Farming and Foraging: Indirect effects of management on bird biology through changing distributions of food and predators

Jenny Claire Dunn

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The candidate confirms that the work submitted is her own and that appropriate credit has been given where reference has been made to the work of others

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Abstract

Farmland songbirds have shown dramatic population declines that have been linked to agricultural intensification. Populations have been impacted via three key factors: a reduction in available nesting habitat, a reduction in the availability of food for nestlings, and a reduction in over-winter food availability. The abundance of nest predators such as corvids, and the presence of sub-clinical disease may also play a part, and this thesis investigates the inter-relationships of some of these five factors along with their potential impacts upon farmland bird populations, using the yellowhammer *Emberiza citrinella* as a model species. It appears that the quality, not the quantity of fledglings has declined, possibly due to delayed life-history effects following on from conditions experienced in the nest. Increases in corvid abundance are associated with declines in chick growth and condition, mediated by behavioural compensation by provisioning adults: these effects are especially marked in large broods and where invertebrate food supply is low; where food supply is high a slightly positive effect of corvid abundance on condition and growth is found, implying an adaptive response by adults to maximise food provisioning in order for chicks to fledge more quickly and thus reduce their risk of predation in the nest. High territory densities, found where the availability of suitable nesting habitat is high, are associated with apparent density-dependent competition for high quality food and reduced chick growth, probably reducing fledgling quality and potentially leading to population sinks in areas of good nesting habitat, or in areas with high corvid densities. Survival analysis from a yellowhammer population sampled over four successive winters indicates that survival is male-biased, probably due to the higher work rates of females during breeding. Survival probability increases with increasing wing length, although analysis of 21 years of ringing data from the same site indicate a significant trend towards decreasing wing length, when controlling for the effects of age and sex. This apparent paradox is likely to have arisen from a decline in wing length of fledglings recruiting into the population as a result of a decline in habitat quality or food availability, both of which have been shown to influence feather growth. Infection by blood parasites showed associations with reduced feather growth and may indirectly influence survival, possibly by compounding food stress over-winter.

Contents

Life history effects on populations: food availability, predation and disease in farmland birds

Abstract

Farmland bird declines across Europe are largely blamed upon reductions in food supply caused by agricultural intensification. Changes in predation pressure through both changing predator numbers and habitat simplification may also contribute to declines. Here, I review recent literature and take a life history approach towards understanding population level impacts of stress-inducing factors, focussing on food shortage, predator pressure and sub-clinical disease, in influencing farmland bird populations during both the breeding and non-breeding season. I discuss the likely impacts of changing management practices on already pressurised populations.

Introduction

The dramatic declines of farmland bird populations over the past 35 years have been well documented (e.g. Fuller et al. 1995; Potts 1997; Chamberlain et al. 2000) and are now known to be linked to the intensification of agriculture over the same period (e.g. Fuller et al. 1995; Wilson et al. 1997; Chamberlain et al. 2000; Donald et al. 2001; Donald et al. 2002). The decline in farmland birds is unparalleled by those associated with any other habitat (Fuller et al. 1995) and in 1999, 116 species of birds associated with farmland, comprising 20% of the European avifauna, were of conservation concern (Krebs et al. 1999). Whilst the current population status of farmland birds as a group appears to have stabilised, the indicator value is currently around 55% of the 1970 value and the apparent stabilisation is due to the balancing of the many still-declining species with some species whose populations have increased over the same time period (Eaton et al. 2008). Since the 1940s, around 50% of all hedgerows have been removed and yield has increased almost fourfold (Robinson and Sutherland 2002); however the resulting effects upon agricultural biodiversity have been catastrophic (Krebs et al. 1999; Robinson and Sutherland 2002; Green et al. 2005). Whilst many farmland birds have significant associations with other habitats (Virkkala et al. 2004), their reliance upon agricultural land for one or more aspects of their life-history appears causal in their declines (Fuller et al. 1995; Gregory and Baillie 1998; Donald et al. 2001) and may be associated with reductions in genetic diversity (Lee et al. 2001). Even countries with only moderate levels of agricultural intensification show a decrease in their farmland bird populations (Donald et al. 2002; Kujawa 2002). Whilst both the mechanisms behind the declines and the measures needed in order to begin to reverse the process are less clearly understood, a reduction in farming intensity provides a better habitat for farmland birds and conversely, more intensive farming is associated with both a poorer breeding performance (Siriwardena et al. 2001) and lower densities of birds (Wolff et al. 2001). This review aims to summarise the drivers behind environmental change during the period of declines: namely agricultural intensification, changes in predator numbers, and other impacts such as sub-clinical disease and climate change. The mechanisms by which these drivers have an impact upon populations, both directly and indirectly, will then be explored; finally, government schemes that attempt to mitigate the effects of environmental change and reverse the declines in avian populations will be discussed.

Drivers of change

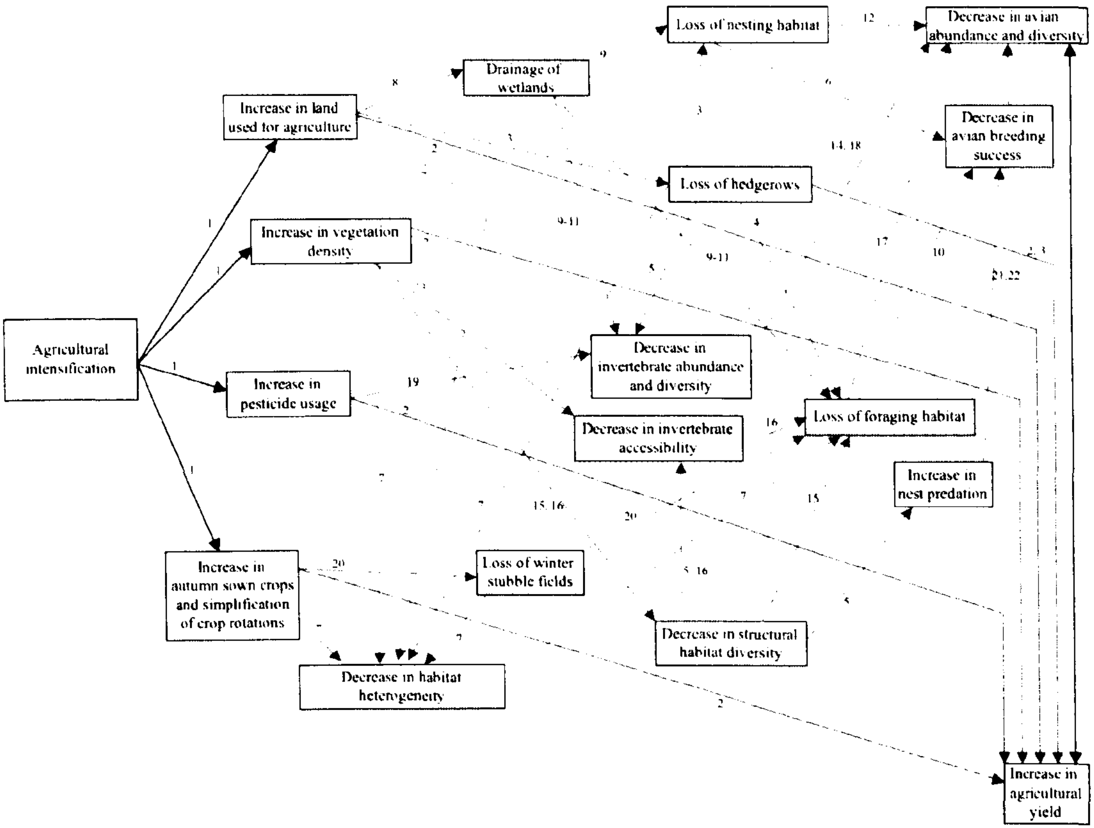

Figure 1. Highlighting some of the mechanisms by which agricultural intensification has led to a reduction in avian biodiversity on farmland with a resulting trade-off between agricultural yield and avian biodiversity. Red lines indicate a negative impact; blue lines indicate a positive impact; double ended lines indicate a trade-off. Numbers on arrows represent citations; these are not intended to be exhaustive. 1 Fuller et al. 1995; 2 Chamberlain et al. 2000; 3 Robinson and Sutherland 2002; 4 Benton et al. 2003; 5 Haddad et al. 2000; 6 Heikkinen et al. 2004; 7 Clough et al. 2005; 8 Weibull et al. 2000; 9 Atkinson et al. 2005; 10 Butler and Gillings 2004; 11 Fuller et al. 2004; 12 Clergeau and Fourcy 2005; 13 Morris et al. 2001; 14 Macdonald and Johnson 1995; 15 Osborne 1984; 16 Whittingham and Evans 2004; 17 Atkinson et al. 2004; 18 Orians and Wittenberger 1991; 19 Zedler 2004; 20 Gillings et al. 2005; 21 Yom-Tov 1974; 22 Komdeur and Kats 1999.

The intensification of agriculture through the introduction of mechanisation has been the most evident driver of environmental change since the 1960s: this will be discussed in detail here, and some of its effects on farmland bird populations will be reviewed. However, agricultural intensification is not the only cause of changes to the agricultural environment: changes in predator numbers have also had an impact upon farmland bird populations. Clinical and sub-clinical disease may play a part, both directly and indirectly, and there is increasing evidence that climate change has significant impacts upon the reproductive performance of some species. These aspects of environmental change will also be examined.

Agricultural intensification

Population crashes associated with agricultural intensification are not limited to avian species (e.g. Rands and Sotherton 1986; Wilson et al. 1999; Bell et al. 2001; Schmidt et al. 2005; Schweiger et al. 2005); groups of organisms in multiple taxa have been affected, with the majority being habitat specialists (Siriwardena et al. 1998; Robinson and Sutherland 2002).

Many aspects of agricultural intensification are thought to have detrimentally affected farmland species: some of these are highlighted in Figure 1. These factors are intrinsically interlinked, and commonly result in a decrease in habitat heterogeneity at many spatial scales. Heterogeneity will be discussed, as will some of the more significant impacts upon farmland bird populations, namely: habitat loss, a reduction in summer invertebrate availability, and a reduction in the availability of over-winter food. Each of these will be explored in turn.

Habitat heterogeneity

The reduction in habitat heterogeneity associated with the increase in mechanisation of agriculture and simplification of crop rotations is thought to play a key role in the reduction of farmland bird abundance and diversity (Benton et al. 2003). It seems logical that in the long term, a reduction in biodiversity at one trophic level will lead to a corresponding reduction in biodiversity further up the food chain (e.g. Haddad et al. 2000) and that a decrease in habitat diversity may also play a part in reducing the diversity of insects available to foraging birds (Haddad et al. 2000; Vickery et al. 2001; McCracken and Tallowin 2004; de Souza and Martins 2005; Schweiger et al. 2005).

Heterogeneity can take many forms and is relevant at many spatial scales. For example, at the landscape scale the spatial structure of bird distribution patterns is thought to be caused by the distribution of habitats either important to or avoided by birds (French and Picozzi 2002; Heikkinen et al. 2004; Robinson et al. 2004), although habitat quality is also important (Gillings and Fuller 1998; Gates and Donald 2000; Profitt et al. 2004). At the farm scale, mixed management practices are thought to be crucial to farmland bird populations, especially in the winter (Wilson et al. 1997; Siriwardena et al. 2000; Atkinson et al. 2002; Moreira et al. 2005; Calladine et al. 2006; Henderson et al. 2009; Mackenzie and Whittingham 2009); even during the summer, adult productivity is associated with the availability of a wide variety of foraging habitats (Anderson et al.

2002; Berg 2008). At the local scale an increase in the structural and botanical diversity of hedgerows and the area of non-cropped habitats is positively associated with bird abundance and diversity (Hinsley and Bellamy 2000; Herzon and O' Hara 2007; Whittingham et al. 2009). Heterogeneity is not only important for avian species but also for farmland biodiversity in general (e.g. Weibull et al. 2000; Benton et al. 2003; Smith et al. 2004; Clough et al. 2005; Marshall et al. 2006).

The declines of farmland bird species are frequently associated with range contractions (Fuller et al. 1995) and local extinctions (Robinson et al. 2001), which have in some cases been associated with a loss of arable land in pastoral-dominated landscapes (Robinson et al. 2001). The overall effect of management intensification has resulted in a spatial and structural uniformity over arable landscapes (Benton et al. 2003; Atkinson et al. 2005); this intensive habitat lacks the structural and botanical diversity necessary to encourage the diversity of invertebrates required as food by farmland birds (Alvarez et al. 2000; McCracken and Tallowin 2004), whilst also reducing both the detectability and accessibility of invertebrate prey (Butler and Gillings 2004). The enhancement of habitat diversity within the farmed landscape through the inclusion of scrub, ruderal vegetation and grasslands is expected to be beneficial to farmland birds through the provision of roosting, foraging or nesting resources (Fuller et al. 2004). In cases where large colonies of gregarious birds such as the Starling *Sturnus vulgaris*, cause significant crop damage it has been suggested that this may be reduced by increasing habitat heterogeneity, proving beneficial to both birds and farmland productivity (Clergeau and Fourcy 2005).

Hedgerows form a vital nesting and foraging habitat for declining farmland species such as the Yellowhammer *Emberiza citrinella* (Bradbury et al. 2000; Morris et al. 2001; Cornulier et al. Under review), and larger hedgerows with a high botanical diversity are generally associated with a higher species richness of nesting birds (e.g. Arnold 1983; Green et al. 1994; Parish et al. 1994; Macdonald and Johnson 1995; Sparks et al. 1996; Hinsley and Bellamy 2000). The presence of tree species and dead timber within hedgerows are also important to avian species diversity (Osborne 1984; Green et al. 1994; Parish et al. 1994; Macdonald and Johnson 1995) and the number of trees and amount of hawthorn in hedgerows positively influences bird abundance (Walker et al. 2005). However, some species prefer shorter, less dense hedgerows for nesting (Green et al. 1994; Whittingham and Evans 2004) and other species such as the Corn Bunting

Miliaria calandra, show a preference for territories without hedgerows (Mason and Macdonald 2000). It is therefore crucial to improve the heterogeneity of hedgerow habitats to make provision for all requirements (Green et al. 1994; Benton et al. 2003).

Within grassland the reduction in species diversity and increase in sward density (Wilson et al. 2005) have led to a corresponding reduction in the availability and accessibility of invertebrates valuable to birds (Atkinson et al. 2004; McCracken and Tallowin 2004; Atkinson et al. 2005; but see also Devereux et al. 2006), whilst also influencing exposure to weather and predation risk (Atkinson et al. 2004; Wilson et al. 2005). Many of the invertebrates present within intensively managed grassland are either not accessible to birds through the dense sward or impenetrable soils, or are too small to be utilised by birds (McCracken and Tallowin 2004). This corresponds to local extinctions of granivorous passerines within grassland over the past 25 years (Robinson et al. 2001) and is additionally supported by the preference of insectivorous species for unimproved grassland, where insects are more accessible within a shorter and less dense sward (Atkinson et al. 2004; Barnett et al. 2004). Whilst taller sward heights are associated with a greater diversity and abundance of invertebrates and may, to some extent, act as an invertebrate source (Atkinson et al. 2004), this may reduce both their detectability and accessibility (Butler and Gillings 2004) as well as increasing perceived predation pressure in patches with longer and more visually obstructive vegetation (Butler et al. 2005). As a result, many species of bird tend to avoid fields with a taller sward (Wilson et al. 1997; Atkinson et al. 2004; Atkinson et al. 2005) due to an increase in perceived predation risk, which is associated with an increase in scanning time and a corresponding decrease in time spent foraging (Whittingham et al. 2004). A mosaic of long and short grass to increase within-field heterogeneity would improve nesting and foraging habitat for species such as the Yellow Wagtail *Motacilla flava* (Bradbury and Bradter 2004) and increase bird diversity during the winter (Whittingham and Devereux 2008): the same principle applied to grass margins is thought to benefit granivorous passerines such as the Yellowhammer in the breeding season (Perkins et al. 2002; Douglas et al. 2009).

Habitat change

The availability of nesting habitat is vitally important in determining species distribution (e.g. Raphael et al. 2002) and territory density (Toepfer and Stubbe 2001). For example, the distribution of the Blue Tit *Parus caeruleus* in the breeding season is largely determined by the distribution of structural resources such as tree holes (Pulido and Díaz 1997). Essentially, safe nest sites and a close proximity to a good foraging area are the two most important requirements for breeding habitat in farmland bird species (Part and Söderström 1999). Nest site selection is usually complex and often important at several spatial scales (Orians and Wittenberger 1991). Territories may be selected on the basis of food availability (Davies and Lundberg 1984; Traba et al. 2008), habitat availability (Orians and Wittenberger 1991) or may be clustered on the basis of mating behaviour (Tarof and Ratcliffe 2004). High territory densities usually occur in high quality habitats (Davies and Lundberg 1984) although this may result in apparent competition through indirect mechanisms such as increased nest predation at high nesting densities (Nilsson et al. 1985; Schmidt and Whelan 1998). Territory density can also influence behaviour and reproductive success (Penteriani 2003; Sillett et al. 2004); thus, birds clustered together at high breeding territory densities in patches of favourable habitat are not necessarily the most productive in terms of individual breeding output (Sillett et al. 2004).

Agricultural intensification has led to the loss of around 50% of Britain's hedgerows since the 1940s, due to an increase in mechanisation (Robinson and Sutherland 2002). This has led to a reduction in both foraging and nesting habitat for farmland birds (Robinson and Sutherland 2002) which does in some cases show strong associations with population declines (Cornulier et al. Under review). At the local scale, there has been a corresponding loss of structural and botanical diversity in many remaining hedgerows, leading to an increase in nest predation risk (Hinsley and Bellamy 2000; Whittingham and Evans 2004) and a decrease in invertebrate availability to species for which hedgerows form an important foraging habitat (Whittingham and Evans 2004).

Agricultural intensification is a major contributor to the loss and degradation of wetlands worldwide (e.g. Zedler 2004), with detrimental effects upon multiple taxa (e.g. Jenkins et al. 2003). Aquatic habitats such as drainage ditches within arable are important in providing invertebrate food resources for species such as the Yellow Wagtails and the Tree Sparrows *Passer montanus*, (Anderson et al. 2002; Bradbury and Bradter 2004; Field and Anderson 2004) and are thought important factors in territory selection for Corn Buntings (Mason and Macdonald 2000). Yellow Wagtail breeding territories are positively associated with fields containing shallow-edged pools during summer: a reduction in the availability of such fields is likely to have led to a decline in suitable nesting habitat for this species (Bradbury and Bradter 2004).

The introduction of novel crops for energy production is also likely to have an effect on farmland bird species by altering the farmland environment further (Bellamy et al. 2009). Crops such as miscanthus may be beneficial in the short term for some species as they tend to contain higher abundances of both non-crop plants and the insects that associate with them (Bellamy et al. 2009). However, miscanthus itself tends to be associated with fewer invertebrates than the crops it replaces; thus, in the long term any benefits are thought likely to diminish as crop management improves with experience (Bellamy et al. 2009). The responses of birds to novel crops are likely to be species-specific, and the consequences of any change will need to be assessed independently for each bird species (Neumann et al. 2009).

Invertebrate availability

Agricultural intensification is associated with a significant decrease in invertebrate availability: one reason for this is the reduction in invertebrate accessibility caused by increased vegetation density (Atkinson et al. 2005) and others include the decline in invertebrate food resources such as weed seed-banks, and the increased use of pesticides, which lead to reduced invertebrate numbers *per se* (Marshall et al. 2003; Morris et al. 2005; Hart et al. 2006). The abundance, diversity, detectability and accessibility of invertebrates during the breeding season play a key role in avian distribution (Ambrosini et al. 2002) and reproductive success (McCarty 2001; Boatman et al. 2004; Wilson et al. 2005; Hart et al. 2006). Whilst many adult farmland birds are granivorous, the majority rely upon invertebrate food with which to sustain their young. Decreases in invertebrate detectability and accessibility may be instigated by a decrease in structural habitat diversity, combined with a corresponding increase in sward density (Vickery et al. 2001; Devereux et al. 2004): the majority of foraging within crops occurs within the tramlines, where food is more accessible and potential predators are more visible (Odderskaer et al. 1997).

Changes in invertebrate food accessibility (Barnett et al. 2004), quality or quantity are thought to be, at least in part, responsible for passerine population declines through a reduction in fledging success and resulting recruitment (Benton et al. 2002; Boatman et al. 2004; Morris et al. 2005; Hart et al. 2006) as well as a requirement for a higher adult work rate during the breeding season (Tremblay et al. 2005), likely to have implications for adult over-winter survival (Bradbury et al. 2003). The application of insecticides and pesticides during the breeding season has been directly linked to declining breeding performance in some passerine species such as Yellowhammer and Corn Bunting (Boatman et al. 2004; Morris et al. 2005; Hart et al. 2006), through a decrease in the availability of invertebrate prey (Moreby and Southway 1999); additionally, strong circumstantial evidence is present for a detrimental effect of herbicides (Boatman et al. 2004; Newton 2004). However, the population level effects of these chemicals are unknown (Boatman et al. 2004).

A decrease in breeding performance due to a reduced availability of invertebrate prey does not explain the population declines in all farmland bird species affected. For example, the breeding performance of Reed Buntings *Emberiza schoeniclus*, Turtle Doves *Streptopelia turtur*, Skylarks *Alauda arvensis*, Tree Sparrows, Yellowhammers and Corn Buntings was higher during the periods of population decline than during those of stability or increase (Peach et al. 1999; Siriwardena et al. 2000; Cornulier et al. 2009). However, the production of a larger quantity of offspring does not itself imply that fledglings are of sufficient quality to survive their first winter: over-winter survival is crucial in maintaining the populations of farmland passerines.

