in magpie density at a landscape scale (per 1km²) did not differ as much at a local scale (within 1km²). For example, within this area habitat defined by farm management such as field size (and therefore hedgerow length which influenced magpie density at a landscape scale), is likely to be consistent. At a local scale, magpie nests were instead positively associated with availability of pasture (grazed grassland) within 125m of the nest site. Magpies have been shown to preferentially associate with grassland (Møller, 1983), particularly that which is grazed by livestock (Birkhead, 1991; Waite, 1984). Surface and soil dwelling grassland invertebrates are an important part of magpie diet (Holyoak, 1968; Tatner, 1983) and the biomass of certain invertebrates is higher in permanent grassland (Tucker, 1992). The shorter sward in grazed pasture also provides easier access (Vickery et al., 2001).

At an even finer scale, magpie nest site choice was driven by tree species availability. Of the trees available within a 6m radius of the nest site, magpies favoured nest sites in hawthorn and blackthorn trees. These species are early leafing and spiky, making it difficult for carrion crows (which were the main predation threat at this site) to access the nest (Baeyens, 1981b). Magpies have generally been found to prefer to nest in trees which provide camouflage (Antonov & Atanasova, 2002; Jokimäki et al., 2017) and a protective canopy (Tatner, 1980).

Proximity to nesting conspecifics also affected magpie nest site choice. Active magpie nest sites were ~80m further apart than if randomly distributed. Similar patterns of nest spacing have been found elsewhere (Vines, 1981). These inter-nest distances could have been driven by food availability however, provision of food

does not necessarily increase magpie breeding density (Dhindsa & Boag 1990), or induce magpies to occupy empty territories (Hogstedt, 1981). Therefore, it seems likely that magpie nest sites were, at least in part, chosen to avoid conspecifics.

In summary, nest site choice was driven by the availability of a pasture and the proximity of conspecifics, at the local scale, and at a tree level, by the protection offered by some tree species against nest predation (Birkhead, 1991). There was no evidence that magpies preferentially selected nest sites due to the presence of songbird nests. It may still be that magpie nest site choice does increase the chance of them encountering some songbird nests, specifically those songbirds which have preferences for nest sites in similar habitat types, for example a preference for thorny hedgerows (*Chapter Five*). Farmland songbirds have been shown to prefer denser hedges (Dunn et al., 2016), and the hawthorn and blackthorn that magpies favour also tend to have a dense structure.

However, the nest sites that were occupied more frequently during all three years of study, and were therefore presumed to be of higher quality (Møller, 1982), were more likely to be found in trees other than hawthorn and blackthorn, such as beech (*Fagus sylvatica*). Hawthorn and blackthorn tended to be less frequently available within 6m of these regularly used nest sites, only within 6m of ~50% of nest sites compared to ~90% of the less frequently used nest sites. It does seem counter intuitive that the most frequently used sites would not contain the preferred nest trees but these sites may be favourable due to other habitat factors. For example, these sites had 3 times as much pasture as frequently occupied sites with hawthorn nest trees.

Perhaps most interestingly, the number of songbird nest sites was lower in the vicinity of the regularly used magpie nest sites than in the vicinity of less frequently used magpie nest sites, independent of the availability of songbird nesting habitat. Prey species may avoid areas with higher predation risk if they can detect evidence of predators (Lima, 2009; Fontaine & Martin, 2006). Songbird species have been shown to avoid the breeding sites of corvid predators at a fine-scale when their broader habitat preferences, for example for foraging habitat, overlap (Roos & Pärt, 2004). It may be easier for songbirds to avoid nest sites which are more predictably occupied by nest predators, than nest sites used less frequently (Suhonen et al.,

1994; Hunter et al., 2016). However, this predator avoidance behaviour could have negative effects on the prey species; restricting habitat choice may be a detrimental if resources are limited (Butler et al., 2005; Festa-Bianchet, 1988).

6.5.3 Individual scale habitat selection

Magpies differed between individuals when selecting home range areas and habitats within those areas. We found larger home ranges than those previously measured in rural environments for both methods that we used to calculate home range (MCPs and fixed-kernel density) (Birkhead, 1991; Kang et al., 2012). Our most conservative measure (MCP) predicted an average home range size of 18 ha. (6.2 – 39.5 ha.). Radio-tracking the magpies enabled us to monitor the birds without disturbing them, but it may be that using this method to measure home range caused the discrepancy between our findings and previous studies. These previous studies have utilised observations of aggressive interactions to identify magpie territory borders (Vines, 1981), and it may be that the radio-tracked area represents an area larger than birds would actively defend. In addition, we may have identified larger home ranges because our field site had relatively poor habitat compared to other studies. If home range sizes are inversely related to habitat quality, populations in more food-rich habitats may be able to exist at higher densities (Birkhead, 1991; Antonov & Atanasova, 2002). Our smallest home range sizes were located in valley bottom habitats near farmyards (which provide a good food source) and were similar in size to those found in other studies (Baeyens, 1981a).