Over-winter food availability

The main factor thought to be driving the population changes within farmland bird species is over-winter survival (Peach et al. 1999; Siriwardena et al. 2000; Gregory et al. 2004) of both adults and fledglings due to a reduction in food availability in the non-breeding season (Greenwood 1995; Robinson and Sutherland 2002). A reduction in winter food availability has been blamed for the widespread declines of the House Sparrow *Passer domesticus*, across the south of England, due to local extinctions (Hole et al. 2002). However, there is a general dearth of research on post-fledging survival rates and the winter ecology of farmland bird species (Siriwardena et al. 2000; Atkinson et al. 2002).

Winter habitat selection by granivorous birds is largely determined by food availability (Robinson and Sutherland 1999), but differences between species are still apparent. Yellowhammers are frequently restricted to foraging close to hedgerows, whereas Skylarks often forage in the centre of fields but begin foraging closer to field margins as seed densities decline throughout the winter (Robinson and Sutherland 1999). Interestingly, in cultivated fields containing autumn-sown cereals, winter seed density declines with increasing distance from field margin; however this trend is not seen within stubble fields where seed density is relatively constant across the field (Robinson and Sutherland 1999); as such, stubble is thought critical to winter habitat selection (Mason and Macdonald 2000).

A key factor in the reduction in over-winter food availability is the loss of over-winter stubbles (Peach et al. 1999; Gillings et al. 2005) due to an increase in autumn sown crops. Stubbles are of most benefit to granivorous birds due to their provision of both spilt crop and weed seeds (Moreira et al. 2005): there is evidence suggesting that changes in winter food availability within rural landscapes have driven population changes in many species (e.g. Browne and Aebischer 2003; Robinson et al. 2005). Stubbles preceded by crops with reduced pesticide inputs are preferred by Cirl buntings *Emberiza cirlus*, implying a long-term impact of pesticide application beyond the breeding season in some species (Bradbury et al. 2008). The same principles that apply to grassland foraging also apply to stubbles, with granivorous passerines preferring to forage on plots with shorter stubble as visibility is improved and thus perceived predation risk is decreased (Whittingham et al. 2006). Birds also select seed-rich patches for foraging, emphasising both the need to grow cereal-based crops annually (Perkins et al. 2008) and the need for increased heterogeneity at the farm scale as many farmland passerines have relatively restricted ranges during the winter months (Calladine et al. 2006). Supplementary over-winter feeding has been shown to be a key factor in increasing annual fecundity in many avian species (Richner 1992; Boland et al. 1997; Nagy and Holmes 2005) with knock-on effects upon population size as a result of an increased annual recruitment either during the year of feeding (Nagy and Holmes 2005) or in subsequent years (Wernham and Bryant 1998). The now widespread availability of supplementary food in gardens is thought to be responsible for extensive population increases in many avian species (Chamberlain et al. 2005), and it has been suggested that the provision of supplementary food for farmland species at artificial feeding sites has the potential to halt, or even reverse, population declines (Siriwardena et al. 2007), although these results are not always consistent (Siriwardena and Stevens 2004). Over-winter food supplies run out at different times of year for different species, and it is thought that current management practices do not provide enough food during late winter (Siriwardena et al. 2008)

Predation

Predation risk and food availability are the two key ecological factors determining the body mass of birds (Gosler 1995; Rands and Cuthill 2001); as such the interplay between them is thought to have played a key role in farmland bird declines (Fuller et al. 1995; Siriwardena et al. 2000; Evans 2004). The pattern in predator populations is not unambiguous (reviewed in Evans 2004) and the increase in avian predators has been shown to be not directly related to passerine population declines (Thomson et al. 1998). However an increase in perceived predation risk may be more important than actual predation risk (Møller 1988; Cresswell 2008): perceived predation risk may influence survival through indirect effects; for example, when food supplies are unpredictable, decreasing body mass when predators are abundant also increases starvation risk (MacLeod et al. 2006). Birds exhibit diurnal weight gain, as predicted by mass-dependent predation, storing enough fat to survive but not enough to impede their escape from predators (Witter and Cuthill 1993; Gosler 1995; MacLeod et al. 2005). Poor foragers, and birds foraging in poor environments, tend to be of higher body mass than good foragers, or those foraging in good environments, in order to survive with an unpredictable food supply (Cresswell 2003; MacLeod et al. 2007). In some cases mass-dependent predation risk has been directly linked to population declines (MacLeod et al. 2007; MacLeod et al. 2008), and other species exhibiting population declines also respond to predation risk as if it is mass-dependent (van der Veen 1999).

An increase in the abundance of aerial predators such as the Sparrowhawk (Newton et al. 1999), again combined with a decrease in habitat complexity, may lead to an increase in perceived predation risk upon the foraging adult bird, which may in turn alter their foraging habitat choice (Rodríguez et al. 2001; Profitt et al. 2004) or foraging tactics (Barta et al. 2004). This may lead to a decrease in either foraging efficiency (Whittingham et al. 2004; Whittingham and Evans 2004) or time spent foraging when perceived predation risk is high (van der Veen 1999).

Predation is the major cause of nest failure in birds (Ricklefs 1969; Crick et al. 1994), and variation in nest predation risk can influence the reproductive success of adult birds, both directly and indirectly through changes in behaviour. The decrease in habitat complexity associated with agricultural intensification may make both nests and birds more accessible to mammalian predators as well as corvids (Whittingham and Evans 2004), which occur at high densities within agricultural landscapes (Andrén 1992) and whose populations have increased dramatically in farmland environments since the 1960s (Gregory and Marchant 1995). Corvids are considered to be the main nest predators in farmland environments (Bradbury et al. 2000): songbird nests located near to corvid nests have a higher risk of predation (Nilsson et al. 1985; Luginbuhl et al. 2001) and the abundance of breeding passerines is positively associated with corvid control measures (Stoate and Szczur 2001) with more individuals nesting in areas with a reduced risk of nest predation (Fontaine and Martin 2006); however, there is no direct evidence for the increase in corvid populations leading to an increase in nest predation (Gooch et al. 1991).

It was Skutch (1949) who first proposed that the reason for tropical birds not raising larger broods might be that an increased level of parental activity around the nest attracts the attention of predators and increases the risk of nest predation (Skutch 1949). Nest predation does, in fact, influence many aspects of breeding biology. When nesting in areas with an increased risk of nest predation, individuals will choose nest sites with more vegetation cover (Eggers et al. 2006), as less visible nests with increased vegetation cover are less likely to be depredated (Cresswell 1997; Matessi and Bogliani 1999; Pasinelli and Schiegg 2006) especially by corvids, which are visually-oriented predators (Eggers et al. 2005; Muchai and du Plessis 2005; Remes 2005). Birds may also invest less in their reproductive attempt by reducing the size of their clutch (Doligez and Clobert 2003; Eggers et al. 2006), or the size and mass of their eggs (Fontaine and Martin 2006). Behaviour during incubation is also influenced by nest predation risk: species with a higher risk of nest predation have evolved strategies to compensate for this and take fewer, longer off-nest bouts in order to reduce activity around the nest (Conway and Martin 2000). In species where females are fed by males at the nest, feeding rate increases with a reduction in nest predation risk (Ghalambour and Martin 2002; Fontaine and Martin 2006). Food availability also influences incubation behaviour, with females spending less time off the nest, and thus reducing the risk of nest predation when food is abundant (Rastogi et al. 2006).

Parental activity during chick provisioning is the main cause of activity around the nest, and can be strongly influenced by the risk of nest predation. When predator activity is high, parents reduce their provisioning rate to nestlings (Eggers et al. 2005; Fontaine and Martin 2006) as high parental activity is associated with a higher risk of predation (Martin et al. 2000). However, parents can usually compensate for this temporary reduction in provisioning rate, either by increasing provisioning rate when predators are less active (Eggers et al. 2005), or by increasing parental load (Finney et al. 2001; Eggers et al. 2008). Parents may also compensate behaviourally for poorly-concealed nests (Remes 2005), with visits to nests with low vegetation cover ceasing entirely during times of high predator activity whilst nest visits to well-concealed nests continue, albeit at a lower rate (Eggers et al. 2008). Food availability may also influence both the likelihood of predation and the ability of adults to compensate for any predator-induced reduction in provisioning rate: often other factors such as temperature may influence prey abundance (Low et al. 2008) which may limit the ability of parents to compensate for any reduction in provisioning rate during times of high predator activity. However, evidence for a reduction in provisioning rate impacting on chicks has only been found where adults reduce chick provisioning to reduce predation risk to themselves, not to their chicks (Scheuerlein and Gwinner 2006; Riou and Hamer 2008) and may in some cases result in earlier fledging (Harfenist and Ydenberg 1995). In agricultural landscapes, the reduction in food may lead to longer parental foraging trips (Brickle et al. 2000) leaving nests more vulnerable to opportunistic nest predators (Yom-Tov 1974; Komdeur and Kats 1999), and may also reduce the ability of parents to compensate for predator-induced behavioural modifications. The potential for a starvation-predation trade-off at the nest level has received little attention, and the impact of perceived predation risk upon life history factors is significant: this will be discussed in detail later.

Climate change

Not all factors adversely affecting farmland birds are directly linked to agriculture. Turtle doves have reduced in breeding range by 25% and declined in number by 70% over the past 30 years (Browne and Aebischer 2003). Climate change, in particular global warming, is thought to have led to a shortening of the breeding season for this species (Browne and Aebischer 2003). It is thought that this shortening of the breeding season, whilst inevitably reducing breeding performance, may additionally have brought the birds out of synchronisation with the peaks in abundance of food availability, thus compounding the detriment to the population (Crick et al. 1997; Browne and Aebischer 2003). This trend has also been found in the Bullfinch *Pyrrhula pyrrhula*, which was found to start laying between 17 and 18 days later in the 1990s than in the same geographical region in the 1960s (Profitt et al. 2004).

However, many other species such as the Pied Flycatcher *Ficedula hypoleuca*, have shown an advancement of laying date, thus extending their breeding season (Both and Visser 2005). This advanced laying date has been shown, in many cases, to correspond with the advancement of the food peak crucial to nestling success (Banbura 1997; Both and Visser 2005) although temperature *per se* has also been implicated as a causal factor in advancing reproduction (Stevenson and Bryant 2000). The constraints of food availability on laying date have also been shown in Blue Tits, where the timing of breeding is reliant upon the development of caterpillars, their main chick food (Nilsson 2000).

Climate effects are also important, with mean annual rainfall and mean winter soil temperature having significant effects upon first year survival rates in Lapwing *Vanellus vanellus*, (Peach et al. 1994). Rain detrimentally affects Yellowhammer nestlings (Bradbury et al. 2003) as females spend more time brooding and less time foraging with increasing rain (Johnson and Best 1982); this species is positively affected by daily hours of sunshine (Bradbury et al. 2003). Temperature also influences the survival, mass and growth of nestlings (Dawson et al. 2005) and fledglings (Greño et al. 2008) and may also affect the resources invested in reproduction (Cooper et al. 2005): for example, Great Tits *Parus major*, breeding in colder nest boxes lay smaller eggs than those breeding in warmer boxes (Nager and Van Noordwijk 1992), inevitably impacting upon the future demography of the population (Metcalfe and Monaghan 2001).

Mechanisms of declines: Life history

The fitness of an individual is measured by its ability to maintain the presence of its own genes in the population, through reproduction; life-history trade-offs occur as the result of a finite availability of resources. Firstly, some of the direct mechanisms of impact will be discussed: these are separated into summer effects during the breeding season and over-winter effects during the non-breeding season. Indirect mechanisms, such as delayed life-history effects, will then be examined

Direct summer effects

Reproductive allocation requires decisions as to the number of offspring to produce and the resources to invest in each: in birds, measurements are made in terms of clutch size, egg size and number of broods per year. Food availability is thought to be a key factor in determining resource allocation decisions (Martin 1987): some of the impacts an abundant food supply can have upon reproductive decisions are highlighted in Figure 2.

It was originally proposed that clutch size was determined by the number of young parents were capable of raising (Lack 1954); however more recent egg-addition experiments have indicated that parents are capable of raising more young than they commonly do (Monaghan and Nager 1997; Monaghan et al. 1998). It is argued that these experiments do not necessarily indicate that an individual is not maximising its fitness by raising as many young as possible (Charnov and Krebs 1974): adding 'free' eggs or young reduces the costs associated with egg laying, but may detrimentally affect the survival of both the fledged young and their female parent (Murphy 2000).

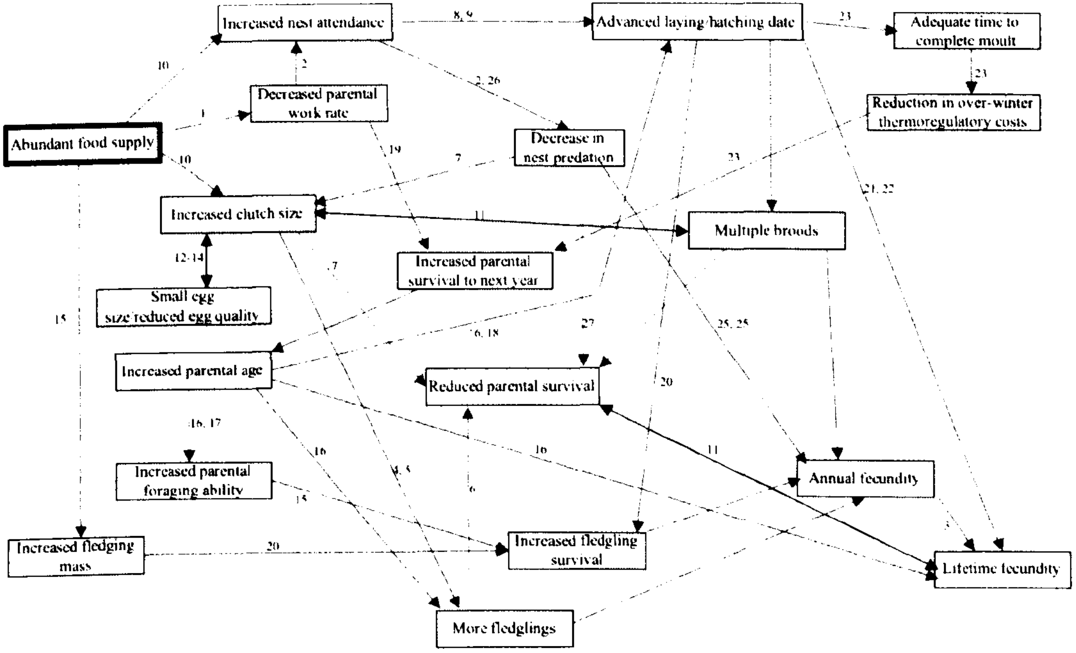

Figure 2. Illustrating some of the effects an abundant food supply can have upon avian reproductive decisions and ultimately upon lifetime fecundity. These impacts are discussed further in the text. Blue lines indicate positive effects; red lines indicate negative effects and black double arrowed lines indicate trade-offs. Numbers indicate citations: these are not meant to be exhaustive; arrows lacking citations indicate postulations. 1 Wernham and Bryant 1998; 2 Komdeur and Kats 1999; 3 Metcalfe and Monaghan 2001; 4 Monaghan and Nager 1997; 5 Monaghan et al. 1998; 6 Murphy 2000; 7 Julliard et al. 1997; 8 Svensson and Nilsson 1995; 9 Nager et al. 1997; 10 Sanz 1996; 11 Martin 1995; 12 Benton et al. 2005; 13 Pinowska et al. 2004; 14 Nager et al. 2000; 15 Davies 1987; 16 Nol and Smith 1987; 17 Ainley and Schlatter 1972; 18 De Forest and Gaston 1996; 19 Davies et al. 2005; 20 Lindén et al. 1992; 21 Verboven and Visser 1998; 22 Norris 1993; 23 Nilsson and Svensson 1996; 24 Rogers et al. 1997; 25 Ferretti et al. 2005; 26 Andersson and Wiklund 1978; 27 McCleery et al. 1996

Whilst differences in clutch size may to some extent indicate differences in parental and territory quality (Nilsson 2000) there remains a theoretical optimal clutch size which depends upon food availability (Török et al. 2004). However this optimal clutch size is rarely seen despite the implications for future reproductive potential (Török et al. 2004). It is thought this is because food availability largely constrains reproductive success (Martin 1987) and females cannot predict food availability at the start of the breeding season; thus in years where food availability is high, fewer than optimal young are raised (Török et al. 2004) although this may be disputed in Tree Sparrows, which exhibit an increased clutch size with an increase in food availability (Anderson 1977). In this species, however, an increase in breeding density is associated with a reduction in average clutch size, potentially as a result of increased competition for available food resources (Anderson 1977). Increasing clutch size initiates other trade-offs: for example as clutch size increases, so does parental work-rate; however each nestling receives a reduced food load (Stoehr et al. 2001) leading to a slower growth rate and a lower fledging mass (Wright et al. 1998). Interestingly, a reduced clutch size appears to increase adult survival, emphasising the costs of reproduction (Julliard et al. 1997).

Many avian species exhibit hatching asynchrony, thought to be a mechanism of clutch size optimisation according to available food resources (Magrath 1989): when food is scarce asynchronous broods have shown to be more productive (Magrath 1989; Forbes et al. 2002). An abundant food supply may also increase levels of hatching asynchrony (Eikenaar et al. 2003); whilst this is nearly always detrimental to the last hatched young this may be partially compensated for by an increased egg size increasing the survival chance of the last hatched young (Rosivall et al. 2005). In species that usually only fledge one chick, the second chick is thought to act as insurance (Humphries et al. 2006). An abundant food supply prior to and during incubation has been shown experimentally to advance both laying date (Svensson and Nilsson 1995; Nager et al. 1997) and hatching date in some species through an increased nest attendance (Sanz 1996); in others an increase in food availability increases egg size (Wiebe and Bortolotti 1995) and clutch size (Nager et al. 1997); however there appears to be no long-term influence upon fledging success (Svensson and Nilsson 1995). Extra food supplied to nestlings does not positively influence their own fledging success, but increases the fledging success and body condition of their siblings the next year through a reduced parental work rate (Wernham and Bryant 1998), although the parents themselves are unaffected in terms of body condition (Wernham and Bryant 1998).

Clutch size is inversely related to the number of broods per year (Martin 1995): whilst it has been proposed that this is due to an energy trade-off limiting total egg production (Martin 1995) it now appears that it is not the biosynthetic cost of egg production *per se* that limits clutch size, but the necessity of timing the onset of reproduction so that peak food demands from chicks coincide with peak food availability (Nilsson and Råberg 2001). It has been shown in soil mites that a trade-off exists between female fecundity and the per-egg provisioning of protein (Benton et al. 2005); this has also been demonstrated in Tree Sparrows where large eggs are thought to contain more vitamins, hormones, anti-oxidants and microelements (Pinowska et al. 2004) and in gulls where as the clutch size grows beyond three the proportions of lipid and water within the egg decrease and increase respectively (Nager et al. 2000).

Egg size is thought to reflect parental quality of both sexes (Amundsen and Stokland 1990), with females in good body condition tending to lay larger eggs (Wiebe and Bortolotti 1995). Egg volume largely determines chick weight at hatching (Schifferli 1973; Furness 1983) and a positive correlation is generally found between egg size and nestling growth and survival (e.g. Furness 1983; Wiebe and Bortolotti 1995; Pinowska et al. 2004). However, this effect decreases with increasing nestling age (Smith and Bruun 1998): for many species this is thought to be a reflection of egg size *per se* as opposed to an effect of parental quality directly (Furness 1983; Amundsen and Stokland 1990; Wiebe and Bortolotti 1995). However, as chick growth rate is also correlated with food provisioning levels (Barlow and Croxall 2002; Takahashi et al. 2003; Tobón and Osorno 2006) adults may potentially invest more effort in chicks from larger eggs (Lorentsen 1996). However, parental quality has a marked effect upon nestling condition and fledging success through provisioning rate (Davies 1986) and parental effort during the chick-rearing period is regulated by parental body condition (Lorentsen 1996).

The majority of farmland passerines are multi-brooded: in such birds, trade-offs have been exhibited between broods within the same year. For example, Song Sparrows *Melospiza melodia*, with successful first broods raised fewer young in later broods (Nol and Smith 1987); supplementary feeding increased the number of breeding attempts (Arcese and Smith 1988). In Tree Sparrows, not all pairs lay a third brood; those females that do have generally reared fewer young in their first two broods and are also heavier than females who have raised many young in their first two broods (Sasvári and Hegyi 1994).

Direct winter effects

Parental age is considered important in terms of chick survival: young birds in general do not have sufficient foraging skills to sustain both themselves and a chick (Orians 1969; Recher and Recher 1969; Ainley and Schlatter 1972; Desrochers 1992; Forslund and Pärt 1995; De Forest and Gaston 1996; Espie et al. 2000): this phenomenon relates mainly to foraging ability as chick mass is related to parental age and not to previous reproductive experience (Ainley and Schlatter 1972; Nol and Smith 1987) and is independent of confounding environmental effects (Daunt et al. 1999). First time breeders also have higher baseline levels of corticosterone than older breeding birds, indicating increased stress and depleted body reserves as a consequence of reduced foraging abilities (Angelier et al. 2007). Parental age is positively related to egg size (Furness 1983), clutch size (Desrochers and Magrath 1993) and both mass and number of chicks (Ainley and Schlatter 1972). Older birds tend to have more successful breeding attempts per season and thus raise more young to fledging (Nol and Smith 1987).