Habitat selection of the home range was not significantly different from random. This may partially be explained by our possible over-estimation of home range within our fairly uniform local area; there may not have been significant overall habitat variation for large subsections to differ from the whole. However, within the home ranges, we found that territorial magpies tended to preferentially utilise hedgerow and, to a lesser extent, grass than expected considering their availability within their home range. Most of the radio-tracking data was collected when magpies on this site were incubating eggs and provisioning young, so we would expect them to spend time near/in the nest site in the hedge. The latter tracking period at the beginning of the moult period (Cramp et al., 1994), when we might also expect birds to spend time under cover (Verbeek, 1972).

The radio-tracking period also corresponded to the songbird breeding period, it may be that magpies are spending a disproportionate amount of time in hedgerows at the same time as songbirds are likely to be nesting in these hedgerows. This overlap in habitat use may facilitate an increase in predator-prey encounter rate (Evans, 2004).

The preference seen for grass within the home range, as with the preference for pasture around the nest site, may be linked to food availability (Tucker, 1992). Further evidence for this preference is provided by magpies' responses to simulated territorial intrusions. The birds were less likely to react to intrusions in crop, compared to those in grass or field margins. As we would not expect the visibility of the dummy to vary meaningfully between these habitats, we examined possible alternative explanations for the difference in response rates between habitats. Birds engage in more vigorous defence of their territory when it contains a more valuable resource (Camfield, 2006; Foltz et al., 2015). It may be that territory holders are less likely to defend crop habitat because it is less valued (Arnott & Elwood, 2008).

6.5.4 Conclusions

Magpie habitat preferences varied depending on the spatial scale of habitat variation considered. Songbird association with magpies could also vary depending on the spatial scale considered. At both a landscape and local scale, magpies may share some broad overlapping habitat requirements with songbird species, particularly those that nest in hedgerows. However, we did not find that shared habitat preferences caused songbirds to nest in especially high density around magpie nests; in fact, we found some evidence that when songbirds could reliably predict magpie nest site occupancy they avoided nesting near magpies. By avoiding predator breeding sites songbird prey species may be pushed into habitat that is otherwise sub-optimal. Habitat loss caused by agricultural intensification, combined with increased predator numbers may have compounded this indirect effect of predation on songbird species. Provision of good quality breeding habitat may facilitate local scale separation between magpies and songbird species, especially in landscape areas where magpies persist at a high density.

Chapter Seven

General Discussion



7.1 INTRODUCTION

Farmland songbird populations have declined rapidly in the UK in recent decades (Newton, 2004; Donald et al., 2001), and this decline has coincided with the population growth of many predators, including corvids, which are known to predate songbird eggs and chicks in the nest (hereafter referred to as nest predation) (Thomson et al., 1998; Schaefer, 2004; Stevens et al., 2008). Therefore, we might expect corvid removal or decline to correspond with an increase in songbird populations. However, analysis of the relationship between corvid population growth and songbird decline has not found evidence of cause and effect (Thomson et al., 1998; Gooch et al., 1991; Gibbons et al., 2007), and meta-analyses of experimental predator removal studies have shown that corvid removal does not always increase songbird breeding success and population numbers (Madden et al., 2015).

There are several possible reasons why we do not always observe the expected relationship between corvid removal/decline and songbird population numbers. This thesis attempted to explore possible explanations for this confused picture.

- i) It may be that corvids are simply not frequent predators of songbird nests. If this is the case, we should not expect corvid removal to improve songbird breeding success (*Chapter Two*).
- ii) Interspecific differences in songbird breeding biology may mean that some songbirds are more vulnerable to predation by visually oriented avian predators such as corvids (*Chapter Two*). Previous studies which found that corvid removal did not increase songbird breeding success may have considered songbird species which are not vulnerable to corvid predation.
- iii) Even if songbird species do suffer high nest predation rates, it may be that some songbird species are able to compensate for losses of eggs and chicks during the nest period. There are several possible mechanisms here. Firstly, mortality caused by nest predators may be compensatory, whereby predators only take eggs and chicks that would otherwise be lost due to other causes of mortality. Secondly, songbird species may be able to compensate for losses due to nest predation by having repeat broods. In this case post-breeding population numbers would be unaffected by changes in nest predation rates. Thirdly, songbird population numbers

may not be limited by losses during the nesting period. Their life history strategy may be adapted to suffering high losses at these early stages, and their population numbers may instead be limited by losses at other later life history stages (*Chapter Three*). For these songbird species removing corvids, and reducing mortality caused by corvid predation of nests, would not be expected to affect overall population numbers.