In some long lived avian species such as petrels, any detriment in environmental conditions which may lead the parent to work harder in order to supply the same amount of food to the young, impacts detrimentally upon the chick instead of the parent (Mauck and Grubb 1995): this has also been shown to be the case in Pied Flycatchers (Moreno et al. 1999). Females forced experimentally to invest more in reproduction one year were consistently less likely to breed during the next year (Nager et al. 2001): however it is generally thought that long-lived species may reduce their investment in their offspring during a sub-optimal year, instead of compromising their future reproductive success (Wernham and Bryant 1998; Croll et al. 2006). Birds are also likely to invest more in, or take more risks for chicks that are in good condition (Rytkönen et al. 1995; Riou and Hamer 2008), with these young being more likely to subsequently recruit into the breeding population (Rytkönen et al. 1995).

Food availability has a profound impact upon reproductive success, through increasing parental provisioning rate and consequently chick growth (Tobón and Osorno 2006): supplementary food can influence the numbers of fledglings per brood (Wiehn and

Korpimäki 1997) and nestlings with a poor food supply in the nest tend to reach a lower mass and size than those with unlimited food (Richner et al. 1989); immune function and subsequent survival may also be lower for birds fed a poor diet as nestlings (Birkhead et al. 1999). Whilst nestlings can compensate to some extent for periods of reduced growth by either catch-up growth (Nilsson and Svensson 1996; Hegyi and Török 2007), delayed fledging (Bize et al. 2003), or both (Bize et al. 2006), catch-up growth inevitably involves accelerated growth of certain body structures at a cost to others (Bize et al. 2006), with long-term implications for survival (Metcalfe and Monaghan 2001).

Early developmental conditions impact upon an individual later in life (Lindström 1999; McCarty 2001; Beckerman et al. 2002; Lummaa and Clutton-Brock 2002; Beckerman et al. 2003), for example through a reduced lifespan and consequently a reduced reproductive output (Birkhead et al. 1999; Metcalfe and Monaghan 2001). This occurs even if conditions in adulthood are beneficial: key reproductive traits are determined by juvenile growth conditions (Taborsky 2006). If resources are unpredictable it may therefore be beneficial for individuals to jeopardise their future reproductive success by investing highly in the current brood (Davies et al. 2005). This may have implications for farmland passerines through applications of pesticides throughout the breeding season and the unpredictability of nest predator abundance, combined with other factors that create unpredictability in insect availability and potentially impact significantly upon future population success.

Factors influencing fledgling survival appear to vary between species: for example, in Collared Flycatchers *Ficedula albicollis*, fledging mass appears most important for juvenile survival (Lindén et al. 1992), whereas in Great Tits other factors such as hatching date are also influential (Lindén et al. 1992). The proportion of large food loads provided to Corn Buntings is positively associated with fledging success, whereas parental work rate *per se* is unrelated (Hartley and Shepherd 1994). In some species such as the Spotted Flycatcher *Muscicapa striata*, it is thought that a reduced survival in the first year of life is largely responsible for their population declines (Freeman and Crick 2003); however this species is also affected by factors on migration and at its wintering grounds (Kirby et al. 2005).

Hatching date is a key factor in survival and future reproductive success in some species: young fledged earlier in the season have a greater probability of surviving and being recruited into the breeding population (Norris 1993; Verboven and Visser 1998). However, in males there is a further impact upon future success in individuals fledging late and surviving over-winter: these individuals produce fewer offspring in their first year of breeding (Visser and Verboven 1999), having a detrimental effect upon their lifetime reproductive success; this effect was not evident in females (Visser and Verboven 1999). Despite this there appears to be no evidence that birds compensate for this by producing a higher proportion of female offspring later in the season.

The provision of supplementary food leads to an advancement of laying date in many species (Källander 1974; Arcese and Smith 1988) suggesting that food availability may be a limiting factor in determining optimal laying date: this is supported by the fact that laying date was only affected in individuals with lower quality territories; in high quality territories where food was sufficient, laying date was not affected (Svensson and Nilsson 1995). However age or experience may also be a factor: older birds frequently begin breeding earlier than younger birds (Nol and Smith 1987; Desrochers and Magrath 1993; De Forest and Gaston 1996; Cabezas-Diaz et al. 2005). The mechanism behind laying date may be related to the timing of moult: delayed breeding is thought to constrain moulting in adults so that the feathers produced have a lower insulating capacity (Nilsson and Svensson 1996). These birds incur greater thermoregulatory costs over winter and their future reproductive success may also be affected (Nilsson and Svensson 1996).

Between species, adult longevity is strongly inversely related to adult fecundity (Martin 1995), the general rule being that species producing many young quickly will die sooner. This can be seen at lesser extremes within avian species (Davies et al. 2005) and trade-offs between adult fecundity and survival are thought to be due to food limitation (Martin 1995)

Indirect effects

The trade-off between predation and starvation is a crucial life history trade-off: in birds, predation may take the form of either nest predation, or predation on foraging adults. Under non-breeding conditions small passerines may be expected to minimise the amount of time spent carrying costly food reserves that might reduce their chance of escape if attacked by a predator (Rands and Cuthill 2001). However, conditions of food availability are not always predictable, and so food resources must often be taken when available (Rands and Cuthill 2001): within a predictable environment birds spend more time feeding in the afternoon to gain enough food supplies to enable them to survive overnight (Olsson et al. 2000). Food availability can influence predation risk indirectly in flocking birds, where interference competition for food can increase the risk of predation through increased movement of foraging birds (Minderman et al. 2006); the detectability of food also interacts with predation risk (through habitat structure), with birds more willing to feed on more obvious prey under higher predation risk (Jones et al. 2006). Perceived predation risk on foraging adults is also important: if perceived predation risk is high, due to either a higher predator density or a visually obstructive foraging habitat, scanning rate will increase (Whittingham et al. 2004) and body mass may decrease accordingly (Lilliendahl 1997). However, foraging and vigilance are not necessarily mutually exclusive: feeding rate in Chaffinches has been shown to partially determine vigilance (Cresswell et al. 2003). As perceived predation risk may be altered by changes in habitat structure (Hinsley and Bellamy 2000; Evans 2004), the effects of agricultural intensification are likely to have had an impact upon farmland bird populations through an increase in perceived predation risk (Fuller et al. 1995; Evans 2004).

Whilst it has long been known that predation is a key factor in shaping life history, the importance of the sub-lethal effects of predation have only relatively recently been realised (Krebs et al. 1995; Boonstra et al. 1998; Beckerman et al. 2002; Zanette et al. 2003; Clinchy et al. 2004). Predation risk can cause chronic stress, impacting on both reproductive success and long-term population dynamics (Hik 1995; Krebs et al. 1995; Boonstra et al. 1998) and may have a detrimental impact upon the foraging behaviour of animals (Beckerman et al. 1997). Low food availability has been linked to high baseline levels of corticosterone, the stress hormone (Kitaysky et al. 1999) and in many species, predation pressure and lack of food can act synergistically to induce chronic stress, with its associated consequences (Krebs et al. 1995; Karels et al. 2000; Zanette et al. 2003; Clinchy et al. 2004; Sih et al. 2004). Ground Squirrels, *Spermophilus parryii plesius*, (Karels et al. 2000) and Song Sparrows (Zanette et al. 2003) exposed to a reduced predation pressure double their population density and produce another 1.3 young respectively and, when given additional food, increase population density 4 – 7 fold and produce another 1.1 young respectively (Karels et al. 2000; Zanette et al.

2003). However, when exposed to a combination of additional food and reduced predation pressure, Ground Squirrels increased their population density 19 fold (Karels et al. 2000) and Song Sparrows raised an extra 4 young (Zanette et al. 2003).

Nest predation has a significant influence upon the evolution of life histories (Martin and Clobert 1996) and commonly accounts for the majority of all nest failures (Wilson et al. 1997; Zanette and Jenkins 2000; Brickle and Peach 2004). Whilst the factors affecting nest predation rates are diverse (Weidinger 2002), habitat simplification may make nests more conspicuous, and nest predation has been found to increase with the proportion of agricultural land in the surrounding landscape (Tewksbury et al. 2006): it has been suggested that the management of landscapes may decrease the impact of predation (Schneider 2001). High levels of nest predation may create demographic sinks, where the population is reliant upon immigration in order to maintain itself: this may contribute significantly to long term population declines (Rogers et al. 1997). In life-history terms, nest predation is thought more important in determining clutch size, parental incubation rate and nestling growth rate than food availability (Ferretti et al. 2005). If a nest is predated it may be beneficial to lay a repeat clutch; however, as predation risk is high fewer eggs may be preferable (Julliard et al. 1997; Nilsson 2000) as less foraging effort would be required to sustain the nestlings leaving more time to defend the nest (Komdeur and Kats 1999; Schmidt and Whelan 2005). In addition, the lower food requirements of a smaller brood are less likely to attract the attention of a visually oriented nest predator (Martin et al. 2000; Eggers et al. 2005; Fontaine and Martin 2006). Interestingly, individuals not themselves subject to nest predation also exhibit a reduced clutch size, emphasising the importance of perceived risk (Julliard et al. 1997).

Whilst investing more time in nest defence may be a logical strategy when the risk of nest predation is high (Andersson and Wiklund 1978; Komdeur and Kats 1999), it is only practical against certain predators, such as corvids, and not against rodents (Schmidt and Whelan 2005). This is supported by evidence that larger species with conspicuous nests, which are more likely to be predated by corvids, are likely to expend more energy in nest defence than smaller species with better concealed nests, which are more likely to be predated by rodents (Weidinger 2002). There is evidence that corvid predators may utilise parental activity to locate nests (Eggers et al. 2005; Muchai and du Plessis 2005), increasing the risk to eggs and nestlings in areas of high nest predation

(Eggers et al. 2005). Some species have been shown to alter their foraging behaviour in areas of high nest predation in order to reduce adult activity around the nest at times of high predator activity (Eggers et al. 2005), whereas other species increase their guarding activity at times of peak predator activity (Sasvári and Hegyi 2000).

Logic may suggest that birds suffering high levels of nest predation might be more stressed than those whose nests remain unpredated (Scheuerlein et al. 2001); as such it may be thought that their life expectancy would be relatively short. Conversely, a study of Great Tits showed that adults with nests that suffered a high predation rate were more likely to survive longer when compared to adults with nests suffering a low predation rate (McCleery et al. 1996). This is thought to be due to a reduction in reproductive investment in terms of competition and foraging effort (McCleery et al. 1996). This phenomenon particularly affected females, with female survival showing a strong relationship with the number of successful breeding attempts, indicating that egg-laying may not be as restrictive a physiological limitation in breeding as raising the young once hatched (McCleery et al. 1996). This concurs with metabolic evidence which indicates that the biosynthetic cost of egg production does not limit clutch size (Nilsson and Råberg 2001). It is however thought likely that there is a ceiling to adult energy expenditure whilst chicks are in the nest as a reduction in brood size corresponds to a reduction in adult work rate; however the converse is not true (Tinbergen and Verhulst 2000).

A recent study (Descamps et al. 2009) indicates that reproductive costs may be higher when another stress-inducing factor is present; in the case of this study the stress-inducing factor is a virulent disease which, when present, lowers survival of females with large clutches (Descamps et al. 2009). This concurs with the observations of Sih et al (2004), that two stress-inducing factors can act synergistically to amplify the effects of either one (Sih et al. 2004), whilst also highlighting the importance of disease, both clinical and sub-clinical, in influencing avian populations.

The status of disease in avian populations, and mortality caused thereby, is largely unknown owing to the difficulties associated with finding carcasses before their removal by predators or scavengers (Prosser et al. 2008). However, parasitic diseases such as avian malaria are known to be present in many avian populations at high prevalence worldwide but at sub-clinical levels (Valkiunas 2005). Whilst sub-clinical parasitism on its own is known to be associated with increased corticosterone levels (Applegate 1970), but may have relatively minor implications for hosts in terms of host fitness and behaviour (Sundberg 1995; Moore 2002), when combined with other factors such as reduced food availability and increased predation risk, it may have synergistic effects (Sih et al. 2004). The status and potential consequences of blood parasites for fitness in farmland bird populations in Britain are unknown.

Mitigating the Effects of Environmental Change

As the intensification of farming is thought to be mainly responsible for farmland bird declines it is widely accepted that farmland management practices are capable of reversing these declines (Green and Stowe 1993; Stowe et al. 1993; Ormerod and Watkinson 2000; Wolff et al. 2001). Even species such as Bullfinch and Reed Bunting, which are only reliant upon farmland for certain aspects of their life history, are thought to be able to benefit from a more sympathetic management approach on agricultural land (Gregory and Baillie 1998). This has resulted in the introduction of several government schemes, the most recent of which: the Countryside Stewardship Scheme and the Environmental Stewardship Scheme; were introduced in 2002 and 2005 respectively and are thought to provide an optimistic outlook for declining avian farmland species (Smallshire et al. 2004) such as the Cirl Bunting (Peach et al. 2001). These schemes provide financial benefits for farmers who manage their land responsibly in wildlife terms (Defra 2005). Options under the schemes include the provision of beetle banks, over-winter stubbles, buffer strips and other features contributing towards an increased farm-level biodiversity (Smallshire et al. 2004), although an increase in overall biodiversity does not necessarily bring benefits for endangered species (Kleijn et al. 2006) and some options show benefits at the field scale but not the farm scale (Stevens and Bradbury 2006). Of these options, many have proven beneficial to biodiversity in terms of invertebrates (Collins et al. 2003) and consequently vertebrates (Vickery et al. 2002; Holland 2004). However, the recent abolition of compulsory set-aside by the EU (Defra 2009) has the potential to reverse the positive effects of these schemes.

Margin management

Favourable management of natural aspects of farmland such as hedgerows and riparian strips in order to increase structural and spatial complexity may be crucial in terms of both increasing invertebrate abundance and diversity and reducing predation rates on farmland birds (Hinsley and Bellamy 2000). Both the size of hedgerows and the presence of trees are positively associated with a greater diversity and abundance of farmland birds (Hinsley and Bellamy 2000; Deschênes et al. 2003) and an increase in hedgerow complexity is likely to reduce the visibility of nests to predators. Reducing pesticide drift may have a crucial effect upon the density of invertebrates such as phytophagous insects within field margins (de Snoo 1999), with a consequential impact upon farmland bird populations through an increase in food supply. Leaving three metre buffer zones unsprayed around the edge of a crop has been shown to be effective at reducing pesticide drift (de Snoo 1999) and is thought unlikely to affect weed levels within the crop (Smith et al. 1999). Similarly, leaving a margin uncropped has incontrovertible benefits for invertebrate biodiversity (Thomas and Marshall 1999; Meek et al. 2002; Marshall et al. 2006): whilst the composition of the margin differentially affects the invertebrate community composition, cropped margins consistently have a lower biodiversity than any alternative margin treatment (Thomas and Marshall 1999; Meek et al. 2002). The presence of hedgerows and grass margins allows the recolonisation of cropped habitats by invertebrates following spraying (Alvarez et al. 2000) and are a preferred foraging habitat for declining species such as the yellowhammer (Perkins et al. 2002; Douglas et al. 2009). The best options in terms of providing summer avian food supplies appear to come from grass or wildflower strips, uncropped wildlife strips and rotational set-aside strips, as well as conservation headlands (Vickery et al. 2002); all of these options increase biodiversity by providing a diverse sward.

Beetle banks have been shown to be important over-wintering refuges for a wide variety of invertebrates (Collins et al. 2003), the densities of which have been shown to increase over successive winters, resulting in higher invertebrate densities in beetle banks than in field margins (MacLeod et al. 2004). Uncut margins of silage fields have also been shown to increase the diversity of invertebrates (Haysom et al. 2004), several of which form important components of chick-diet for farmland bird species (Hartley and Quicke 1994; Brickle and Harper 1999). Increasing the abundance of invertebrates crucial to the reproductive success of granivorous passerines is likely to have significant beneficial impacts upon farmland bird populations (Douglas et al. 2009), as well as farmland biodiversity as a whole.

Stubble and tillage

The manipulation of tillage systems may also benefit birds, through an increased accessibility of seed resources (Cunningham et al. 2004; Holland 2004). Non-inversion tillage, or conservation tillage, involves disturbing the surface of the soil whilst leaving a high proportion of the previous year's stubble at the soil surface (McLaughlin and Mineau 1995; Cunningham et al. 2004). Whilst the increased availability and accessibility of weed seeds and crop residues is unequivocal (McLaughlin and Mineau 1995; Cunningham et al. 2004; Holland 2004), the benefits in terms of invertebrate availability are less clear and non-inversion tillage may be only marginally beneficial when compared to more traditional tillage systems (McLaughlin and Mineau 1995; Kromp 1999; Cunningham et al. 2004). The response of bird species to management depends on both their diet and habitat specialisation (Ondine et al. 2009) and farmland specialists tend to do better on conventionally managed farms when compared to farms with conservation tillage (Ondine et al. 2009)

The loss of over-winter stubbles is thought to be a key factor in the reduction in winter food availability for granivorous passerines (Peach et al. 1999; Mason and Macdonald 2000; Gillings et al. 2005) and even where stubbles are available they are thought insufficient to support avian populations during late winter (Siriwardena et al. 2008). The most beneficial stubbles for the majority of granivorous birds are those with a relatively sparse stubble and significant areas of bare ground (Moorcroft et al. 2002; Butler et al. 2005) which allow a higher visibility of predators and accessibility of food (Butler et al. 2005). Skylark and partridges, however, prefer taller stubble: increasing the structural heterogeneity of available stubble is therefore thought to improve its value as foraging habitat (Butler et al. 2005) with beneficial knock-on effects upon the over-winter survival of farmland birds and consequently population size (e.g. Peach et al. 1999; Siriwardena et al. 2007).

Set-aside and game cover crops

Winter food supplies for granivorous birds may be provided through naturally regenerated rotational set-aside strips and game cover crops (Vickery et al. 2002); these encourage significantly higher densities of insectivorous and granivorous passerines, as well as gamebirds, than are found on conventionally farmed crops (Henderson et al. 2000; Henderson et al. 2004; Parish and Sotherton 2004).

Game cover crops may consist of a variety of species, including kale, quinoa, sunflower, phacelia and buckwheat. These provide significantly higher densities of both weed seeds and invertebrates than conventional crops (Parish and Sotherton 2004) and attract the highest densities of birds in grassland regions where they increase the heterogeneity of the landscape more than in arable regions (Parish and Sotherton 2008). However, alternative compositions of these crops benefit different bird species, with quinoa being used by Tree Sparrows and finches, seeded cereals supporting high bunting densities and kale supporting the highest avian species richness (Henderson et al. 2004). It is thought that even relatively small areas of game cover crop would be beneficial to bird populations through a greater over-winter food availability (Henderson et al. 2004; Stoate et al. 2004) leading to a increased survival to the next breeding season (e.g. Siriwardena et al. 2000).

Set-aside is a vital aspect in increasing farmland biodiversity (Van Buskirk and Willi 2004) and may be an important factor in reversing farmland bird declines (Poulsen et al. 1998; Sotherton 1998), although the percentage of land now required to be left as set-aside in the UK was reduced to 0% in 2008 (Defra 2009). The location of set-aside is an important factor in determining the selection of summer territories in some species such as the yellowhammer (Whittingham et al. 2005). It is important as a foraging habitat for many species as in most cases it is preferred to cereal crops (Chamberlain et al. 1999) owing to the abundance of invertebrates on set-aside habitat (Wilkin 2003; Bright 2004); however correct management of set-aside land is crucial in order for its value to be realised (Poulsen et al. 1998; Sotherton 1998). Skylark breeding success, in terms of both number of fledglings per hectare and the density of successful nests, is considerably higher in set-aside than in other cereal crops as breeding often starts earlier (Poulsen et al. 1998), with implications both for annual fecundity, parental survival and ultimately population size. Research is needed to establish the magnitude of the detriment to farmland bird populations of the loss of set-aside in the landscape (Risely et al. 2009).

Organic farming

Organic farming is widely heralded as the solution to the loss of biodiversity precipitated by the intensification of agriculture (Fuller et al. 2005; Hole et al. 2005); instead of regulation via conventional pesticides, organic farming relies on an internal regulation through functional agrobiodiversity (Altieri 1999): this works by increasing the biodiversity of the agricultural landscape in order to reduce the impact of crop pests specific to any one crop (Altieri 1999; Roschewitz et al. 2005). Practically, there are three main organic management practices: a preservation of mixed farming and a corresponding increase in habitat heterogeneity; sympathetic management of non-cropped habitats; and a significant reduction in the use of inorganic pesticides and fertilisers (Hole et al. 2005).

Organic farming appears to be effective in increasing biodiversity throughout all trophic levels, through an increase in both abundance and species richness of organisms (Feber et al. 1997; Beecher et al. 2002; Hutton and Giller 2003; Bengtsson et al. 2005; Fuller et al. 2005). Whilst the scales of response vary between taxa (Fuller et al. 2005), it remains unclear at which spatial scales organic management is important, and whether organic patches of habitat within a conventional farm are any less beneficial than a whole farm organic regime (Hole et al. 2005). Indeed it is thought that the variation across taxa found by Fuller *et al.* (2005) is likely to be a result of isolation: this recent study concluded that the extension of organic farming would be a step towards the restoration of biodiversity (Fuller et al. 2005).

Organically farmed fields have been shown to support a higher proportion of weeds beneficial to farmland birds (Moreby et al. 1994) along with higher densities of invertebrates such as spiders (Moreby et al. 1994), important components of chick diet in many granivorous passerine species (Brickle and Harper 1999; Cummins et al. 2000; Orszaghova et al. 2002). As a result, farmland birds appear to prefer organic farmland to conventional, as shown by the presence of a greater abundance and diversity of birds on organic when compared to non-organic farms (Beecher et al. 2002; Fuller et al. 2005; Mackenzie and Whittingham 2009): in one study no bird species was found to be more abundant on a conventional than an organic farm (Beecher et al. 2002). Organically farmed arable has also been shown to be preferred to conventionally farmed crops by some declining farmland species such as the Skylark (Wilson et al. 1997). However other studies have shown less striking results: in southern Britain, few significant differences were found in bird densities between organic and conventional farms outside of the breeding season (Chamberlain et al. 1999), although organic field boundaries supported a higher density of 8 out of 18 bird species (Chamberlain et al. 1999), and Piha et al. (2007) found that organic farming influenced neither bird density nor species richness (Piha et al. 2007).

Whilst organic farming practices clearly have beneficial effects upon farmland wildlife (but see also Kragten and de Snoo 2007) it is considered likely that these stem from the lower intensity agricultural practices and increased habitat diversity rather than any specific features of organic farming (Krebs et al. 1999; Mackenzie and Whittingham 2009): indeed organic farming does not appear to be beneficial in an already heterogeneous landscape (Piha et al. 2007). However, there remains little doubt that both organic farming and the Stewardship Schemes are beneficial to farmland bird diversity, through an increased availability of habitat and food for farmland birds and their young both during the breeding season and over-winter.

Conclusion and Introduction to Thesis

The catastrophic declines in farmland bird populations over the past 35 years are unlikely to be due only to the direct effects of agricultural intensification. As habitat and food availability have been modified, so farmland bird species have had to modify various aspects of their life history, leading to reductions in fledging success, over-winter survival and ultimately population size. The impact of both adult predation and nest predation, again due to changes in habitat structure and food supply, as well as increases in some species of predator, may have been overlooked; however, this review emphasises the impact of these factors upon interlinked aspects of farmland bird life-history. Government schemes and changes in farming practice recommended to increase farmland biodiversity are likely to benefit farmland bird populations through an increase in summer and winter food availability combined with a reduced risk of predation; however these may need to be extensively taken up before widespread benefits can be visualised.

The aims of this thesis are to address some of the gaps in knowledge highlighted by this review, using the declining Yellowhammer *Emberiza citrinella* as a focal study species. Chapter 2 investigates broad aspects of nesting ecology, foraging ecology and chick life history in this species, including whether nesting habitat may have changed in response to habitat changes induced by agricultural intensification, and which factors may influence the choice of foraging site by adults foraging for chicks. Chapter 3 asks whether independent stress-inducing factors such as reduced chick food availability and increased nest predation risk can act synergistically at the nest level to influence chick condition and growth through changing parental foraging behaviour. Chapter 4 explores whether territory density, at three different scales, influences parental behaviour or chick growth and whether density dependence may be important in declining populations through clustering of territories in fewer, high quality, habitat patches. Chapter 5 investigates whether parents react differently to various factors influencing nesting ecology and considers sex differences in time budgets during chick provisioning. Chapter 6 describes the results of an exploratory study into the potential effects of sub-clinical disease in Yellowhammer populations, through an investigation of blood parasite prevalence, identity, and association with morphological variables during the winter months. Finally, Chapter 7 uses mark-recapture data to examine factors influencing survival in this species and Chapter 8 summarises the conclusions of the thesis.

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Chapter 2: Nesting and foraging ecology of yellowhammers *Emberiza citrinella*

Abstract

Yellowhammer nesting and foraging ecology were investigated during the breeding seasons of 2006 – 2008. Yellowhammers nested most frequently in hedgerows, with some nests also found in herbaceous vegetation. Mean clutch size was similar to that found in other studies, as was mean fledgling number per successful nest. The percentage of nests successfully fledging at least one chick was similar to both recent (2000) and historic (1960) studies, indicating no evidence of any change in fledging success since the start of the yellowhammer population decline. Predation accounted for the majority of nest failures, followed by abandonment and whole-brood starvation. Mean nest height was significantly greater than that of a study in 1960, being nearly double in the current study: this may indicate either changes in nest site selection or differences in the availability or structure of suitable nesting habitat (nests in vegetated ditches are under-represented in the current dataset). No hedgerow features differed between nest site locations and randomly selected sites within the same territory, indicating that the selection of a territory containing high quality nesting habitat is more important than small-scale habitat selection for nest sites, which is more likely to depend on local habitat features such a suitable support structure in an area of high vegetation cover. When compared with control sites within a similar microhabitat, foraging sites did not differ in terms of vegetation height, density, cover or invertebrate abundance. However, foraging sites had a lower vegetation density, as well as a higher invertebrate abundance at higher vegetation densities than did control sites within a different habitat, indicating that foraging sites are selected according to a vegetation structure that allows a greater accessibility to invertebrates, and that where accessibility at foraging sites is lower and may incur a greater predation risk (through a reduced visibility of predators at higher vegetation densities), there is a payoff in terms of increased invertebrate availability. Parental provisioning rate decreased with increasing vegetation cover at foraging sites in areas of high invertebrate abundance, probably due to an increased amount of time spent scanning for predators; conversely where invertebrate abundance was low, provisioning rate increased with increasing vegetation cover, probably due to a positive correlation between vegetation cover and invertebrate abundance, and suggesting that adults in low food environments may be forced to take more risks when foraging for food for their young.

Introduction

Populations of farmland birds have been declining in recent years due to aspects of farmland management associated with agricultural intensification (e.g. Fuller et al. 1995; Chamberlain and Fuller 2000). The majority of these declines began in the mid to late 1970s (Fuller et al. 1995) but that of one species, the Yellowhammer, is unique (Bradbury and Stoate 1999). This species apparently did not begin its decline until the late 1980s (Kyrkos et al. 1998) but since then it has undergone an estimated population reduction of 54% (Eaton et al. 2008). Unlike populations of many other farmland birds whose populations have now begun to stabilise, yellowhammer populations remain in decline (Eaton et al. 2008).

Nesting habitat appears to be a factor limiting Yellowhammer populations, with population density strongly associated with the densities of hedgerows and vegetated ditches (Kyrkos et al. 1998; Bradbury et al. 2000; Stoate and Szczur 2001; Whittingham et al. 2005). Nests tend to be built in herbaceous vegetation in ditches, or in the base of hedgerows (Bradbury et al. 2000), although Yellowhammer nests in hedges are more susceptible to predation than those in herbaceous vegetation (Stoate and Szczur 2001). Generally, nests with higher levels of vegetation cover are less susceptible to predation by visually-oriented predators such as corvids (e.g. Cresswell 1997; Eggers et al. 2006), which are the main nest predators of birds in the agricultural landscape (Andrén 1992) and also the main nest predator of the Yellowhammer (Bradbury et al. 2000). Depredation is the main cause of nest failure in many farmland species, including the Yellowhammer (Bradbury et al. 2003) and the Reed Bunting (Brickle and Peach 2004).

Yellowhammer breeding population density increases with the proportion of land growing cereals and with increasing crop diversity (Kyrkos et al. 1998). This is likely to be linked to foraging requirements during the breeding season: whilst adult yellowhammers are granivorous, all chicks are fed invertebrates as well as unripe cereal grain (Stoate et al. 1998). Nestling mortality has been linked to weather variables such as cold temperatures and increased rainfall that decrease both numbers and activity levels of invertebrates (Stoate et al. 1998; Bradbury et al. 2003) and a reduction in the growth and body condition of chicks, as well as an increase in brood reduction, has been linked to the use of pesticides during the breeding season, through a decrease in invertebrate populations (Morris et al. 2005; Hart et al. 2006). Habitat type and structure can also influence the availability of invertebrates to foraging birds: grass margins, hedges and ditches are selected over cropped areas for foraging (Perkins et al. 2002). Within cropped areas, broad-leaved crops and bare ground are favoured, with cereal crops being utilised more often as the cereals ripen (Stoate et al. 1998; Morris et al. 2001) and non-cropped habitats increase in vegetation density, reducing invertebrate accessibility (Douglas et al. 2009).

An interaction between food abundance and accessibility in predicting foraging site suitability, mediated by habitat structure, was proposed by Morris et al. (2001). Whilst Perkins et al. (2002) found no difference in the use of cut and uncut margin patches for foraging, their sample size was small and they suggest that an interaction between prey abundance and accessibility may explain their observations (Perkins et al. 2002). In a larger scale study, Douglas et al. (2009) found cut margins to be used more often than uncut margins by foraging Yellowhammers, indicating that accessibility to prey plays a large part in determining the selection of foraging habitats (Douglas et al. 2009). Predation risk to foraging adults may also play a part in habitat selection: Yellowhammers are sensitive to perceived predation risk (van der Veen 1999) and time exposed to predators is thought more important to survival than an adaptive reduction in body mass to reduce predation risk for this species (van der Veen 1999). Thus, the choice of foraging habitat may be influenced by perceived predation risk mediated by habitat structure (Whittingham et al. 2004; Whittingham and Evans 2004; Whittingham et al. 2006) as well as through food abundance and accessibility.

Neither the abundance of nesting habitat, nor the availability of foraging habitat are sufficient to explain Yellowhammer population declines in areas where cereal cultivation remains predominant (Kyrkos et al. 1998). A study by Whittingham et al. (2005) indicates that winter habitats are important in predicting where birds will locate summer breeding territories, and that the presence of set-aside fields is particularly important (Whittingham et al. 2005). It remains to be seen what effect the reduction in set-aside abundance (Langton 2008) as a result of the lowering of the percentage of compulsory set-aside to 0% in 2008 will have on Yellowhammer populations.

This chapter aims to address some key gaps in knowledge of Yellowhammer nesting and foraging ecology. Firstly, nesting ecology and nest-site selection at the within-hedgerow scale will be examined to determine whether specific microhabitats within a hedge are selected for nesting, and by comparison of nest height data with data from

1960 (Peakall 1960), the possibility that changes in nesting ecology have occurred concurrently with yellowhammer population declines will be examined. Other factors influencing nest survival and fledging success are explored further in Chapter 4.

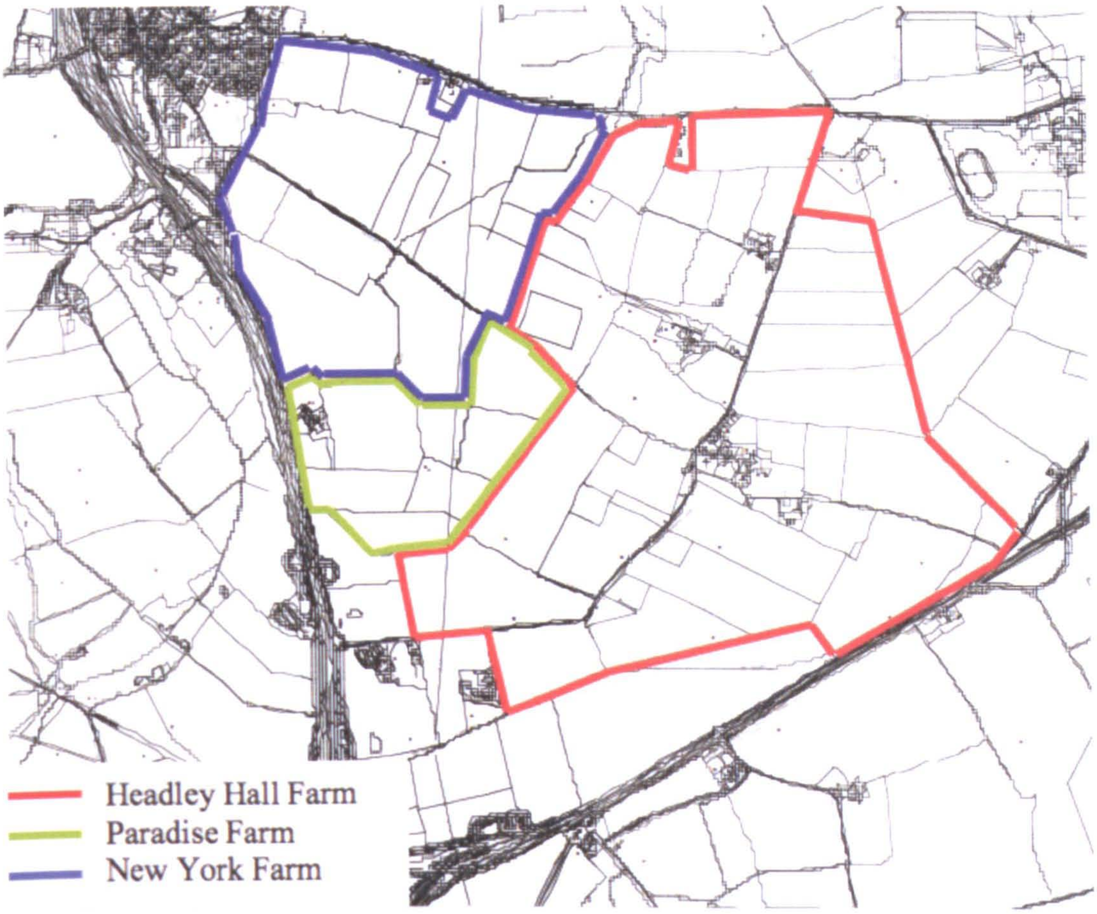
Studies of Yellowhammer foraging site selection have mostly looked at site selection at the habitat scale (e.g. Stoate et al. 1998; Morris et al. 2001; Perkins et al. 2002). Yellowhammer foraging habits have been linked to bare ground and a short sward (Stoate et al. 1998; Douglas et al. 2009) and Yellowhammers are sensitive to predation risk (van der Veen 1999) which can be influenced by foraging habitat structure (Whittingham et al. 2004; Whittingham and Evans 2004). This study compares foraging sites with randomly placed control sites, both within the same microhabitat, for example tramlines within a crop, and within a different microhabitat in order to determine important features influencing habitat choice at the within-field scale. Habitat features of foraging sites will also be linked to parental provisioning rate, to determine whether features of foraging sites may influence foraging success.

Methods

Sites

Fieldwork was carried out between April and August during 2006, and between May and July during 2007 and 2008 on three farms near Bramham, Yorkshire in 2006 (Figure 1) and 12 farms during 2007 and 2008 across Gloucestershire, Hampshire, Wiltshire and West Sussex. Fields were bounded by ditches, hedges, tree-lines, fences, grass margins or green lanes. Land use consisted of a combination of arable crops (spring and winter wheat, spring and winter barley, oilseed rape, vining peas, potatoes, field beans, and sugar beet), grass grown for silage, set-aside (grass-sown and natural stubble re-growth), agroforestry with arable set-aside and pasture grazed by cattle.

Fig. 1. Map showing locations of three farms from which yellowhammer nest and foraging data were collected during 2006. © Crown Copyright/database right 2009. An Ordnance Survey/EDINA supplied service



Nest Data

Territorial pairs were located by repeated observations of singing males and foraging pairs. Once pairs had been located, observations allowed the approximate positioning of a nest to be detected; nests were then located by a systematic search of this region. The height of the nest above ground, and vegetation type within which the nest was built were recorded, along with the height and width of the hedge at the nest site. Distance to the nearest songpost was also recorded: a songpost was defined as a piece of vegetation prominent above the rest of the hedge such as those used by male yellowhammers; these tended to be tree branches, the top of elder bushes, or long hawthorn stems.

To determine whether adult yellowhammers exhibited selection for particular nest site features within hedgerows, measurements were obtained from random sites within 25m either side of the nest. Sites were selected through the use of random numbers marked along a 50m measuring tape; at each site hedge height, width and the distance to nearest songpost (measured as above) were recorded. To establish whether nest positioning may have changed since before the yellowhammer population decline, data on the height distribution of nests were taken from Peakall (1960) and compared to nest height data collected here.

Provisioning and foraging site data

Observations of adult foraging behaviour were carried out on between one and four occasions when chicks were between 2 and 9 days old. The observer was positioned between 50 and 100m from the nest to ensure the birds' behaviour was unaffected by their presence: a previous study observed foraging behaviour from a distance of 30m with no noted effects on behaviour (Stoate et al. 1998). Adults were watched for an hour between 6:00 and 21:00hrs and food provisioning rate was calculated as the number of complete foraging trips per hour. At least one morning and one afternoon watch was carried out for each nest where possible to account for any diurnal variation in foraging patterns. Watches were not carried out during heavy rain or strong winds.

During 2006, data on foraging sites were recorded. The distance of the site from the nest was measured to the nearest 1m using a Bushnell Yardage Pro Sport Laser Rangefinder (Bushnell Performance Optics UK Ltd, Chessington; accuracy ± 1m). Each foraging site that could be accurately located (n=34, 38% of trips) was paired with two control sites 5m from the foraging site. The first control was within the same microhabitat (for example, in a crop tramline) and the second control was in a different microhabitat (for example, in the crop if the foraging site was within a tramline) in a randomly selected direction from the foraging site. For each foraging and control site, vegetation height (± 1cm), vegetation density (as per Douglas et al. in press; ± 1cm) and vegetation cover were recorded. Vegetation cover was assessed using a fisheye lens attached to a Nikon CoolPix p5000 digital camera placed on the ground facing upwards, using a timer to ensure the observer did not appear in the photograph. Photographs were taken at time of day when the camera was not in direct sunlight, as this would confound the contrast between vegetation and sky. Photographs were subsequently analysed using Gap Light Analyser software (Frazer et al. 1999) to derive the percentage of sky visible in the image.

Invertebrate samples were collected from foraging and control sites using a leaf-vacuum (Ryobi RGBV-3100, Marlow, UK) modified by the use of a fine mesh to trap invertebrates and a 1cm wire mesh to keep vegetation out of the sample. Sampling followed the protocol of Douglas et al. (2009), whereby each sampling site consisted of a 1 m square and 5 x 5s sucks were taken from each corner and from the centre of the square. Samples were frozen and subsequently identified to order (Chinery 1993).

Chick Data

Where first egg date was known, this and clutch size were used to predict hatch date; otherwise nests were visited at maximum intervals of 3 days during incubation in order to determine hatch date and monitor nest failures. Where nest failures occurred and the date was unknown, failure was assumed to have occurred at the mid point between the two final visits to the nest. Where nests were discovered at the chick stage and age was unknown, comparisons were made with the feather tract development of chicks of known age (as per Bradbury et al. 2003).

Chicks were measured on two occasions between two and seven days post-hatching, the period of linear growth for this species (Bradbury et al. 2003). Chicks were individually marked on the leg with a non-toxic marker pen to allow the identification of each nestling and measurements were taken of tarsus length (from the foot to the inside of the knee), mass and length of the leading edge of the wing to allow calculation of growth rate. Measurements of tarsus and wing were taken using digital callipers

(±0.1mm) and mass was measured using a pocket scale (±0.1g; Satrue, Taiwan). Nests were checked when chicks were 10 days old to determine fledging success: where a nest contained chicks at 7 days and the nest remained intact but was empty at 10 days (making predation of chicks immediately prior to fledging unlikely), the chicks were deemed to have fledged successfully.

Statistical analysis

Statistical analysis was carried out using R version 2.7.1 for Mac (www.r-project.org). Statistics are presented as mean ± 1 SE throughout.

Nest analyses

To determine whether features of nest sites differed from features of randomly selected sites within the same territory, a generalised linear mixed-effect model with binomial error distributions was used. Site ID (nest site or random site) was designated as the response variable with vegetation height, vegetation width, habitat and distance to the nearest songpost as predictor variables. Nest ID was designated as a random effect to control for differences between territories. Model comparisons using AIC values were used to determine whether terms significantly improved the fit of the model; those that didn't were removed in a stepwise fashion until only those terms that improved the fit of the model at $p<0.05$ remained. Following model simplification, each term was reinserted into the minimum adequate model (MAM) in turn and compared with the MAM using AIC comparisons to ensure lack of association with the response variable.

In order to determine whether nest positioning has changed since before the yellowhammer population decline, nest height data were classified according to Peakall (1960) in order to allow direct comparison between the two studies. No difference was found in frequencies of nests in height categories between the three years of this study (Poisson GLM: Year*Height interaction, $Dev_{2,15}=3.33$, $p=0.19$) and thus data from these three years were pooled to allow comparisons between the two datasets using a G test.

Foraging analyses

To determine whether or not birds chose foraging sites based on vegetation height, density, cover or invertebrate abundance, two GLMMs with binomial error distributions were constructed using the lmer function within the lme4 package (Bates & Maechler

2009) in R to compare foraging sites to both control sites within the same microhabitat and control sites within a different microhabitat. Predictor variables were vegetation height, density, cover, the abundance of invertebrates >2mm and two-way interactions between invertebrate abundance and vegetation density, height and cover, as well as between vegetation height and density. To control for differences between site localities and between foraging adults, site ID (designated for each pair of foraging and control sites) within Nest ID were designated as random variables.

To determine whether features of foraging sites were associated with parental provisioning rate, a linear mixed-effects model was constructed using the lme function within the nlme package (Pinheiro, 2009) in R. Provisioning rate was designated as the response variable and vegetation cover, height, density, total invertebrate abundance, abundance of invertebrates >2mm in length, distance from nest, trip duration and two-way interactions between invertebrate abundance and vegetation density, height and cover, as well as between vegetation height and density were designated as predictor variables. To control for individual differences, parent ID within nest ID were designated as random factors.

For all models, comparisons using AIC values were used to determine whether terms significantly improved the fit of the model; those that didn't were removed in a stepwise fashion until only those terms that improved the fit of the model at $p<0.05$ remained. Following model simplification, each term was reinserted into the minimum adequate model (MAM) in turn and compared with the MAM using AIC comparisons to ensure lack of association with the response variable.

Results

Nesting ecology

Fifty-one yellowhammer nests were monitored across three breeding seasons between 2006 and 2008. The majority (65%) of nests were found in hedgerows, mostly in hawthorn (*Crataegus* spp.); 15% were found in bramble (*Rubus* spp.) or herbaceous vegetation and 14% were found in herbaceous vegetation associated with a wall or fence. The remaining 6% were found on the ground amongst grasses. The height of nests above ground ranged from 0 to 210 cm with a mean nest height of 82.71 + 7.71 cm.