iv) Corvids may differ in the extent to which they predate nests. Variation in breeding status, time in the breeding season, and differences in personality may affect the nest predation behaviour of corvids. If particularly predatory individuals are not removed, then increases in songbird breeding success and population numbers might not be observed (*Chapter Four*).

v) The chance of corvids encountering (and therefore predating), songbird nests also depends on the habitat use of both songbirds and corvids and how their habitat use interacts. Songbirds may be able to choose nest sites that reduce the probability of corvids encountering their nests. However, songbirds which nest near habitat which corvids are likely to use, may be more likely to be encountered. Understanding the factors that drive habitat selection and nest site choice of songbirds (*Chapter Five*) and corvids (*Chapter Six*), may help identify areas or habitats in which songbirds are likely to be particularly vulnerable to nest predation. It may be that corvid removal only benefits songbirds nesting in particularly vulnerable locations, possibly where preferred nesting habitat is limited, or where corvids exist in high density.

7.2 SUMMARY OF KEY FINDINGS

The simplest explanation for the apparent lack of effect of corvid removal/decline on songbird populations is that corvids do not predate a high number of songbird nests. Yet, evidence I obtained from the literature suggested that corvids are frequent predators of songbird nests. A meta-analysis of reported rates of nest predation attributed to corvids indicated that corvids were frequent predators of songbird nests; on average 10% of songbird nests were lost to corvid predation (*Chapter Two*). This finding was supported by evidence from the field; magpies were identified as the most frequent predators of artificial songbird nests (*Chapter Four*).

However, different songbird species were not found to be equally vulnerable to nest predation by corvids. It may be that only particularly susceptible species

show improvements in breeding success following corvid removal. An analysis of nest predation rates extracted from the literature identified several features of breeding biology which influenced the vulnerability of songbirds' nests to predation by corvids; open nesting species, which placed nests low in vegetation, and had a higher breeding season overlap with magpie breeding season, were particularly susceptible to corvid predation (*Chapter Two*). These findings received additional support from results obtained from field observations. The same factors predicted songbird nest success on a mixed agricultural site where corvid predation was the main cause of nest failure. Open-nesting species had lower breeding success than hole nesting species (*Chapter Five*) and artificial nests were found to be more vulnerable to predation during the magpie breeding season (*Chapter Four*). These susceptible species, such as blackbird (*Turdus merula*) and song thrush (*Turdus philomelos*) were also reported in other studies (see Stoate & Szczur 2001 and White et al. 2008) as being more likely to show increased breeding success in response to corvid removal or decline.

Nevertheless, even for the species identified as more susceptible to nest predation, such as long-tailed tit (*Aegithalos caudatus*), the removal of corvid predators may not lead to an increase in songbird breeding success. The mortality of eggs and chicks (hereafter, referred to as nesting mortality) caused by nest predators, may be compensatory (taking individuals that would otherwise have died due to other causes, such as starvation or exposure). Only when nest predators cause mortality that is additive to nesting mortality caused by other factors, will variation in nest predation affect overall nesting mortality, and therefore breeding success. I found some evidence that mortality caused by nest predation was additive; songbird species that were vulnerable to corvid nest predation, did have higher nesting mortality at a species level (*Chapter Three*).

However, although corvid predation of nests may limit breeding success in susceptible species, previous studies have given no indication that this nest predation limited overall population numbers of these species. Songbird species that were susceptible to corvid predation, and had higher nesting mortality, were not more likely to be in long-term population decline over the period of corvid population increase (*Chapter Three*). It appears that changes in breeding success do not always lead to changes in breeding population numbers. This may be because

mortality at other life history stages, for example first year overwinter mortality, is more important in limiting the overall population numbers of songbird species population numbers (Newton, 1988; Baillie & Peach, 1992; Siriwardena et al., 1998). Corvid removal may therefore only influence the breeding population numbers of species for which mortality during the nesting period also has a significant effect on overall population numbers. For example, linnet (*Carduelis cannabina*) population abundance may have been affected by mortality during the egg period (Drachmann et al., 2002; Siriwardena et al., 2000a).