Clutch size varied from 2 to 5 eggs, with a mean of 3.48 ± 0.14. Brood size ranged from 1 to 4 chicks, with a mean of 2.78 ± 0.14. From nests that successfully fledged at least one chick, the mean number of fledglings was 2.87 ± 0.20; however across all nesting attempts that reached the egg stage, mean fledgling number was 1.375 ± 0.23 fledglings per nest.

Twenty-three nests (45%) successfully fledged at least one chick. Predation accounted for most nest failures (54%), with 19% of nest failures due to starvation of chicks and another 19% of failed nests abandoned during incubation. The remaining 8% of failed nests were destroyed during agricultural operations. Of nests that hatched chicks, brood reduction occurred in 24% of nests; however, when only nests that successfully fledged young were considered, brood reduction affected only 13% of broods.

When nest sites were compared with randomly selected points along the same boundary within 25m of each nest during 2006, none of the features considered differed between nest sites and randomly selected sites (Table 1), indicating that adult yellowhammers do not appear to select for specific features of a hedge when they select nest sites.

In order to determine whether or not yellowhammer nest site positioning might have changed since prior to the yellowhammer population decline, nest height data were compared with that of Peakall (1960). Nest height differed between the two data sets (G test, G_6–30.26, $p<0.001$) with more nests at lower heights in the 1960 dataset (Figure 2).

Table 1. Results of a binomial GLMM determining whether adult birds selected for features of a hedge when choosing a nest site: sites were either nest sites or randomly selected sites along the same field boundary within 30m of the nest. All models contained the random effect of Site ID. Statistics presented for non-significant terms are following reinsertion of the term of interest into the minimum adequate model.

Variable	AIC	Chi sq	p
Null model	79.694		
Habitat	80.139	3.555	0.169
Width	80.378	1.316	0.251
Distance to nearest songpost	81.299	0.396	0.529
Hedge height	81.430	0.265	0.607

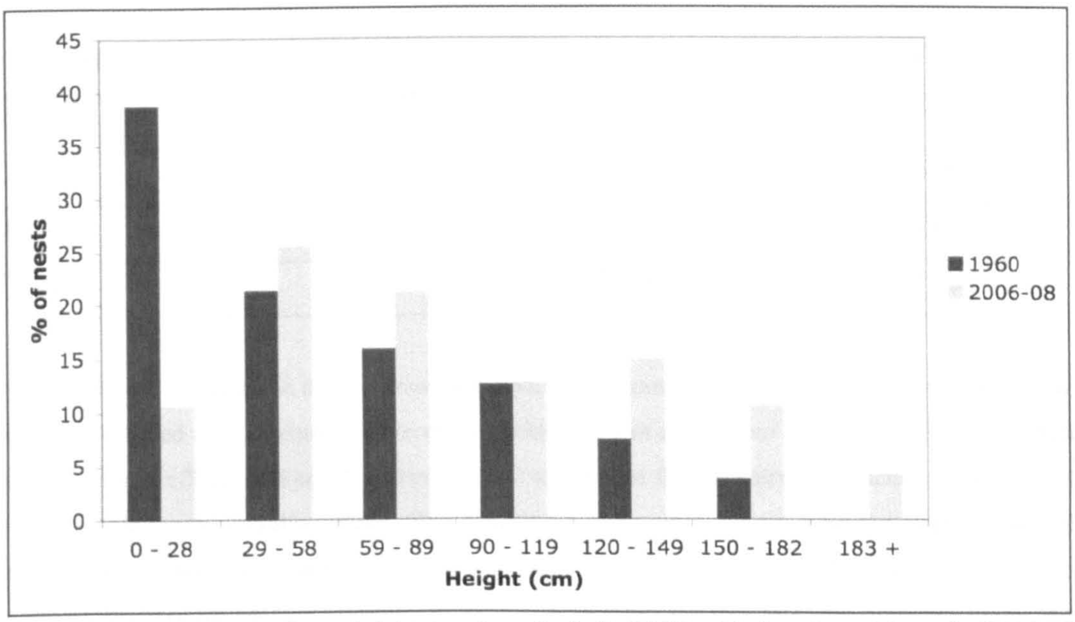


Figure 2. A comparison of nest height data from Peakall (1960) with data from this study (2006-08) indicates differences in nest height between the two datasets (G test, G_6=30.26, $p<0.001$)

Foraging ecology

No differences were found between characteristics of foraging sites and control sites of similar microhabitat (Table 2). However, both vegetation density and the interaction between invertebrate abundance and vegetation cover were found to influence whether a site of different habitat was used as a foraging site (Table 3). Foraging sites had both lower vegetation densities, and more invertebrates at higher levels of vegetation cover than control sites (Figure 3b). Invertebrate abundances were higher at foraging sites than at control sites of different microhabitats.

Table 2. Results of a GLMM comparing foraging sites with control sites of similar microhabitats 5m away from the foraging site. All models contain random effects of Site ID within Nest ID to account for the pairwise structure of the data and differences between foraging adults. Statistics presented for non-significant terms are following reinsertion of the term of interest into the minimum adequate model (MAM). *Model comparisons indicated that this term significantly improved the fit of the model (AIC = 89.20, $\chi^2 = 36.47$, $p<0.01$) and thus the term remains in the MAM but is not considered to significantly influence the response variable. Two-way interactions of Cover * Density ($F_1=0.07$, $p=0.16$), Height * Density ($F_1=0.01$, $p=0.65$), Height * Cover ($F_1<0.01$, $p=0.66$), Invertebrate abundance * Cover ($F_1=0.02$, $p=0.42$), Invertebrate abundance * Density ($F_1=0.02$, $p=0.47$) and Invertebrate abundance * Height ($F_1=0.05$, $p=0.28$) did not significantly improve the fit of the model or influence the response variable and thus were removed from the model.

Variable	**df**	**z**	**p**
Invertebrate abundance	1	-0.649	0.516*
Variable	**AIC**	χ^2	**p**
MAM	89.202		
Cover	87.758	3.443	0.064
Density	91.052	0.150	0.699
Height	90.810	0.391	0.531

Table 3. Terms remaining in the minimum adequate model from a GLMM comparing foraging sites with randomly selected control sites of different microhabitats 5m away from the foraging site. All models contain random effects of Site ID within Nest ID to account for the pairwise structure of the data and differences between foraging adults. For significant terms, parameters estimates and SE are also presented; estimates include intercept values. * Model comparisons indicated that this term significantly improved the fit of the model (AIC=73.530, $\chi^2 = 4.10$, $p=0.04$) and thus this term remained in the MAM but is not considered to significantly influence the response variable. Two-way interactions of Density * Invertebrate abundance ($z_1=-0.80$, $p=0.43$) and Density * Height ($z_1=-0.95$, $p=0.34$) did not significantly improve the fit of the model or influence the response variable and thus were removed from the model.

Variable	**df**	**z**	**p**	**Estimate**	**SE**
Density	**1**	**-0.143**	**0.049**	**-0.418**	**0.032**
Invertebrate abundance	**1**	**-1.963**	**0.044**	**-0.455**	**0.402**
Cover	1	0.485	0.628		
Height	1	-0.688	0.491		
Invertebrate abundance * Cover	**1**	**-2.067**	**0.039**	**-0.017**	**0.008**
Invertebrate abundance * Height	1	1.905	0.057*		

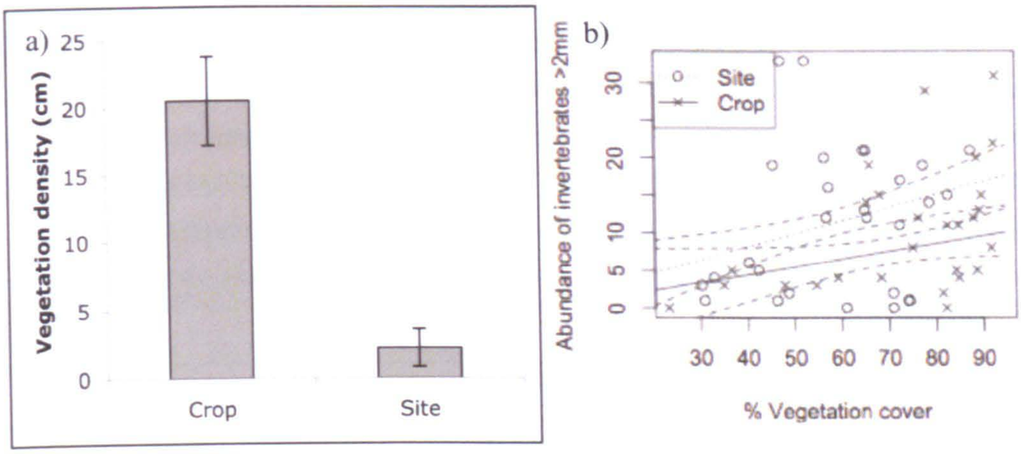


Figure 3. Differences between yellowhammer foraging sites and control sites were influenced by a) Vegetation density and b) An interaction between vegetation cover and invertebrate abundance (Table 3). Bars represent mean ± 1 SE. Lines are predicted from the MAM (Table 3) with mean vegetation density (11.35 cm); dashed lines show ± 1 SE.

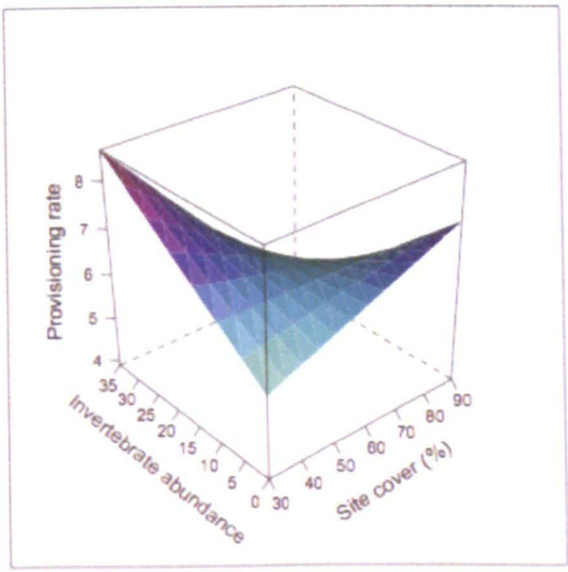


Figure 4. Parental provisioning rate was influenced by an interaction between vegetation cover and invertebrate abundance (LME, $F_{1,10}$=13.78, p<0.01). Surface is predicted from the MAM (Table 4) for mean trip duration (15.8 minutes).

Parental provisioning rate was influenced by an interaction between vegetation cover and invertebrate abundance at foraging sites (Table 4; Figure 4). At low invertebrate abundances, provisioning rate increases with increasing vegetation cover, whereas as high invertebrate abundances, provisioning rate decreases with increasing vegetation cover (Figure 4).

Table 4. Minimum adequate model (MAM) from a LMM determining which features of parental foraging sites are associated with provisioning rate. All models contain random effects of Parent ID within Nest ID. Statistics presented for non-significant terms are from model comparisons following reinsertion of the term of interest into the MAM. *Model comparisons indicated that this term significantly improved the fit of the model (AIC=84.71, χ^2 =11.92, $p<0.01$) and thus this term remains in the MAM but is not considered to significantly influence the response variable. Two-way interactions of Height * Density (AIC=83.05, χ^2 =0.22, p=0.64), Height * Invertebrate abundance (AIC=81.27, χ^2 = 0.70, p=0.41) and Density * Invertebrate abundance (AIC = 79.97, χ^2 =2.81, p=0.09) did not significantly improve the fit of the model or influence the response variable and were thus removed from the model.

Variable	**df**	**F**	**p**	**Estimate**	**SE**
Trip duration	1, 10	3.690	0.084*		
Vegetation cover	1, 10	2.170	0.172		
Invertebrate abundance	1, 10	0.594	0.459		
Cover * Invertebrate abundance	**1, 10**	**13.776**	**0.004**	**-0.003**	**0.001**
Variable	**AIC**		χ^2		**p**
MAM	74.790				
Distance from nest	75.729		1.060		0.303
Vegetation density	76.831		0.001		0.999
Vegetation height	76.558		0.231		0.631

Discussion

Yellowhammer nesting habitat was similar to that found in other studies, with the majority of nests in hedgerows, followed by herbaceous vegetation (Kyrkos et al. 1998; Bradbury et al. 2000; Stoate and Szczur 2001). Preferences appear to differ from the study of Stoate et al. (1998), who state that nests in hedgerows were "located within herbaceous vegetation in field margins, rather than in the shrubby vegetation of the hedge itself" (Stoate et al. 1998): this was not the case in the present study as all nests recorded as in hedgerows were located within hedgerow vegetation, mostly hawthorn. The preference of this species for nesting in vegetated ditches (Bradbury et al. 2000) was not confirmed with this study; however, this is probably a reflection of the paucity of vegetated ditches within the study sites.

The mean clutch size of 3.48 ± 0.14 found in this study compares favourably with the most recent study of Yellowhammer breeding performance: Bradbury et al (2000) found a mean clutch size of 3.27 ± 0.03 from a dataset of over 400 nests within Oxfordshire, Wiltshire and Warwickshire. This figure was significantly lower than that of 3.44 ± 0.70 obtained from the BTO Nest Record Scheme (Robinson 2005) and other datasets with large sample sizes (see Bradbury et al. 2000 for details), and data from this study are more in concordance with these earlier studies (Stoate et al. 1998; Robinson 2005; see Bradbury et al. 2000 for others). Mean fledging success per nest was within the range of Bradbury et al (2000), and 45% of nests successfully fledged at least one chick, compared to 46.5% of nests recorded by Bradbury et al. (2000). When compared with a figure of 45% fledging success in 1960 (Peakall 1960), there appears to have been little change in fledging success since the start of the Yellowhammer population decline.

That predation accounted for the majority of nest failures agrees with other studies (Crick et al. 1994; Bradbury et al. 2000; Hart et al. 2006; but see Stoate et al. 1998 for inter-year variation), and the proportions of other causes of failures are similar (Bradbury et al. 2000), although destruction by agricultural activities is notably lower than recorded by Crick et al (1994), as is the overall failure rate recorded from BTO Nest Record cards pre- 1994 (Crick et al. 1994).

Nest height distribution within this study was found to differ considerably from that of a study by Peakall (1960) undertaken prior to the Yellowhammer population decline, with mean nest height in this study nearly double that found by both Peakall (1960) and more recently by Stoate et al. (1998). Whilst it is possible that this may be partly due to observer bias leading to a reduction in the number of ground nests found during this study, or a reduction in suitable ground habitat such as vegetated ditches, nests were consistently found at greater heights than by Peakall (1960). Whilst Bradbury et al. (2000), found a higher proportion of nests on the ground than within this study, nests located later in the season were consistently higher above the ground than those analysed by Peakall, especially later in the breeding season when nest height tends to increase (Peakall 1960; Bradbury et al. 2000; Stoate and Szczur 2001). This indicates that nesting habitat has altered since the onset of the Yellowhammer population decline, possibly due to changes in nesting habitat and a reduction in suitable nesting habitat, such as a reduction in ditches leading to an increased use of hedgerows, a possible increase in hedgerow height, and a thinning of herbaceous vegetation at hedgerow bases due to increased use of herbicides (Boatman et al. 1994). However, as nest success is unaltered from that recorded by Peakall (1960) there is unlikely to be a direct link between nest habitat alterations and population decline.

Yellowhammers do not appear to select for any of the hedgerow features examined when choosing a nest site within their territory, as there was no apparent difference between nest sites and randomly selected points within the same territory in terms of habitat, hedgerow height or width, or distance to nearest songpost. As variation within the same length of hedgerow within the extent of a territory is likely to be relatively small, it is probable that the selection of a territory containing a length of high quality hedgerow is more important (Whittingham et al. 2005). Selection of nest sites is more likely to be based upon the presence of a suitable support structure in an area of high vegetation cover, neither of which were assessed within this study. Whilst the presence of a songpost such as a tree has been found to be important in territory selection (Whittingham et al. 2005), this had no influence on the selection of nest sites, probably as there was no shortage of songposts such as emergent hawthorn branches or elder branches that are commonly used as songposts by Yellowhammers (Author, pers. obs.).

There was no difference between foraging sites selected by yellowhammers and control sites of similar microhabitat; however microhabitats used for foraging had lower vegetation density and higher invertebrate abundance than control sites 5m away in a different microhabitat, and higher invertebrate abundances at higher vegetation density. This suggests that Yellowhammers initially select foraging microhabitats according to vegetation structure, but then according to food availability, with a lower vegetation cover providing a greater visibility of predators (Whittingham et al. 2004; Whittingham and Evans 2004) and a lower vegetation density providing easier access to invertebrates despite their lower abundance. This also suggests that where Yellowhammers take higher risks by foraging in more dense vegetation, where perceived predation risk is higher (Butler et al. 2005), there is a payoff in terms of an increased invertebrate availability within the microhabitats selected for foraging. This concurs with suggestions made by Morris et al. (2001) and studies by Perkins et al. (2002) and Douglas et al. (2009), suggesting that cutting patches within field margins would improve their value for birds by creating a mosaic of cut patches where accessibility is improved, adjacent to uncut patches where invertebrate abundance remains high (Perkins et al. 2002; Douglas et al. 2009), as this would reduce. This also concurs with a recent study by Douglas et al. (in press) which found Yellowhammer foraging sites to be characterised by lower vegetation height, lower vegetation density and a higher proportion of bare earth than control sites within cereal fields, indicating a higher degree of accessibility to foraging sites. However, Douglas et al (in press) found no differences in the abundance of invertebrates between foraging and control sites, indicating no cost to selecting more accessible foraging habitat.

Parental provisioning rate increased with increasing vegetation cover in areas of low invertebrate abundance, indicating that where food availability is low, parents take more risks by foraging where cover (and invertebrate abundance) is higher in order to ensure sufficient food for their chicks. This may increase their own risk of predation by lowering their visibility of predators. Conversely, when invertebrate abundance is high, provisioning rate decreases with increased vegetation cover, expected when increased vegetation cover leads to an increased time spent scanning for predators and thus decreasing prey capture rate (Whittingham et al. 2004; Whittingham and Evans 2004), although the time spent searching for prey is likely to be decreased where prey is abundant.

This work adds to the growing body of literature emphasising the importance of prey accessibility to foraging birds. Here I demonstrate that invertebrate abundance and vegetation cover interact to influence where birds forage, and how efficiently they can provision their chicks. Whilst increased vegetation cover leads to a higher perceived predation risk to the foraging bird, higher invertebrate abundances associated with increased cover can lead to birds selecting such sites for foraging, with resulting increases in provisioning rates to chicks in areas where invertebrate abundance tends to be low. In areas where invertebrate abundance tends to be higher, provisioning rates to chicks are highest where vegetation cover is low as parents can forage adequately with minimum risk to themselves. This suggests that measures aimed at increasing the abundance of invertebrates in the farmland environment, such as the maintenance of uncropped habitats such as field margins and conservation headlands, can be improved by the establishment of sward heterogeneity within these habitats (Perkins et al. 2002; Douglas et al. 2009) in order to provide a mixture of microhabitats aimed at encouraging invertebrate populations, and microhabitats enabling birds to forage more efficiently.

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Chapter 3. Indirect impacts of nest predation risk on chick growth in a declining farmland passerine

Abstract

Predation risk and food availability can act synergistically to influence breeding success, with population-level consequences. Here I investigate for the first time how nest predation risk, food availability and brood size interact to influence nestling growth using Yellowhammers *Emberiza citrinella* as a model species. I show a significant and sizeable negative impact of local corvid activity upon brood provisioning rate, indicating that yellowhammers are able to assess the level of nest predation risk and adjust their behaviour accordingly. Chick condition and growth were both negatively influenced by corvid abundance and positively influenced by invertebrate abundance in large broods, but not in small broods, indicating that parents raising large broods in unfavourable conditions were unable to compensate fully for the effect of corvid activity on provisioning rate. In areas of high food availability, chick growth has a positive relationship with corvid abundance, indicating that parents maximise the food intake of their chicks to enable rapid growth and minimise the risk of corvid predation. I propose a mechanism by which increasing corvid abundance combined with a decreasing food supply may have precipitated population declines through delayed life history effects.

Introduction

Predation risk and food availability are two key factors shaping the ecology of foraging behaviour (Gosler 1995; Rands and Cuthill 2001): as such the interplay between the two is thought to have played a crucial role in farmland bird declines (Evans 2004). The importance of the sub-lethal effects of predation risk have only relatively recently been realised (Krebs et al. 1995; Clinchy et al. 2004; Cresswell 2008): increased predation risk can alter behaviour, impacting upon both reproductive success and long-term population dynamics (Boonstra et al. 1998; Clinchy et al. 2004) and may act synergistically with a lack of food to induce chronic stress, with associated consequences for reproductive success (Krebs et al. 1995; Clinchy et al. 2004). Predation risk and food availability may also act synergistically at the nest level, mediated by parental behaviour.

Nest predation is the most important cause of nest failure among many small passerines (Ricklefs 1969; Crick et al. 1994) and has the potential to contribute significantly to long term population declines (Rogers et al. 1997). Skutch (1949) hypothesised that increased levels of parental activity around the nest would increase the risk of nest predation (Martin et al. 2000), supported by recent evidence (e.g. Martin et al. 2000; Eggers et al. 2005). Avian predators such as corvids, whose populations have increased since the onset of agricultural intensification (Gregory and Marchant 1995), are more likely to predate poorly concealed nests and behavioural compensation by parent birds may be more likely in areas of high corvid abundance (Remes 2005).

In many farmland bird species the availability of invertebrate chick food has been detrimentally affected by various aspects of agricultural intensification, leading to a reduction in invertebrate availability through increased vegetation density (Douglas et al. 2009) and a reduction in invertebrate numbers per se through altered land-use (Møller 2001) and a decline in invertebrate food resources such as weed seed banks (Hart et al. 2006). The abundance, diversity, detectability and accessibility of invertebrates during the breeding season play a key role in reproductive success (e.g. Hart et al. 2006) and this reduction in invertebrate availability is thought to be a driving factor behind the population declines of many farmland passerines (Møller 2001; Hart et al. 2006).

Changes in parental provisioning behaviour, induced by any causal factor, may have both direct and indirect consequences for nestlings. High provisioning rates are usually associated with high chick growth rates and good nestling condition (e.g. Takahashi et al. 2003), increasing the likelihood of fledging success (e.g. Schwagmeyer and Mock 2008) although this may be confounded by the amount of food brought back per visit (parental load), food quality (Wright et al. 1998) and compensatory growth (Nilsson and Svensson 1996). As early developmental conditions impact upon an individual later in life (Beckerman et al. 2002; Taborsky 2006), for example through a reduced lifespan and a reduced reproductive output (Metcalfe and Monaghan 2001), any reduction in chick growth rate or condition may have long-term population-level implications.

The Yellowhammer *Emberiza citrinella* is a farmland passerine whose population has declined by 55% between 1967 and 2006 in the UK (Baillie et al. 2009). The majority of nest failures in this species are due to predation (Crick et al. 1994) and corvids are considered the main nest predator of Yellowhammer nests in the UK (Bradbury et al. 2000). The species is also influenced by invertebrate abundance, with chick growth, body condition and fledging success all associated with the abundance of invertebrates around the nest (e.g. Hart et al. 2006).

This species provides an opportunity to test three hypotheses involving the potential consequences of nest predation risk and chick food availability for provisioning behaviour and chick growth, through impacts on nest predator abundance and chick food availability:

Hypothesis 1) Farm management influences both corvid abundance and invertebrate abundance. I predict that conventionally managed farms will have lower invertebrate abundances, due to the use of pesticides avoided by organic farming practices, and higher corvid abundances as corvid population increases have been linked to agricultural intensification (Gregory and Marchant 1995).

Hypothesis 2) Corvid activity and invertebrate abundance influence the rate at which adult Yellowhammers provision their young. I predict that high levels of corvid activity will be associated with low provisioning rates as adults reduce the risk of nest predation by reducing activity around the nest, and that high invertebrate abundances will be associated with high provisioning rates as adult birds maximise the food intake of their chicks.

Hypothesis 3) Corvid abundance and invertebrate abundance interact to influence chick mass and growth. In areas of high corvid abundance and low invertebrate abundance it is predicted that foraging adults will be unable to compensate for reductions in provisioning rate during times of high corvid activity, resulting in both a decrease in chick mass and a reduction in chick growth.

Methods

Sites

Fieldwork was carried out during May – July 2007 and 2008 on eighteen farms in Wiltshire, Hampshire, Gloucestershire and West Sussex, UK. Farms consisted of pairs of organic and conventional farms (herein referred to as under differing managements), grouped into clusters of four in the vicinities of Chichester, Andover, Salisbury and Swindon and matched according to soil type, farm size, geography and ratio of arable to livestock.

Nest and Chick data

Territorial pairs and nests were located and monitored using standard methodology (Bradbury et al. 2000; described further in Chapter 2). Chicks were measured on two occasions between two and seven days old, the period of linear growth for this species (Bradbury et al. 2003). Chicks were individually marked on the leg with a non-toxic marker pen to allow the identification of each nestling and measurements were taken of tarsus length (from the foot to the inside of the knee), mass and length of the leading edge of the wing to allow calculation of growth rate. Measurements of tarsus and wing were taken using digital callipers (+/-0.1mm) and mass was measured using a pocket scale (+/-0.1g; Satrue, Taiwan)

Foraging data

Observations of adult foraging behaviour were carried out on between one and four occasions when chicks were between 2 and 9 days old. The observer was sat between 50 and 100m from the nest to ensure the birds' behaviour was unaffected by their presence: a previous study observed foraging behaviour from a distance of 30m with no noted effects on behaviour (Stoate et al. 1998). Adults were watched for an hour between 6:00 and 21:00hrs and foraging rate was calculated as the number of complete foraging trips per hour. At least one morning and one afternoon watch was carried out for each nest where possible to account for any diurnal variation in foraging patterns. Foraging watches were not carried out on days when rain was heavy as this increased the likelihood of the brood being incubated by the female and reduced invertebrate availability, thus reducing provisioning rate.

Chick food availability

Invertebrate samples were collected from foraging and control sites using a leaf-vacuum (Ryobi RGBV-3100, Marlow, UK) modified by the use of a fine mesh to trap invertebrates and a 1cm wire mesh to keep vegetation out of the sample. Sampling followed the protocol of Douglas et al. (2009), whereby each sampling site consisted of a 1 m square and 5 x 5s sucks were taken from each corner and from the centre of the square. The majority of yellowhammer foraging trips are within 200m of their nest and 60% are within 100m (Morris et al. 2001, cited in Hart et al. 2006), and field margins are a favoured foraging habitat of this species (Douglas et al. 2009). Thus, this sampling strategy was designed to get a comparable measure of invertebrate abundance within potential foraging habitat. During 2007, samples were taken from ten patches within the margin habitat on either side of the hedgerow between 0 and 50m from the nest at 25m intervals. Analysis showed no significant difference in invertebrate abundance between ten samples and a subset of four samples (GLMM, $\chi^2_{1,17}=0.014$, $p=0.906$), so in 2008 four samples were taken within the margin habitat on both sides of the hedgerow 50m from the nest. Samples were collected immediately following each foraging watch but not if conditions were wet as this impeded the efficiency of the vacuum sampler (Hart et al. 2006). Samples were stored in 70% methanol prior to being identified to order. Subsequently, the abundance of invertebrates in orders known to be important in yellowhammer chick diet was calculated (Hart et al. 2006). Invertebrates smaller than 2mm in length were excluded from the total count as these are unlikely to be important in nestling diet (Morris and Bradbury 2002).

Predator abundance

The abundance of potential avian nest predators was assessed through the use of transects and point count surveys for corvids (Magpies *Pica pica*, Carrion Crows *Corvus corone*, Rooks *Corvus frugilegus* and Jackdaws *Corvus monedula*), key nest predators in agricultural landscapes (Andrén 1992) and the main nest predators of the yellowhammer in the UK (Bradbury et al. 2000). Corvid activity shows considerable temporal variation (Luginbuhl et al. 2001); thus, transects were designed to provide a "farm-scale" level of corvid abundance that would be more relevant in models of chick condition and growth (herein "corvid abundance"), whereas point counts were designed to assess the temporally relevant corvid activity (herein "corvid activity") for models of parental provisioning rate.

Transects consisted of two 1km transects which were walked on each farm on three separate occasions between May and July during both 2007 and 2008, according to standard methodology (Marchant et al. 1990). Point count surveys were carried out for 20 minutes immediately prior to each adult foraging watch: the total abundance of corvids within 100m of the nest was recorded.

Statistical analysis

Linear mixed-effects models (LMMs) from the nlme library (Pinheiro et al. 2009) in R (R Core Development Team 2006) were fitted to data using maximum likelihood fits to allow model comparisons and subsequent simplification; data were transformed where necessary to meet the assumption of normality of random errors (Crawley 2007). Random effects of Chick ID within Nest within Farm, or a subset thereof, were included where appropriate to control for non-independence of repeated measures and effects of different parental quality. Model comparisons using AIC values were used to determine whether terms significantly improved the fit of the model; those that didn't were removed in a stepwise fashion until only those terms that improved the fit of the model at $p<0.05$ remained. Following model simplification, each non-significant main-effect was reinserted into the minimum adequate model (MAM) in turn and compared with the MAM using AIC comparisons and likelihood ratio tests to ensure lack of association with the response variable. Although model simplification by stepwise-deletion has been criticised in the literature (Whittingham et al. 2006), a recent study validated this method of producing predictive models (Murtaugh 2009).

Two mixed-effects models were run to determine the influence of farm management on each of corvid abundance and invertebrate abundance. Insect abundance was square root transformed to meet the assumptions of an LMM; the residuals of the model for corvid abundance would not transform to normality and thus a GLMM with poisson error distributions was fitted. To control for repeated measures from the same farm, farm ID was included as a random effect within each model. Within the corvid model, month, year and management were included in the model as main effects; for invertebrate abundance, management, month, time of day, year and temperature were included in the model as main effects; examination of the raw data indicated possible quadratic relationships with time of day and temperature and thus quadratic relationships with these terms were included in the model.

Provisioning rate was designated as the response variable in an LMM to determine whether corvid activity and invertebrate abundance influenced parental provisioning rate. Corvid activity, invertebrate abundance, brood size, farm management, year, chick age and quadratic terms for temperature and time of day were included as main effects and all two-way interactions between brood size, corvid abundance and invertebrate abundance were also included in the maximal model. To determine whether any effect on provisioning rate was temporally adapted to reduce the risk of nest predation (i.e. a response to the abundance of corvids in the immediate region of the nest at that time rather than are generally present in the wider landscape), farm-scale corvid abundance was substituted into the model above as a main effect in place of corvid activity and the model rerun with the same model structure and main effects.

Chick condition was assessed by chick mass when controlling for the size of the chick (wing length) using measurement from chicks of 5-7 days old. Measurements from chicks of these ages were used as external factors were thought likely to have had time to exert an influence on mass by this age. Wing length was used, as wing length at fledging is crucial to fledging success and thus is less variable than other measures of size (Nilsson and Svensson 1996). Growth was assessed by tarsus measurements, as tarsus growth is likely to be more variable than wing growth (Nilsson and Svensson 1996). For the growth model, second measurement was designated as the response variable, with first measurement and hours between measurements as main effects to control for the stage of growth and the amount of growth in between measurements.

In both models, corvid abundance, invertebrate abundance, brood size, management, parental provisioning rate, year, chick age, Julian day and time of measurement were designated as main effects; all two-way interactions between brood size, corvid abundance and invertebrate abundance, along with the interaction between chick age and provisioning rate, between invertebrate abundance and provisioning rate and between invertebrate abundance and farm management were also included in the maximal model. Examination of the raw growth data indicated a possible quadratic relationship with second tarsus length; however the fit of the model containing the linear term to the data was better than that containing the quadratic terms, so the model containing the linear term was used (AIC linear model: -321.05; AIC with quadratic terms: -318.30).

Results

Twenty-nine nests were monitored on thirteen farms during 2007 and 2008. Provisioning data were collected on between one and four occasions for each of the seventeen of these nests on twelve farms that hatched successfully (2.71+/-0.24 foraging watches per nest); condition data were collected from 45 chicks within sixteen nests and growth data from 42 chicks within fifteen nests.

Management effects on nest predator abundance and chick food availability

Both invertebrate abundance and corvid abundance varied between farms (Appendix 1), although this did not differ between organic and conventionally managed farms (Tables 1 & 2). However, the power of these tests to detect a statistical difference if one was present was very low (Corvid abundance: power=0.15, Invertebrate abundance: power=0.08) due to high variation within the data and consequently a small effect size (given in Tables 1 & 2 for illustration). Farm scale corvid abundance was significantly influenced by year and by month (Table 1) with a higher abundance in 2008 compared to 2007 (2007: 70.89 +/- 10.59; 2008: 109.93 +/- 29.53), and increasing throughout the season (May: 80.69 ± 14.16; June: 82.15 ± 16.93; July: 89.09 ± 31.75 corvids per farm). Invertebrate abundance was influenced by month (May: 18.00 ± 2.51; June: 47.04 ± 2.24; July: 43.29 ± 2.35), year (2007: 45.98 ± 2.04; 2008: 34.49 ± 2.29) and showed quadratic relationships with temperature and time of day (Table 2).

Table 1. Results of a generalised linear mixed-effects model determining which variables influence corvid abundance. All models contain random effects of Farm ID to control for effects of repeated measures from the same farm. Statistics presented for non-significant terms are following reinsertion of the term of interest into the minimum adequate model (MAM).

Variable	**df**	**z**	**p**	**Estimate**	**SE**
Month (May)	1, 5	5.017	<0.001	-0.077	0.026
Month (June)				-0.059	0.026
Month (July)				0.136	0.027
Year (2008)	1, 5	7.031	<0.001	0.243	0.035
Variable	**df**	χ^2	**p**	**Estimate**	**SE**
Management (Conventional)	1	1.038	0.308	0.663	0.640

Table 2. Results of a generalised linear mixed-effects model determining which variables influence invertebrate abundance. All models contain random effects of Farm ID to control for effects of repeated measures from the same farm. Statistics presented for non-significant terms are following reinsertion of the term of interest into the minimum adequate model (MAM).

Variable	**df**	**F**	**p**	**Estimate**	**SE**
Time^2	1, 194	9.413	0.003	-0.006	0.002
Temperature^2	1, 194	8.051	0.005	0.004	0.002
Year (2008)	1, 194	5.363	0.022	0.524	0.226
Month (July)	2, 194	12.428	<0.001	0.836	0.337
Month (June)				1.267	0.247
Month (May)				-2.102	0.292
Variable	**df**	**LRT**	**p**	**Estimate**	**SE**
Management (Conventional)	1, 10	0.080	0.778	-0.063	0.227

Parental provisioning behaviour

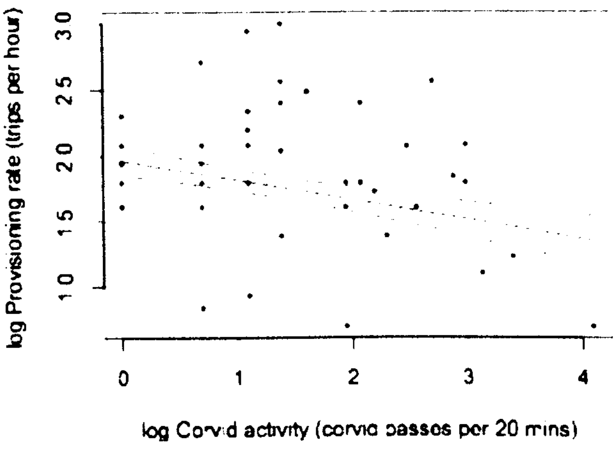


Figure 1. Parental provisioning rate decreases with increasing corvid activity (LMM, $F_{1,24}$=8.46, p<0.01). Points show raw data; solid line is predicted provisioning rate from the MAM with mean chick age (4.76 days) and brood size (2.85 chicks); dashed lines show standard error.

Corvid point counts prior to provisioning watches were undertaken on 46 occasions for 17 nests. Corvid activity significantly influenced parental provisioning rate (Table 3) with a decrease in provisioning rate with increasing corvid activity (Figure 1). Chick age and year both significantly influenced provisioning rate (Table 3), with higher provisioning rates to older chicks and in 2008 than 2007 (2007: 5.45 ± 0.56; 2008: 8.26 ± 1.25 trips per hour). When substituted into the previous model in place of corvid activity, corvid abundance had no effect upon provisioning rate (GLMM, $F_{1,24}$=0.30, p=0.62).

Table 3. a) Results of a linear mixed-effects model determining which variables influence the rate at which Yellowhammer parents provision their chicks. All models contain random effects of Nest ID within Farm ID to control for effects of parental quality and localised geographical variation. Back-transformed parameter estimates are presented for significant terms. b) Statistics presented for non-significant terms are following reinsertion of the term of interest into the minimum adequate model (MAM). *Model comparisons indicated that this term significantly improved the fit of the model (LRT_1=4.152, p=0.042) and thus this term remains in the MAM but is not considered to significantly influence the response variable. Two-way interactions of invertebrate abundance x corvid activity (LRT_1=0.051, p=0.822) and corvid activity x brood size (LRT_1=0.258, p=0.612) did not significantly improve the fit of the model or influence the response variable and thus were removed from the model.

a) Variable	**df**	**F**	**p**	**Estimate**	**SE**
Insect abundance	1, 24	0.295	0.592	0.011	0.005
Corvid activity	**1, 24**	**8.459**	**0.008**	**-0.019**	**0.008**
Brood size	1, 24	2.211	0.150	0.710	0.200
Chick age	**1, 24**	**5.820**	**0.024**	**0.088**	**0.048**
Year (2008)	**1, 4**	**7.941**	**0.048**	**0.713**	**0.193**
Insect abundance x Brood size	1, 24	3.684	0.067*	-0.004	0.002

b) Variable	**df**	**LRT**	**p**
Temperature^2	1	1.368	0.242
Time of day^2	1	0.393	0.531
Management	1	1.970	0.160

Chick mass and growth

Chick growth was influenced by all two-way interactions between corvid abundance, invertebrate abundance and brood size (Table 5; Figure 3), and chick mass was influenced by two-way interactions between corvid abundance and brood size, and invertebrate abundance and corvid abundance (Table 4; Figure 2). Large broods showed reduced mass and size growth with increasing corvid abundance and increased growth with increasing invertebrate abundance, whilst small broods showed the opposite trends (Tables 4 & 5; Figures 2a, 3a & 3b). Chick mass and growth decrease with increasing corvid abundance; however, this effect is reduced in areas of high invertebrate abundance (Tables 4 & 5; Figures 2 and 3).

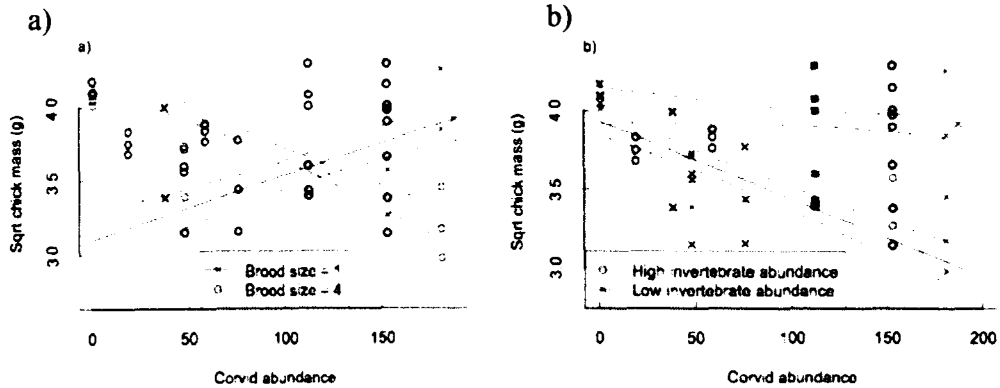
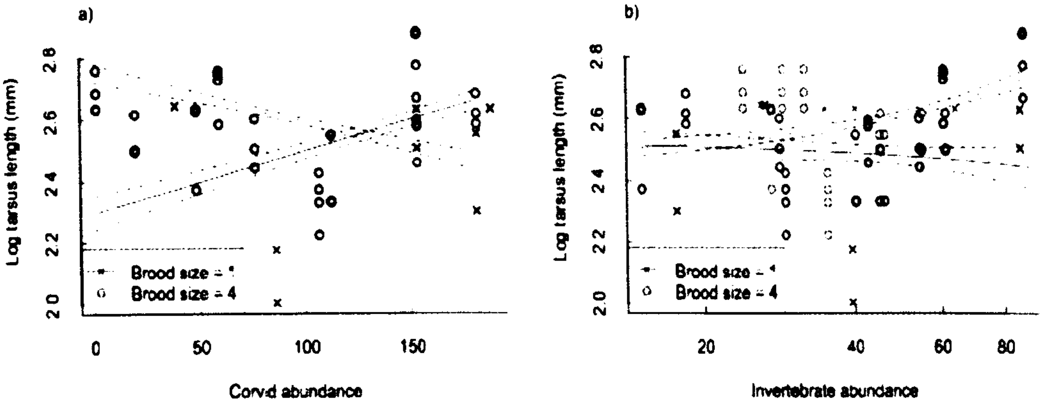


Figure 2. Interactions between a) Brood size and Corvid abundance (GLMM, $F_{1,8}$=9.92, p=0.02) and b) Corvid abundance and Invertebrate abundance (GLMM, $F_{1,50}$=4.45, p=0.04) both influenced chick mass when controlling for size. Points show raw data; Lines are predicted from the MAM with mean values for wing length (14.96 mm), provisioning rate (8.46 trips per hour), chick age (5.67 days), Time of day (13:41) a) Invertebrate abundance (51.0 invertebrates) and b) Corvid abundance (93.1 corvids). Dashed lines represent SE.