Although, the varied results of previous predator removal studies may be partially explained by between-species differences in vulnerability to nest predation (Madden et al., 2015; Côté & Sutherland, 1997), within-species variation in response to predator removal/decline has also been found (Chiron & Julliard, 2007; Baláz et al., 2007). It therefore cannot just be variation in prey that causes variation in the effect of corvid removal on songbird species. The predators may also differ in their effect on prey. Corvids vary, both within and between species, in their ecology and foraging behaviour. These differences may affect the extent to which individuals predate songbird nests (Weidinger, 2009) and the effect of predator removal on songbirds may vary depending on the individual predators removed.

I found that the extent to which magpies predated songbird nests did vary. Magpie predation of nests was affected by the breeding status of the magpies, predation of nests was higher inside the territories of breeding magpies. Territory holders can develop a detailed knowledge of local habitat, which may increase their chances of encountering prey within that area (Møller, 1988; Linnell et al., 1999). However, the artificial nests placed inside magpie territories were only more likely to be predated than those outside when nests were exposed later in the breeding season (no nests placed outside of magpie territories were predated by magpies in July, compared to 20% of nests placed inside of territories). Territorial magpies, the breeding individuals, continued to predate nests late in the breeding season. This is likely to be when the magpies were provisioning dependent young. Magpies could have been selecting particularly nutrient-rich food to increase the growth rates of their young (Annett & Pierotti 1989; Sará & Busalacchi 2003).

However, nest predation also varied between magpie territories even though all the territories were occupied by breeding birds which may have been provisioning young. Within populations some individual predators may be dietary specialists, selecting specific prey such as eggs and chicks, rather than a more varied generalist diet (Slagsvold, 1980a). I found some evidence that nest predation was higher inside particular magpie territories. These differences between territorial locations could be due to difference in attributes of individual birds; due to attributes of the territories (habitat variation); or to a combination of the two (particularly predatory birds may be more likely to hold territories with specific habitat characteristics). As this research was only carried out in one year, during which individuals did not move between territories, we could not separate these possible explanations. However, we did find some evidence that individuals which occupied territories where nest predation rates were higher differed in other behaviour. Artificial nests placed in territories in which the owners had a stronger response to simulated territorial intrusion were more likely to be predated. It may be that underlying behavioural variation influenced differences in predation behaviour (Blackwell et al., 2016). If individual predators do differ in predation behaviour, only the removal of the most predatory individuals is likely to increase songbird productivity. Understanding what causes this variation in predation behaviour may therefore facilitate the identification and control of these particularly predatory individuals. For example, on my field site it could be that pairs or individual magpies that most strongly defend their territories could also be those most likely to predate nests within those territories.

Although differences in songbird susceptibility to nest predation, and magpie propensity to predate nests may explain some of the variation in the effect of corvid removal on songbird species, there may be some circumstances where even the removal of particularly predatory individuals does not benefit vulnerable songbird species. To affect the breeding success of songbird species, magpies must encounter their nests. The likelihood of magpies encountering songbird nests is affected by the habitat use of both magpies and songbirds. The extent to which their habitat use overlaps and interacts may also be affected by variation in the farmland habitat.

Habitat factors are likely to affect many aspects of a prey species' vulnerability to predation. For example, specific habitat types may allow prey to better avoid

predators or provide better protection from predators (Dunn et al., 2016; Baines et al., 2004; Coates & Delehanty, 2010). On the mixed farmland site, I studied there was some evidence that songbirds were choosing nests sites which were further away from predators and sites which provided increased physical protection from predators (*Chapter Five*). Magpies were recorded as the most common nest predators (*Chapter Four*) and songbird nests were generally further from magpie nests, than expected if distributed randomly. However, songbird nests were also more likely to be located in hedges with a denser structure. This dense structure is likely to reduce the accessibility of the nest site to predators. Indeed, I found that nests in these denser hedges were more likely to be successful independent of how close the songbird nests were to magpie nests. Mirroring the finding from my analysis of nest predation rates reported in the literature (*Chapter Two*), hole nesting species on my field site had higher breeding success and were 50% more likely to produce a fledged brood per territory. Nests in sites which were harder for predators, particularly corvids, to access, were more likely to produce fledged chicks.

Songbirds may select nest sites that reduce their risk of predation. However, the chance of songbird nests being encountered by predators will also be affected by the predator's own habitat selection and this may depend on the predator's nest site or foraging preferences. Defining the habitat preferences of predators could therefore help identify areas where prey may be particularly vulnerable. I found that magpie habitat selection in a mixed rural environment was scale-dependent; at a landscape scale, it was driven by availability of hedgerow, which provided nest sites, and roads, which provided a food source in the form of roadkill. At a local scale, magpies avoided conspecifics, selected nest trees that provided protection and cover and preferred sites with a higher proportion of preferred foraging habitat (pasture). Individual level measures of habitat selection derived from radio tracking of magpies and observations of magpie defence behaviour demonstrated that even within territories magpies preferentially utilised certain habitats; specifically, their preferred foraging habitat (pasture) and nesting habitat (thorny hedgerows) (*Chapter Six*).