Table 4. a) Results of a linear mixed-effects model determining which terms influence chick mass. All models contain random effects of Chick ID within Nest ID within Farm ID to control for effects of parental quality and localised geographical variation. Back-transformed parameter estimates are presented for significant terms. b) Statistics presented for non-significant terms are following reinsertion of the term of interest into the minimum adequate model (MAM). *Model comparisons indicated that this term significantly improved the fit of the model (LRT_1=8.38, p<0.01) and thus this term remains in the MAM but is not considered to significantly influence the response variable. The invertebrate abundance x farm management interaction (LRT_1=2.85, p=0.09) did not significantly improve the fit of the model or influence the response variable and thus were removed from the model.

a) Variable	df	F	p	Estimate	SE
Wing length	1, 50	1283.01	<0.001	-0.237	0.081
Provisioning rate	1, 50	5.37	0.022	0.432	0.107
Chick age at measurement	1, 50	362.90	<0.001	2.820	0.195
Time of measurement	1, 50	126.93	<0.001	0.185	0.017
Invertebrate abundance	1, 50	6.63	0.005	-0.156	0.063
Brood size	1, 8	0.79	0.409	-0.082	1.200
Corvid abundance	1, 8	5.97	0.043	0.036	0.021
Age x Provisioning rate	1, 50	21.99	<0.001	-0.067	0.017
Invertebrate abundance x Brood size	1, 50	3.14	0.081*	0.055	0.019
Invertebrate abundance x Provisioning rate	1, 50	8.46	0.012	-0.001	0.001
Corvid abundance x Brood size	1, 8	6.84	0.034	-0.024	0.008
Invertebrate abundance x Corvid abundance	1, 50	4.42	0.048	0.001	0.001

b) Variable	df	LRT	p
Year	1	0.440	0.507
Julian day	1	0.842	0.359
Management	1	3.028	0.082



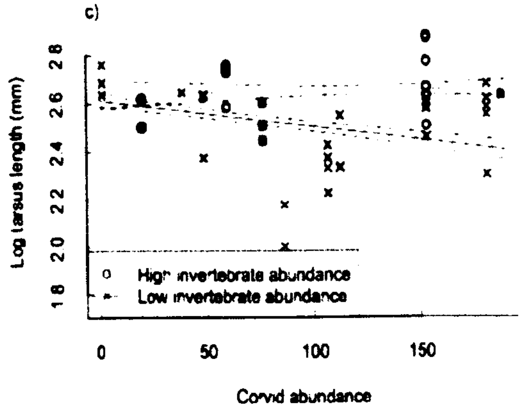


Figure 3. Chick growth was influenced by interactions between brood size and a) corvid abundance (GLMM, $F_{1,105}=34.83$, $p<0.01$) and b) invertebrate abundance (GLMM, $F_{1,105}=8.12$, $p<0.01$), as well as between c) corvid abundance and invertebrate abundance (GLMM, $F_{1,105}=5.41$, $p=0.02$). Points represent raw data; lines are predicted from the MAM (Table 4) with mean values for 1st tarsus length (10.13 mm), hours between measurements (46.11 hours), invertebrate abundance (46.04 invertebrates), corvid abundance (93.32 corvids) and brood size (3.15 chicks), on conventionally managed farms. Dashed lines represent SE. b) Note log x-axis.

Chick mass was also influenced by interactions between chick age and provisioning rate, and invertebrate abundance and provisioning rate, and by the time of day at which chicks were measured. Chick growth was influenced by an interaction between invertebrate abundance and farm management.

Table 5. a) Results of a linear mixed-effects model determining which terms influence chick growth. All models contain random effects of Nest ID within Farm ID to control for effects of parental quality and localised geographical variation. Back-transformed parameter estimates are presented for significant terms. b) Statistics presented for non-significant terms are following reinsertion of the term of interest into the minimum adequate model (MAM). *Model comparisons indicated that this term significantly improved the fit of the model (LRT_1=8.38, p<0.01) and thus this term remains in the MAM but is not considered to significantly influence the response variable. Two-way interactions of invertebrate abundance x provisioning rate (LRT_1=0.06, p=0.81) and chick age x provisioning rate (LRT_1=0.01, p=0.92) did not significantly improve the fit of the model or influence the response variable and thus were removed from the model.

a) Variable	**df**	**F**	**p**	**Estimate**	**SE**
1st tarsus measurement	1, 105	646.31	<0.001	0.153	0.010
Management (Organic)	1, 2	52.59	<0.001	0.221	0.134
Hours between measurements	1, 105	39.45	0.024	0.014	0.003
Brood size	1, 105	2.02	0.158	0.229	0.082
Corvid abundance	1, 9	0.01	0.922	0.006	0.001
Invertebrate abundance	1, 2	9.79	0.002	-0.009	0.005
Day	1, 105	0.32	0.574*	0.005	0.001
Management x Invertebrate abundance	1, 105	8.21	0.005	-0.008	0.003
Brood size x Corvid abundance	1, 105	29.59	<0.001	-0.003	0.001
Corvid abundance x Invertebrate abundance	1, 105	6.05	0.016	0.001	0.001
Invertebrate abundance x Brood size	1, 105	5.59	0.020	0.003	0.001

b) Variable	**df**	**LRT**	**p**
Year	1	0.103	0.748
Chick age	1	0.169	0.681
Provisioning rate	1	0.105	0.746
Time of measurement	1	0.871	0.351

Discussion

Neither invertebrate abundance nor corvid abundance differed significantly between the organic and conventional farms used in this study, although the power of these tests was low. This is in contrast to previous studies that indicate higher invertebrate abundances on organic farms than conventional, and a concurrent study on the same study farms found differences in invertebrate abundances in the field margins (D. Gabriel, pers. comm.), although this study investigated invertebrate diversity as opposed to the abundance of specific orders important to Yellowhammer chicks (Hart et al. 2006). Whilst organic farming is generally thought to be beneficial to invertebrates, results very according to taxa (Fuller et al. 2005); for example, one comprehensive large-scale study found inconsistent results with both spiders and carabids within field margins, whereby only spider abundance post-harvest was significantly higher on organic farms (Fuller et al. 2005).

The lack of effect of management on corvid abundance may be considered surprising given the increase in corvid populations since the 1960s (Gregory and Marchant 1995), which has been associated with an increase in improved grassland (Barnett et al. 2004). A concurrent study on the same study farms found a higher abundance of corvids or organic farms (D. Gabriel, pers. comm.). However, in the long-term this population trend is thought to stem from a reduction in control measures rather than an increase in available food or habitat (Gregory and Marchant 1995), and factors influencing corvid population size are likely to act at a larger scale than that of the individual farm.

I show a strong negative correlation between corvid activity and parental provisioning rate. As corvids are visually oriented nest predators (Andrén 1992), activity around the nest when corvids are abundant may increase the risk of nest predation (Skutch 1949). These results indicate that adult Yellowhammers are able to assess the risk of nest predation from corvids, and reduce their provisioning rate when the risk to the nest is high, as has been shown in other species (e.g. Eggers et al. 2005). The lack of association between corvid abundance and parental provisioning rate adds further weight to this argument, indicating that behavioural compensation varies temporally, and that parents are able to assess the current risk to their nest and adjust their provisioning behaviour accordingly.

Invertebrate abundance had no effect on provisioning rate, indicating that either food may not have been limiting, differences in parental load may mask impacts on provisioning rate, or that reducing the risk of nest predation takes precedence over ensuring that chicks are well fed. The latter hypothesis seems more plausible, as previous studies have shown invertebrate abundance to be critical in influencing chick growth, body condition, and fledging success (e.g. Hart et al. 2006); conversely, there is no evidence to suggest that nest predation rates increased concurrently with corvid population increases (Baillie et al. 2009), implying that behavioural compensation for corvid nest predation risk may be highly sensitive to changes in corvid abundance and thus independent of food availability.

Chick mass and growth were both influenced by interactions between brood size and both corvid abundance and invertebrate abundance. Large broods showed decreased condition and growth with increasing corvid abundance, and increased condition and increased growth with increasing invertebrate abundance. Conversely, small broods show the opposite trends. Whilst the lower food requirements of small broods may negate the requirement for compensatory behaviour under predation risk, another possibility becomes apparent when considering that the majority of small broods have already undergone brood reduction through starvation of one or more chicks. As starvation occurs due to an inadequate food supply, surviving chicks may subsequently exhibit compensatory growth as their share of the food supply increases (Nilsson and Svensson 1996).

That corvid abundance influences nestling growth, measured over a period of days, implies that parents are unable to compensate for the reduction in provisioning rate induced by increased corvid activity, either through increasing provisioning rate when corvid activity is reduced, or by increasing load size (Eggers et al. 2005; Eggers et al. 2008). This indicates that food is limiting and is further supported by the interactive effect of invertebrate availability and corvid availability on chick growth. In areas of low food abundance, growth decreases with increased corvid abundance, indicating that food availability limits parents' ability to increase provisioning rate when nest predation risk is low. However, in areas of high food abundance, growth appears to increase with corvid abundance. This result is curious and appears counterintuitive; however, it is possible that where food is abundant but access to the nest to provision chicks is mediated by corvid activity, and thus unpredictable, that parents may overcompensate, both by increasing load size when provisioning rate is reduced (Eggers et al. 2008), and by increasing provisioning rate when corvid activity is low (Eggers et al. 2005). This would allow the maximum possible growth of chicks in order that they fledge quickly and are thus removed from the risk of nest predation.

Food availability and predation risk have been found to interact to influence reproductive success in both mammals (Krebs et al. 1995) and birds (Clinchy et al. 2004). This study both supports this interaction at the nest level, and provides evidence for a behavioural mechanism, mediated by parent birds, by which this effect may occur. Previous studies (Krebs et al. 1995; Clinchy et al. 2004) demonstrate these effects through predator exclusion and food addition, with consequent increases in reproductive success. However, here I suggest that two distinct factors associated with changes in farmland management: a decline in invertebrate food availability and an increase in nest predator abundance; may act detrimentally, both separately and interactively, to influence chick biology in a declining passerine species.

Implications

Here I rely on observations rather than experimental manipulations to demonstrate non-lethal impacts of nest predation risk on nestlings as a consequence of behavioural compensation for nest predation risk by parent birds: the implications of this at the population level are likely to be significant. Yellowhammers have undergone considerable population declines since the onset of agricultural intensification (Baillie et al. 2009), conincidental with, if slightly behind, the increase in populations of corvids (Gregory and Marchant 1995). A previous study demonstrated that increasing magpie numbers showed no relationship with nest failure in Yellowhammers (Gooch et al. 1991) but my results indicate it is merely the presence of corvids that influences parental behaviour with negative consequences for chick growth and condition. There is ever-increasing evidence to suggest that conditions early in life are important in determining the life-history trajectory of an individual (Metcalfe and Monaghan 2001; Taborsky 2006), with birds that suffer a reduced growth rate or undergo compensatory growth in the nest suffering subsequently in terms of body size and lifespan (reviewed in Metcalfe and Monaghan 2001). This is supported by the fact that Yellowhammer breeding productivity was higher during periods of decline then previously (Cornulier et al in prep) indicating that fledgling quality, not quantity, has declined.

It is therefore conceivable that in areas of high corvid density, nestlings that experience reduced growth rates and poor condition whilst in the nest may have lower survival rates post-fledging and a lower reproductive success should they survive to breed, leading to a long-term reduction in recruitment to the breeding population and a consequent population sink. As Yellowhammer territory availability is restricted partially by the availability of territories containing suitable habitat (Bradbury et al. 2000), territories within high corvid areas with suitable habitat may act as ecological traps resulting in the long-term population declines seen in this species.

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Appendix 1. Summary of invertebrate and corvid data on each of the farms surveyed. Invertebrate abundance is number of chick food invertebrates per sample (Hart et al. 2006); corvid activity is number of flying corvids within 100m of the nest during a 20 minute period prior to each provisioning watch; corvid abundance is the number of corvids sighted during a 1km transect. Both insect abundance and corvid abundance differed between farms (Insect abundance: LM, $F_{11,199}=6.34$, $p<0.001$; Corvid abundance: LM, $F_{11,25}=6.00$, $p<0.001$); however corvid activity showed only a marginal difference between farms (GLM: $F_{11,34}=1.97$, $p=0.06$). Data displayed are mean ± SE.

Farm Number	**Management**	**Invertebrate abundance**	**Corvid activity**	**Corvid abundance**
1	Organic	53.67 ± 3.68	0.75 ± 0.48	19.33 ± 3.84
2	Organic	26.25 ± 1.50	1.00 ± 0.58	38.33 ± 11.10
3	Conventional	28.17 ± 5.18	3.33 ± 2.03	1.00 ± 0.58
4	Conventional	60.60 ± 10.49	4.00 ± 1.08	59.33 ± 40.01
5	Conventional	24.80 ± 8.18	5.33 ± 2.85	48.33 ± 12.03
6	Organic	27.66 ± 3.11	7.50 ± 1.74	146.83 ± 19.76
7	Conventional	56.73 ± 4.53	11.57 ± 8.06	153.00 ± 58.00
8	Organic	33.32 ± 4.49	4.00 ± 2.52	106.50 ± 20.50
9	Organic	40.50 ± 3.09	21.67 ± 4.33	86.00 ± 13.65
10	Conventional	42.25 ± 11.14	2.00 ± 0.00	49.67 ± 8.41
11	Organic	49.87 ± 3.55	0.00 ± 0.00	187.67 ± 80.63
12	Conventional	41.20 ± 5.40	10.00 ± 4.65	76.00 ± 12.12

Chapter 4. Effects of farm management on Yellowhammer territory density and consequences for bird behaviour

Abstract

Territory availability is determined by the resources available, and breeding density can impact upon parental behaviour, chick growth and survival. Here I investigate factors influencing territory density in a declining farmland passerine, the Yellowhammer (*Emberiza citrinella*), and consider whether breeding densities at two different scales are associated with nest survival, parental provisioning rate or chick growth. Territory numbers were strongly positively associated with hedgerow length and the length of boundaries with dense herbaceous vegetation, the favoured nesting habitats of this species. Territory numbers declined by 42% on the same farms during the two years of the study, probably due to a wet breeding season during 2007. Nearest neighbour distance, a measure of local territory density, interacted with brood size to influence parental provisioning rate and suggests that food availability (although possibly not quality) is relatively constant across territories. Growth rates of chicks suggest density-dependent competition for high quality food in areas of high local territory density. Both provisioning rate and growth rate were higher on conventionally managed farms than on organic farms; however this may be as a consequence of a higher abundance of nest predators on organic farms leading to depressed provisioning rates and growth rates, rather than from bottom-up effects of food availability. These data suggest that the availability of suitable nesting habitat is the limiting factor behind Yellowhammer territory densities, and that patches of suitable nesting habitat allowing high breeding densities may not provide sufficient food to allow maximal growth rates of Yellowhammer chicks.

Introduction

Population densities of animal species are regulated by both density-dependent and density-independent processes (e.g. Sæther and Engen 2002); however, the mechanisms behind many of these processes are poorly understood (e.g. Sillett et al. 2000; Sibly and Hone 2002). Knowledge of the mechanisms of population regulation is key to the understanding of population dynamics (Sutherland and Norris 2002) and to gaining an insight into both how species have responded to past environmental change and how they will respond to future change (e.g. Sæther et al. 2000; Sillett et al. 2000; Sibly and Hone 2002; Sutherland and Norris 2002).

Density-dependent effects in avian populations are largely due to either competition for food (Johnson et al. 2006) or territories (Rohner 1997) and may also be related to the density of predators or parasites, whereby territories nearer to potential predators are less likely to be occupied than those further away (Roos and Pärt 2004), and higher densities of birds are associated with higher densities of parasites (Møller et al. 2006). Density-independent effects are generally associated with weather, which can either act separately (Sæther and Engen 2002), or compound density-dependent effects on food supply (Alatalo and Lundberg 1984; Brouwer et al. 2009).

The mechanisms by which density impacts on a species' life history depend on its ecology. For example, increased breeding densities are associated with reduced clutch sizes in some species (Perrins 1965; Both 2000) but not in others (Both 2000), and have also been associated with increased nest failure due to both predation (Dunn 1977; Chalfoun and Martin 2009; Elmberg et al. 2009) and nest parasitism (Arcese et al. 1992). Reproductive fitness is consistently influenced by territory density: in Great Tits *Parus major*, the probability of a pair nesting, the growth rate and subsequent recruitment of fledglings, and adult survival are all negatively influenced by increasing territory density (Both and Visser 2000). Similar relationships with nestling weight, size and fledging success are found in Pied Flycatchers *Ficedula hypoleuca* and Seychelles Warblers *Acrocephalus sechellensis* (Alatalo and Lundberg 1984; Brouwer et al. 2009), and experimentally in Black-throated Blue warblers *Dendroica caerulescens*, probably as a result of males spending more time foraging (Sillett et al. 2004). In all these cases, density dependence is thought to be due to competition for food between breeding pairs and is compounded by an increase in this effect when poor weather limits the available food supply (Alatalo and Lundberg 1984; Brouwer et al. 2009).

There are two conflicting schools of thought regarding the relationship between food availability and territory size. The food-maximizer model (Ebersole 1980) predicts that high food abundance allows males to hold larger territories as they require less time to forage and have more time available to defend a territory, supported by empirical evidence from Rock Pipits *Anthus petrosus* (Arvidsson et al. 1997). Conversely, the food maintenance model (Thresher, 1977 cited in Ebersole 1980) predicts that males hold territories large enough to provide the resources they need and thus where food is readily available, territories should be smaller, especially where the costs of territorial defence are high (Hixon 1980; Eberhard and Ewald 1994). This is supported by a range of empirical evidence (e.g. Davies and Lundberg 1984; Davies and Hartley 1996) and is considered the more frequent determinant of territory quality, whereby high territory densities are associated with a high quality habitat that has a higher carrying capacity and can thus support more individuals (Vander Werf 2004). These models should not necessarily be thought of in terms of food being the only factor influencing territory quality: other resources such as nest site availability may also influence territory size and thus territory densities.

Beyond access to food, territory density impacts on other physiological and behavioural traits (Rohner 1997). Males in areas of high breeding density can have higher plasma testosterone levels, causing an increase in aggressive behaviour (Silverin 1998), which can lead to nest abandonment (Hötker 2000). Vocal behaviour can also be affected: the breeding density of conspecifics can influence the honesty of vocal signals (Penteriani 2003), although this behaviour is not always consistent between species and may be linked to the risk of extra-pair paternity (Tarof et al. 1998). The frequency of territorial song may also reflect the quality of a territory, with males on food-rich territories having more time available to sing than those on territories with lower food availability (Berg et al. 2005), which can also translate into a higher reproductive success (Hoi-Leitner et al. 1993). An increasing territory density is generally thought to increase the risk of extra-pair paternity (e.g. Mougeot 2000): whilst many studies show extra-pair young to be fathered by males in neighbouring territories (Webster et al. 2001), extra-pair males are not necessarily nearest neighbours (Sundberg and Dixon 1996; Woolfenden et al. 2005). In order to reduce the risk of cuckoldry, males may increase their time spent mate-guarding prior to laying where breeding densities are higher (Mougeot 2000). Levels of extra-pair paternity may also vary with habitat quality independently of territory density: numbers of extra-pair young are frequently higher in low-quality territories or when food availability is low (Václav et al. 2003; Rubenstein 2007) possibly due to females seeking copulations from males in higher quality territories, or from males in low quality territories having little time for mate guarding; consequently male territorial behaviour may vary in severity according to habitat quality (Newton 1992).

However, birds may be lured into ecological traps and thus attain a lower breeding success in habitats that may, at the start of breeding, appear superior (Donald and Vickery 1999; Remes 2003; Nordby et al. 2009). This can be most marked in areas that receive high levels of anthropogenic disturbance (Gilroy and Sutherland 2007). For example, in agricultural habitats that are intensively managed, both vegetation structure and the fauna it supports can change dramatically following the application of pesticides, herbicides or following physical management such as the mowing of vegetated margins, which may all detrimentally impact on nesting success. Many farmland songbirds have declined significantly since the onset of agricultural intensification (Fuller et al. 1995) and whilst areas of high territory density are thought to reflect high quality habitat, the associations between territory density and reproductive parameters in farmland songbirds have only rarely been investigated (but see Donald and Vickery 1999).

The Yellowhammer, *Emberiza citrinella*, is a medium sized, socially monogamous bunting that has undergone dramatic population declines since the mid-1980s (Baillie et al. 2009). Territory density in this species is associated with the availability of suitable nesting habitat such as hedgerows and ditches, and birds show preference for short, wide hedgerows with no trees (Green et al. 1994; Kyrkos et al. 1998); consequently the removal of these habitat features seems likely to have contributed to population declines (Bradbury et al. 2000). Yellowhammers have high levels of extra-pair paternity, which largely benefits older, more colourful males (Sundberg and Dixon 1996) although there is no evidence of a density-dependent effect on the numbers of extra-pair young in this species (Sundberg and Dixon 1996). Indirect effects, through changes in behaviour, may have greater implications for Yellowhammer populations than previously anticipated (Chapter 3), and this chapter aims to explore the implications that territory density may have for chick growth and reproductive success through impacts of breeding density on adult behaviour.

Using natural variation in territory density of Yellowhammers across a number of farms under differing management practices, I explore the correlative associations between territory density, breeding behaviour and reproductive success in a declining farmland passerine and address the following questions:

1) Which habitat variables are associated with territory density?
2) Is territory density associated with reproductive success?
3) Is territory density associated with parental provisioning rate?
4) Is there an association between territory density and chick growth?

Methods

Sites

Fieldwork was carried out during May – July 2007 and 2008. Territory data were collected on 12 farms in Wiltshire, Hampshire and Gloucestershire, UK, in 2007 and on 10 of the same farms, 2 different farms within the same region, and 16 additional farms during 2008, extending the study area into West Sussex, Staffordshire, Leicestershire, Derbyshire and Shropshire. Farms consisted of pairs of organic and conventional farms, matched according to soil type, size, geography and ratio of arable to livestock and clustered into groups of four farms in distinct geographical 'clusters'. Additional data on nest success were collected during May – August 2006 from three farms in North Yorkshire, UK.

Territory density and habitat variables

Farms were visited at least three times during each breeding season and territories mapped according to the location of singing males. Each male was observed in order to differentiate between close neighbours singing at different times, and the same bird using more than one song-post within a larger territory. Where farms were too large for adequate coverage within a morning, only a subsection of the farm was surveyed: this subsection was determined both by ease of access and by the location of focal cereal fields for a concurrent project using the same sites (Mean area surveyed per farm: 0.95 ± 0.14 km^2). No territory surveys were carried out under wet or excessively windy conditions as this reduced singing behaviour and made locating and following birds more difficult. Boundary vegetation was also identified for each length of field boundary between intersections; if the boundary vegetation changed within this unit the point at which this change occurred was estimated. Vegetation was classified according to Table 1.