It may be that only songbirds nesting in less well-protected sites or those nesting in close proximity to preferred magpie habitat, which are likely to be directly more vulnerable to predation, benefit from corvid removal. If preferred breeding

habitat is abundant and corvid habitat is limited, corvid removal would not be expected to improve songbird breeding success.

However, if breeding habitat is limited the threat of magpie predation may have additional indirect effects on songbird breeding success. There was some evidence that the habitat preferences of magpies and songbird species overlapped on my field site; both species showed preferences for nesting in hawthorn hedgerows. Yet, songbird nest density was lower around the most frequently used magpie nest sites. This could indicate that songbirds are actively avoiding areas around magpie nests and if preferred habitat is limited, it may be that songbirds are being excluded from optimal habitat. In this scenario, corvid removal may also benefit songbirds which appear to be avoiding the direct threat of corvid predation.

In summary, although, corvids were found to be significant predators of songbird nests generally, I identified several circumstances in which we would not expect corvid removal to benefit songbird species. This may explain the mixed results of previous predator removal studies. It could be that corvid removal is more likely to benefit target songbird species only in certain circumstances; when i) the target songbird species is vulnerable to nest predation, ii) the songbird species is limited at a population level by losses of eggs and chicks, iii) when particularly predatory magpies are removed and iv) when preferred nesting habitat of songbirds is limited, and songbirds are more likely to nest in sites with higher predation risk (i.e. in close proximity to magpies), or songbirds avoiding the threat of magpie predation are more likely to be pushed into otherwise suboptimal habitat.

7.3 IMPLICATIONS OF FINDINGS

7.3.1 Applying the findings of this thesis to the management of corvid and songbird populations

Changes in agricultural habitats, increases in predator populations, and the interactions between the two, are likely to have affected breeding success and population numbers of songbird populations in several ways. Therefore, both habitat management and predator population management have been suggested as possible methods by which songbird population increases on farmland sites might be achieved. The findings of this thesis provide insight into how both these strategies

could be used, specifically to reduce the effect of magpie predation of farmland songbirds.

There is likely to be a trade-off between habitat management and predator population management; in some circumstances, perhaps when predator population density is low, habitat management may be sufficient to reverse songbird population decline, whereas at higher predator densities even exceptional habitat management may not be sufficient to reverse declines in population numbers (Aebischer et al., 2015; Baláz et al., 2007; Dunn et al., 2010; Baines et al., 2004). However, even in the latter case, appropriate habitat management should be in place before management of the predator population is considered. This is because firstly, even if habitat management does not facilitate songbird population increase when implemented alone, any improvements in songbird breeding success or survival, may increase the chance of population recovery when implemented alongside predator removal. For example, provision of foraging habitat could improve songbird survival and breeding success indirectly, increasing population resilience to predation. Secondly, predator control is costly and has animal welfare implications and should only be considered when other options have been explored (Smith et al., 2010).

Indeed, it has been argued that the evidence that nest predators can limit songbird populations is not sufficient to justify predator removal as a solution in any circumstances (Madden et al., 2015). However, it could be that this lack of evidence is due to the absence of well-planned experimental interventions, such as that of Tapper et al. (1996), which are likely to provide the most definite evidence for an impact of predator removal on passerine prey species (Nicoll & Norris, 2010). Furthermore the majority of UK published studies are based on work carried out at one site, Loddington Farm, Leicestershire (Stoate & Szczur, 2005; White et al., 2014; Stoate & Szczur, 2006). This may not be a sufficient sample to draw broad conclusions about efficacy of predator removal in increasing songbird productivity or abundance. Certainly, the weight of evidence is not sufficient to discount the benefits of predator removal entirely. The results of this thesis, in accordance with some previous work (Holt et al., 2008; Fletcher et al., 2010; White et al., 2008), suggest that targeted use of predator control, alongside appropriate habitat management, may still have beneficial effects for some prey species.

7.3.1.1 Predator control

If sympathetic habitat management is in place and songbird breeding success and population numbers have not recovered, this could indicate that predator removal may be influential at a site. The findings of this thesis have several implications for situations where removal of corvids is being considered.

I identified differences between songbird species in susceptibility to corvid nest predation and the effect of losses in the nesting period on post-breeding population numbers. Therefore, before predator removal is implemented, two major considerations must take place. Firstly, it should be asked whether the songbird species at the site are of conservation concern (Eaton et al., 2015), and are those likely to be vulnerable to corvid predation because of their behaviour and breeding ecology. On sites where these criteria are met, confirming that significant corvid nest predation of these vulnerable songbirds species occurs, using an accurate method of nest predator identification, such as camera observations, may be helpful (Mallord et al., 2012; Lariviere, 1999; Schaefer, 2004).

Secondly, it should be established where or not the targeted songbird species are limited at a population level by breeding season losses. Where population demographic data is available, it might be possible to identify species whose populations are likely to be limited by losses of eggs and chicks from the nests (Peach et al., 1999; Baillie & Peach, 1992; Siriwardena et al., 1999) and where population numbers could then be increased through nest predator removal.

In situations where vulnerable species are threatened with local extinction predator removal may be appropriate. However, I also found some evidence that predators differed in their propensity to predate nests. Therefore, if predator removal is carried out, it should be targeted towards particularly predatory individuals as opposed to non-selective removal of all predators. Again, either direct observations or camera observations may help identify the most frequent nest predators at the nest. In this thesis, for example, it appeared that particular individual magpies or magpies which occupied particular territories were responsible for more predation. It may be possible to target particular individuals or particular locations for removal. In the case of the former, individuals could be targeted due to their susceptibility to particular trapping techniques or particular foraging strategy, whereas in the latter

case individuals could be targeted because of their association with particular spatial areas (Swan et al., 2017; Königson et al., 2013; Dickman & Newsome, 2015)

Larsen traps, currently the main method by which corvids are trapped and removed in the UK (Game and Wildlife Conservation Trust, 2014), may already target the most predatory magpies. I showed that nests were predated more when placed within the territories of magpies which were most likely to respond to territorial intrusions. This suggests that aggressive territory holders may show disproportionately high levels of nest predation. As Larsen traps work by eliciting a territorial response in the target bird by using a magpie as decoy, they may be efficient at trapping territorial birds, particularly those birds that are more likely to react to a territorial intrusion (Gregory & Marchant, 1996; Diaz-Ruiz et al., 2010).

Finally, if predators are removed, then both predator and prey species should be monitored before and after removal (Nicoll & Norris, 2010). Although this is likely to be labour intensive and may not always be practical, monitoring of post-breeding numbers and subsequent breeding populations of songbird species would be particularly helpful in detecting long-term benefits of predator removal.

7.3.1.2 Habitat management

The results of this thesis also provide insight into other strategies that could be used instead of, or in addition to, predator control to reduce the impact of magpies on songbird populations. Specifically, the understanding of habitat preferences of magpies and songbirds in mixed farmland gained in this thesis can be used to inform the management of mixed farmland habitats to reduce the chances of magpies encountering songbird nests. This approach should be seen as a minimum requirement that must be met before predator control is considered.

Different management strategies at a landscape scale may reduce the density of generalist predators, including corvids. Firstly, the availability of anthropogenic food sources could be reduced (Stracey, 2011; Marzluff & Neatherlin, 2006; Rodewald et al., 2011). In this thesis magpie nest density was positively associated with availability of roads, possibly due to the supply of road kill. Secondly, where possible, habitat fragmentation could be reversed (Angelstam, 1986; Andren, 1992; Schneider et al., 2012b; Chalfoun et al., 2002). In the mixed farmland landscape studied in this thesis magpie density was increased in areas with small fragments of

woodland set in farmland, possible due to the availability of preferred woodland-farmland edge habitat (Storch et al., 2005; Sanchez-Oliver et al., 2014).

At a local scale, provision of good quality songbird nest habitat, specifically hedgerows with a dense structure, may reduce corvid access to songbird nest sites (O'Connor, 1984; Hinsley & Bellamy, 2000). It has been suggested that hedgerows that are cut semi-regularly (every 3-4 years) are more likely to have dense structure (Dunn et al., 2016). On the farmland site used in this thesis, songbirds preferentially nested in denser hedgerows and nest success was greater in these hedges. However, magpies and songbird species may share preferences for breeding habitat. For example, magpies preferentially nested high in hawthorn hedges whilst songbirds also preferred to nest (lower down) in the dense vegetation provided by hawthorn hedgerows. These shared habitat preferences could increase magpie encounters with songbird nests or exclude songbirds which avoid magpies from preferred habitat. However, as magpies were, at least partly, limited by proximity of conspecifics (*Chapter Six*), increasing preferred breeding habitat might not be sufficient to increase magpie population density. Therefore, providing more breeding habitat may facilitate songbird avoidance of magpie predators – i.e. songbirds would be able to choose nest sites in high quality habitat away from magpie nests (Evans, 2004; Vickery et al., 2004). This would avoid a potential compromise between nesting in good quality habitat and nesting near a predator (*Chapter Five*).

7.3.2 Applying the findings of this thesis to the future research of corvid and songbird populations

This thesis illustrated how variation in the ecology, behaviour and habitat preferences of corvids and farmland songbird species could cause the effect of corvid nest predators on these songbird species to vary. I have also demonstrated how the understanding of these source of variation, gained through this thesis, could be applied to the management of corvid and farmland songbird populations. However, this work was limited to assessing the effect of one predator of farmland songbirds on one, albeit typical, farmland site. The results therefore provide several possible avenues for further investigation, both in terms of possible management strategies and future research.

Firstly, although I was able to identify songbird species that were particularly susceptible to nest predation, and are therefore likely to have suffered increased rates of nest predation as populations of nest predators have grown, I was not able to establish a clear link between a species' susceptibility to nest predation and nation or region wide changes in a species' population numbers. Integrating assessments of nest vulnerability with knowledge of species life history strategies would allow us to identify songbird species that are both i) unusually vulnerable to nest predation by corvids and ii) more likely to be limited at a population level by losses early in life. Identifying these species would more accurately highlight songbird species that might be expected to benefit from reductions in corvid populations or suffer if corvid populations increased. This work requires an extensive knowledge of the life cycle and demography of songbird species, but it is critical if we are to identify where and when we should focus conservation efforts to achieve recovery in overall population numbers of species of interest.

Secondly, there was some evidence that magpies' varied in their propensity to predate songbird nests. There were differences in rates of nest predation between active magpie territories. However, as this aspect of the fieldwork was limited to a single breeding season, it was not possible to determine whether higher predation rates in particular territories were due to the properties of the specific territory or due to the predatory behaviour of the individual territory owner. Future work could utilise natural changes in territory ownership to try and distinguish these two possibilities.

Thirdly, further exploration of the fine-scale habitat use of corvid and songbird habitat use may be beneficial. My work was exclusively descriptive, and it would be beneficial to ascertain (perhaps experimentally) how corvid encounters of songbird nest sites could be reduced through habitat management. For example, it may be possible to examine how different management of hedgerows affects hedge structure, and whether the effect of differences in hedgerows on nest survival are moderated by corvid proximity. It may also be possible to carry out further fine-scale analysis of habitat use by predators. This may help identifying individual differences in habitat use and how these might relate to propensity to take eggs and chicks from nests in certain habitats. In this thesis, we radio tracked magpies in a mixed agricultural environment. The undulating terrain and tall hedges meant we only could locate magpies to within approximately 10m (*Chapter Six*). Other tracking technology

such as GPS, could be used. GPS is more accurate than radio tracking and, unlike radio tracking, does not require the operator to manually search for the focal individual each time the animal is located. Instead location data can be recorded remotely. This would provide a more accurate indication of magpie habitat preferences and a more precise and fine-scale representation of magpie movement through habitat.

Finally, more explicit analysis of the relationship between corvid predation behaviour and trappability may be useful. It may be possible to investigate if/how nest predation behaviour relates to trappability and explore whether more targeted removal of particularly predatory individuals is feasible. For example, the potential relationship between magpie nest predation behaviour and the propensity of magpies to trap in Larsen traps could be tested explicitly (see 7.3.1).

7.3.3 Applying the findings of this thesis to the management of other predator and prey populations

This thesis has focused specifically on variation in the relationship between corvids and the songbird species whose nests they predate. However, the widespread increase in both generalist and invasive predator populations has led to increasing interest in the implementation of predator control as a management option more widely (Goodrich & Buskirk, 1995). The exploration of factors found to influence corvid-songbird relationships carried out in this thesis may provide some insight into other relationships between predator species and their prey.

The nesting biology of some songbird species made them more vulnerable to predation by corvids. The interaction between prey breeding ecology and predator foraging ecology may make some prey more vulnerable to predation by specific predators. Developing a more detailed understanding of how predator foraging ecology and prey biology interact may reveal some general rules that could be applied widely to predict which predators are likely to detrimentally effect particular prey. For example, nest height can affect the relative chance of different predators encountering nests; ground nesting species are more vulnerable to mammalian predation where as those that nest above ground in the shrub are more vulnerable to avian predation (Schmidt, 1999; Weidinger, 2002). Nest defence behaviour may also affect the propensity of different predators to take nests. Smaller nest predators,

such as jays (*Garrulus glandarius*), are less likely to predate the nests of species that engage in more active nest defence (Weidinger, 2009).

It is not only broad interspecific differences in prey ecology that may affect predator-prey relationships. This thesis found some evidence for variation within the predator population in the extent to which predators took songbird nests. Identifying particularly predatory individuals or demographic groups that are likely to be particularly predatory is a growing area of research across taxa (Jennings, 2006; Amar et al., 2004; Graham et al., 2011). Identifying specific individuals that are likely to predate nests may have important management implications since removal of fewer individuals is desirable (Linnell, 2011; Swan et al., 2017). If underlying differences which influence variation in predation behaviour can be detected, this may further aid the targeting of more predatory individuals. These underlying differences could be relatively simple demographic differences, for example, large male feral cats were considered more likely than other feral cats to predate native mammal species in Australia (Moseby et al., 2015; Swan et al., 2017). More complex behavioural differences could also affect individual differences in propensity to predate nests, for example, bolder individuals may be more likely to win aggressive interactions and therefore exploit particular food resources (Cole & Quinn, 2011), but could also be less susceptible to management techniques such as scare devices (Darrow & Shivik, 2009).

Even if the prey species are susceptible to predation and individual predators are likely to predate prey, predators can only predate prey if they encounter them. Variation in the external environment can affect the likelihood of predators encountering prey. Songbird nests in dense hedgerows were less likely to be encountered and predated. The ecological context of predator-prey interactions is likely to be influential. Identifying habitat preferences of both predator and prey, across different spatial scales, may highlight areas where predators and prey are likely to overlap, and where management could be specifically targeted. Particular protection could be given to nests or other prey living in these areas of overlap. For example, by characterising habitats that define the distribution of predatory carnivores it was possible to identify areas where these predators are likely to take livestock (Mladenoff et al., 2007; Treves et al., 2004). As in this thesis, fine-scale (within territory) analysis of predator habitat preferences could be used to identify

areas where prey species are likely to be particularly vulnerable. For example, radio-tracking of individual buzzards (*Buteo buteo*) revealed that they were more likely to take pheasant poults from pheasant release pens with specific habitat characteristics (Kenward et al., 2001).

7.4 FINAL SUMMARY AND CONCLUSIONS

Identifying the causes of the decline of UK farmland songbird populations is a long-standing focus of research. The increase in the numbers of predators of eggs and chicks of songbirds, including corvids, has often been cited as a factor limiting the populations of farmland songbird species. However, direct analysis of the impact of corvids on songbird prey has produced mixed results with little support for the hypothesis that corvids suppress songbird populations.

I explicitly asked why such expected relationships were absent by testing five explanations. Firstly, it is conceivable that magpies in particular, and corvids in general are simply not especially common nest predators. However, I found that 23% of reported nest predation of songbird nests was attributed to corvids. Secondly, it is possible that some species, due to their breeding biology, are not vulnerable to corvid predation of their nests. For example, songbirds which nest in holes, and those with less breeding season overlap with corvids, experience low levels of nest predation by corvids. Including these less vulnerable species in analyses of effects of corvid population change on songbirds may mask more subtle, species-specific consequences of corvid removal/decline. Thirdly, songbirds may differ in the effect that loss of eggs and chicks has on overall population numbers. Songbirds that were susceptible to corvid nest predation did suffer higher nesting mortality, but I could not link this higher nesting mortality to population decline during a period of corvid population growth. Further research is required to better understand how mortality at different life history stages relates to overall population numbers. Fourthly, it is possible that magpies vary in the extent to which they predate nests and if individuals that predate more are not removed, changes in numbers of corvids may not alter the populations of their prey. I found evidence that breeding territorial magpies were more likely to predate nests at certain times of year and there were additional differences in predation rates between these territorial pairs of magpies. If particularly predatory individuals, or those individuals which

occupy territories where predation rates are high, can be identified and selectively removed at critical times, control of corvids could alter the population numbers of songbirds. Finally, it is possible that in many cases, perhaps especially at low corvid population densities, corvids do not encounter nests because either the songbird deliberately selects habitats away from areas frequented by magpies or magpies do not preferentially forage in areas naturally frequented by songbirds. I found that songbirds had clear preferences for nest sites which were further from magpie nests than expected by chance. Additionally, magpies displayed strong preferences for habitats in which to forage. By analysing habitat and nest site selection of both species at the same site it was possible to assess how and where predators were likely to encounter prey species.

Understanding the complexity of situations where predators may be limiting prey species is of importance in conservation, and other areas of research. This thesis highlights the benefits of considering multiple potentially influential factors when trying to understand predator-prey relationships, specifically the importance of considering the breeding ecology, behaviour, and habitat use of both the predator and the prey to better understand how they interact.

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