Territories were mapped in ArcGIS based on the centre of the territory being the song-post atop which each male was observed most frequently. Two measures of territory density were measured: 1) The number of territories per km of boundary features significantly associated with yellowhammer territories, herein referred to as territory density (Bradbury et al. 2000) and 2) The nearest neighbour distance (NND), defined as the distance to the centre of the nearest neighbouring territory (to a maximum limit of 1km where no neighbour was present within this distance). Boundary habitats (as defined in Table 1) were also mapped in ArcGIS and the total length of each boundary habitat on each farm calculated.

Table 1. Classification of boundary habitat vegetation

Habitat	Definition
Hedge	Hedgerow less than 3m in height with <10% canopy cover from trees over 3m in height
Hedge with 10-50% trees	Hedgerow less than 3m in height with 10-50% canopy cover from trees over 3m in height
Hedge with >50% trees	Hedgerow with >50% canopy cover from trees over 3m in height; also includes tree lines with no hedgerow vegetation
Gappy hedge	Hedgerow with >20% gaps along length; also includes rows of solitary bushes
Fence or wall	Fence or other boundary (except hedgerow) adjoined by <1m width of dense herbaceous vegetation.
Fence with vegetation	Fence or other boundary (except hedgerow) adjoined by >1m width of dense herbaceous vegetation

Nest and Chick data

Territorial pairs were located by repeated observations of singing males and foraging pairs. Once pairs had been located, observations allowed the approximate positioning of a nest to be detected; nests were then located by a systematic search of this region. Once nests had been located, the height of the nest above ground, and vegetation within which the nest was built were recorded, along with the height and width of the hedge at the nest site. Nest concealment was judged from photographs taken from a distance of 2m from the nest, from the angle at which the nest was most obvious. Concealment was scored on a categorical scale from 1 (highly visible) to 5 (well hidden); photos were scored blindly according to nest identity or outcome. Chicks were measured as described in Chapter 3. A nest where chicks were still present at 7 days old and where the nest remained intact but was empty when chicks were 10 days (making predation of chicks immediately prior to fledging unlikely) was deemed to have fledged successfully. Where brood reduction was evident, chicks were assumed to have starved and been removed from the nest by parents, as the likely nest predators (corvids, rodents and mustelids) in the study areas were thought unlikely to depredate only one chick. Where the nest was empty and damaged before chicks were eight days old (making fledging) unlikely, chicks were assumed depredated; I did not attempt to identify nest predators.

Behavioural data

Observations of adult foraging behaviour were carried out when chicks were between 2 and 7 days old. Provisioning watches were carried out and provisioning rate calculated as detailed in Chapter 3. Data on corvid abundance and invertebrate availability were collected as described in Chapter 3 and included in the maximal models to control for significant variation caused by these terms. However, significant effects where they have been considered previously (Chapter 3) are not discussed here.

Statistical analysis

Territory number

To determine which factors influenced the number of yellowhammer territories on a farm, a linear mixed-effects model (LMM) was constructed with territory number as the response variable; following transformation the residuals and random effects were normally distributed, meeting the assumptions of an LMM. The lengths of all boundary types (as defined in Table 1), along with farm management (organic vs. conventional), geographic location (cluster) and year were included as predictor variables; to control for pseudoreplication of data from the same farms in different years, farm ID was designated as a random factor. To determine whether management influenced the length of any boundary feature, each boundary type (as defined in Table 1) was designated as the response variable in turn in a generalised linear mixed effects model; farm management and standardised total boundary length per farm were designated as predictor variables in order to determine whether management influenced the length of any boundary feature, whilst controlling for the variation in total boundary lengths between farms. Gaussian error distributions were fitted where residuals were normally distributed; where residuals were non-normal, poisson or quasipoisson error distributions were fitted to models dependent on the dispersion parameter of the model.

The significance of the 'farm management' term was established through deletion of the term and subsequent model comparison of models with and without the term.

Nest success

Variables influencing nest success were investigated following the method of Hazler (2004), which is an extension of the Mayfield method for estimating nest success (Mayfield 1975), allowing its use in logistic regression to examine variables influencing nest survival whilst allowing for the number of days for which nests were observed. Two generalised linear mixed-effects models (GLMM) with binomial error distributions were constructed using the lmer function within the lme4 package (Bates & Maechler 2009) in R. The first model looked at the overall likelihood of nest success, with the response variable of Fail/Obsdays (as defined by Hazler 2004); the second model used the same response variable but omitted nests that failed for reasons other than predation, to examine factors influencing the likelihood of predation.

All models contained nest height, vegetation cover (concealment), year, NND, hedge height and hedge width as predictor variables. Farm ID was designated as a random factor in all three models to control for any localised effects influencing nest success. Model comparisons using AIC values were used to determine whether terms significantly improved the fit of the model; those that didn't were removed in a stepwise fashion until only those terms that improved the fit of the model at $p<0.05$ remained. Following model simplification, each term was reinserted into the minimum adequate model (MAM) in turn and compared with the MAM using AIC comparisons to ensure lack of association with the response variable.

Provisioning rate

To determine whether provisioning rate was associated with territory density at both the local and farm-scale, a linear mixed-effects model was constructed using the lme function within the nlme package (Pinheiro et al. 2009) in R. Provisioning rate was designated as the response variable, with corvid activity, farm management, brood size, invertebrate abundance, chick age, year, NND, farm-scale territory density, and quadratic relationships with temperature and time of day as predictor variables. The maximal model also contained two-way interactions between NND and each of brood size, corvid abundance and invertebrate abundance as these terms were considered likely to interact with local territory density, possibly as a measure of territory quality, to influence the response variable. A two-way interaction between brood size and invertebrate abundance was also included in the maximal model as this term significantly improved the fit of previous models investigating the effect of corvid activity on provisioning rate (Chapters 3 & 5). Nest ID within Farm ID were included as nested random effects within the models to control for the non-independence of chicks within nests, and nests within farms. Model simplification was as described previously.

Chick growth

Growth was assessed by tarsus measurements as tarsus growth is likely to be more variable than wing growth (Nilsson and Svensson 1996). Two linear models were constructed, each testing the importance of interactions with either local or farm scale territory density (sample size and subsequent degrees of freedom did not allow the inclusion of all terms in one model). For both models, second tarsus measurement was designated as the response variable, with first tarsus measurement, hours between measurements and chick age at second measurement as predictor variables to control for stage of growth and time between measurements. Other predictor variables were year, provisioning rate, management, brood size, corvid abundance, insect abundance, both measures of territory density and a quadratic relationship with temperature. Two-way interactions between each territory variable (in separate models) and brood size, management, corvid abundance and invertebrate abundance (as potential measures of territory quality) were included in the maximal model. Nest ID was designated as a random effect in both models to control for non-independence of chicks within nests; Farm ID was not controlled for as the model was looking for associations with variation in farm scale territory density, for which there was one value per farm. Following transformation of predictor variables where necessary, model residuals were normally distributed. Model simplification was as described previously.

Results

Territory number

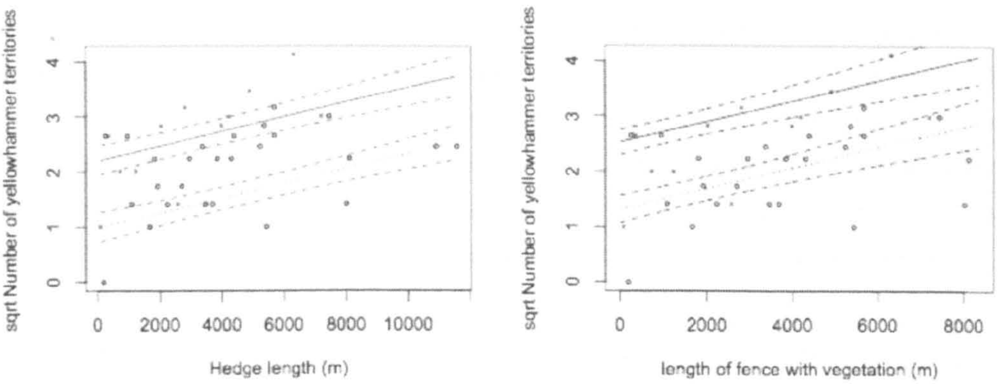


Figure 1. Yellowhammer territory number increases with increasing a) hedge length (LME, $F_{1,5}$=12.88, p=0.02) and b) length of fence with vegetation (LME, $F_{1,5}$=12.50, p=0.02) and differed between 2007 and 2008 (LME, $F_{1,5}$=49.56, p<0.01). Points show raw data during 2007 (crosses) and 2008 (circles); lines are predicted from the MAM (Table 2) with average lengths of other significant boundaries (hedge: 3911 m; fence with nettles: 743.9 m; fence or wall: 1116m; hedge with 10-50% trees: 240.6 m) during 2007 (solid line) and 2008 (dotted line); dashed lines show SE.

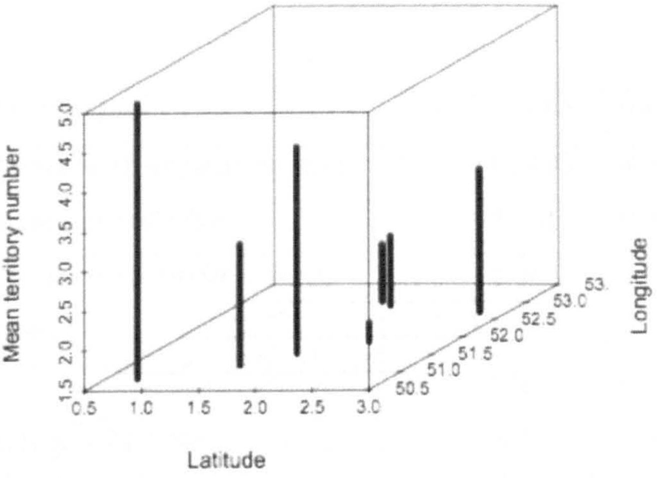


Figure 2. Geographical variation in yellowhammer territory number with longitude and latitude. Bars represent mean values per farm.

Territory data were collected from twenty-eight farms over two years. Yellowhammer territory number was positively associated with the lengths of both hedgerow and fence with dense herbaceous vegetation (Figure 1; Table 2). Territory number also differed between years (2007: 7.58+/-1.29; 2008: 4.69+/-0.52 territories per farm; Figure 1) and geographically (Table 2; Figure 2). As more farms were surveyed during 2008 than 2007, data were reanalysed using only farms surveyed in both years (n=10). Territory numbers remained markedly lower in 2008 than 2007 (LME, $F_{1,5}$=36.26, p<0.01; 2007: 6.6±1.16; 2008: 3.8±0.84 territories per farm). Farm management did not influence territory number (Table 2), and did not influence the length of any boundary type when controlling for the total boundary length on each farm (Appendix 1).

Table 2. Results of an LME investigating the variables influencing the number of yellowhammer territories on a farm. For significant terms, back-transformed estimates and SE are presented. For factors the levels of the estimate and SE are also presented. All models contain Farm ID as a random effect to control for repeated measures from the same farms across years. Terms remaining in the MAM are shown in bold; for non significant terms, statistics presented are following reinsertion of the term of interest into the minimum adequate model (MAM). *Likelihood ratio tests showed these terms to significantly improve the fit of the model (Hedge with 10-50% trees: LRT=5.594, p=0.018; Fence or wall: LRT=7.238, p=0.007), thus these terms remained in the MAM but are not considered to significantly influence the response variable.

Variable	**df**	**F**	**p**	**Estimate**	**SE**
Year (2007)	**1, 5**	**49.564**	**<0.001**	**0.385**	**0.091**
Cluster	**6,21**	**3.737**	**0.011**	**Swindon: -0.898** **Gloucester: 0.597** **Uttoxeter: 1.511** **Chichester: 0.916** **Ashbourne: 0.168** **Shrewsbury: 0.159** **Andover: -0.060**	**0.352** **0.393** **0.331** **0.290** **0.440** **0.325** **0.336**
Hedge (km)	**1, 5**	**12.883**	**0.016**	**0.091**	**0.024**
Fence with vegetation (km)	**1, 5**	**12.498**	**0.017**	**0.151**	**0.040**
Fence or wall (km)	**1, 5**	**5.431**	**0.067***	**-0.079**	**0.038**
Hedge with 10-50% trees (km)	**1, 5**	**4.085**	**0.099***	**0.467**	**0.234**
	df	LRT	p		
Hedge with >50% trees (km)	1	0.798	0.372		
Gappy hedge (km)	1	0.264	0.607		
Management	1	0.831	0.362		

Nest success and productivity

Nest data were collected from 20 nests in 2006, 21 in 2007 and 10 in 2008. Twenty-three (45%) of nests successfully fledged at least one chick. Predation accounted for most (54%) of nest failures, with 19% of nests failing due to starvation and another 19% of nests abandoned during incubation. The remaining 8% of nests were destroyed during agricultural operations. None of the variables tested were associated with the probability of a nest either failing (Table 2) or being depredated (Table 3).

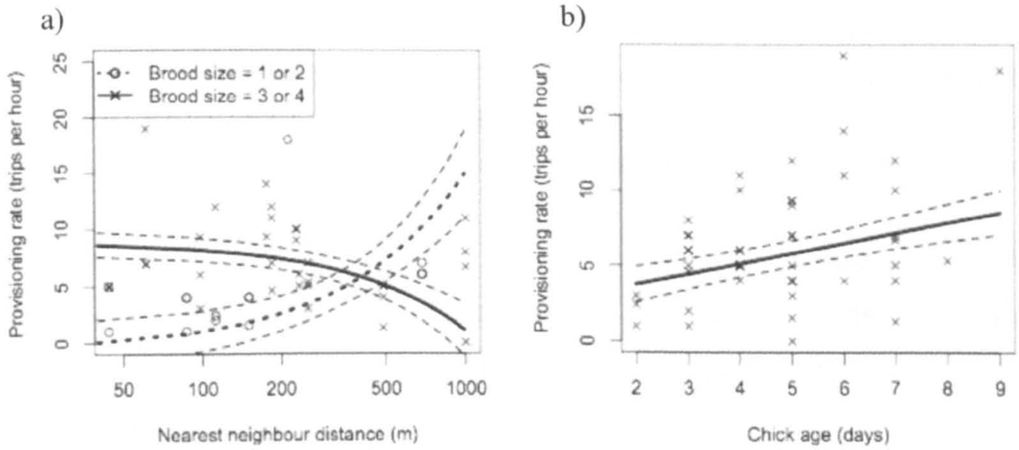
Table 2. Results of a binomial GLM investigating variables that influenced the chances of nests failing, where a failed nest is one that failed to fledge one chick. Farm ID was included in each model to control for localised effects. For non-significant terms, statistics presented are those from model comparisons to determine the influence of the term upon the fit of the model.

Variable	**AIC**	**df**	χ^2	**p**
Null model	12.105			
Nest height	12.900	1	1.205	0.272
Year	13.850	1	0.255	0.614
Hedge height	12.401	1	1.704	0.192
Hedge width	12.262	1	1.843	0.175
NND	13.523	1	0.582	0.446
Visibility	13.982	1	0.123	0.726

Table 3. Results of a binomial GLM investigating factors influencing the likelihood of nest predation, where a successful nest is one that fledged at least one chick, and a failed nest was depredated at either egg or chick stage. Farm ID was included in each model to control for localised effects. For non-significant terms, statistics presented are those from model comparisons to determine the influence of the term upon the fit of the model.

Variable	**AIC**	**df**	χ^2	**p**
Null model	11.285			
Nest height	12.489	1	0.797	0.372
Year	13.107	1	0.178	0.673
Hedge height	12.050	1	1.235	0.266
Hedge width	11.953	1	1.332	0.248
NND	12.629	1	0.657	0.418
Visibility	13.099	1	0.186	0.666

Parental provisioning rate



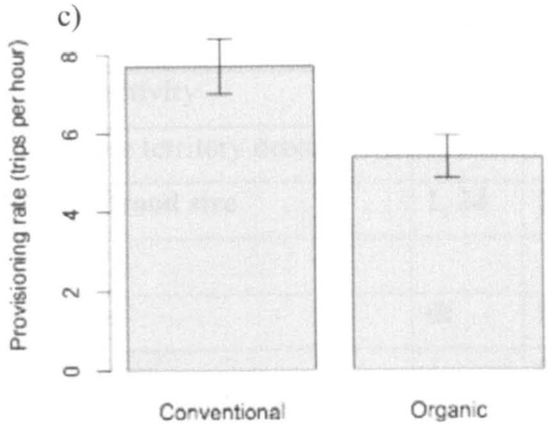


Figure 3. Parental provisioning rate was influenced by a) an interaction between brood size and NND, b) Chick age and c) Management. For a & b) Points represent raw data; lines are predicted from the MAM with mean values of chick age (4.761 days), NND (286.6 m), Brood size (2.848 chicks), invertebrate abundance (43.63 invertebrates), corvid activity (6.696 corvids), farm scale territories (1.876 territories per km significant boundary), under conventional farm management during 2007; dashed lines show SE. For c) bars represent mean values ± 1 SE.

Parental provisioning rate was associated with interactions between local territory density and brood size (Table 4), with provisioning rate increasing with increasing NND in small broods, and decreasing in large broods (Figure 3a). Whilst farm scale territory density remained in the MAM (Table 4), it did not significantly influence parental provisioning rate. Provisioning rate was also influenced by chick age and farm management (Table 4), with increasing provisioning rate with older chicks (Figure 3b), and higher provisioning rates on conventional compared to organic farms (Figure 3c).

Table 4. Results from an LME investigating variables influencing parental provisioning rate. Terms remaining in the MAM are highlighted; estimates and SE are presented for significant terms. For non-significant terms, statistics presented are those from model comparisons to determine the influence of the term upon the fit of the model. Nest ID was included as a random effect in all models to control for non-independence of chicks in the same nest. Two-way interactions of NND x invertebrate abundance (LRT_1=0.15, p=0.70), NND x Corvid abundance (LRT_1=2.56, p=0.11) and Invertebrate abundance x brood size (LRT_1=0.70, p=0.40) neither significantly improved the fit of the model nor influenced the response variable and thus were removed.

Variable	**df**	**F**	**p**	**Estimate**	**SE**
Management (Organic)	**1, 10**	**7.002**	**0.025**	**-2.282**	**1.030**
Chick age	**1, 24**	**12.732**	**0.002**	**0.679**	**0.287**
Year (2008)	1, 2	6.523	0.125*	6.477	1.477
Invertebrate abundance	1, 24	0.138	0.713*	0.063	0.030
NND	1, 2	0.076	0.809	0.024	0.007
Brood size	**1, 24**	**6.768**	**0.016**	**3.185**	**0.811**
Corvid activity	**1, 24**	**5.687**	**0.025**	**-0.090**	**0.050**
Farm scale territory density	1, 2	0.015	0.914*	1.205	0.549
NND x Brood size	**1, 24**	**12.550**	**0.002**	**-0.008**	**0.002**
Variable	**df**	**LRT**	**p**		
Time of day^2	1	0.285	0.594		
Temperature^2	1	0.818	0.366		

* Likelihood ratio tests showed these terms to significantly improve the fit of the model (Year: LRT_1=19.29, p<0.01; Invertebrate abundance: LRT_1=5.43, p=0.02; Farm scale territory density: LRT_1=5.78, p=0.02) and thus they remained in the MAM but are not considered to significantly influence the response variable.

Chick growth

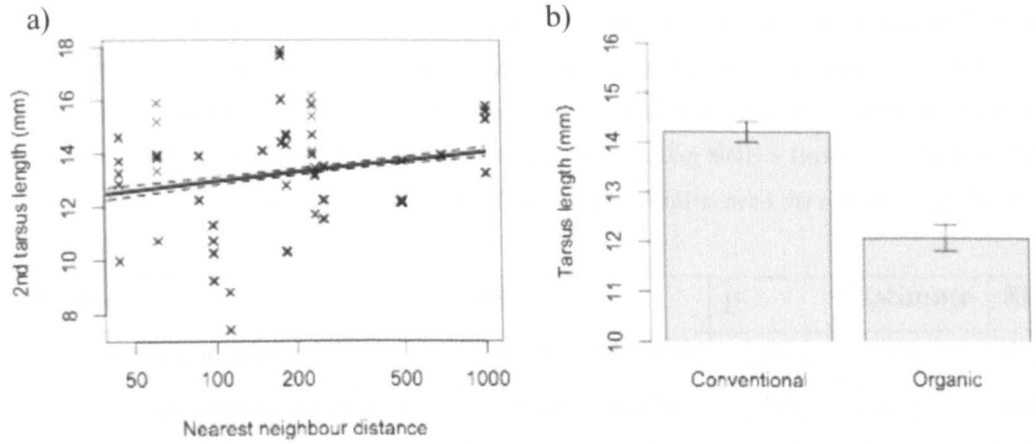


Figure 4. Chick growth was associated with a) NND and b) Management. In a) points represent raw data; the line is predicted from the MAM (Table 5) with mean values of 1st tarsus length (10.37 mm), chick age at second measurement (5.281 days),territory density (2.114 territories per km) and hours between measurements (44.98 hours); dashed lines show SE. In b) bars represent mean ± 1 SE.

Tarsus growth was associated with both nearest neighbour distance (NND) and farm management where the maximal model contained interactions with NND only (Table 5). No interactions with NND were statistically significant (Table 5). Growth increased with increasing NND (Figure 4a), and was higher on conventional farms than on organically managed farms (Figure 4b). In a model containing interactions with farm scale territory density (Table 6), chick growth was associated with an interaction between territory density and farm management (Figure 5).

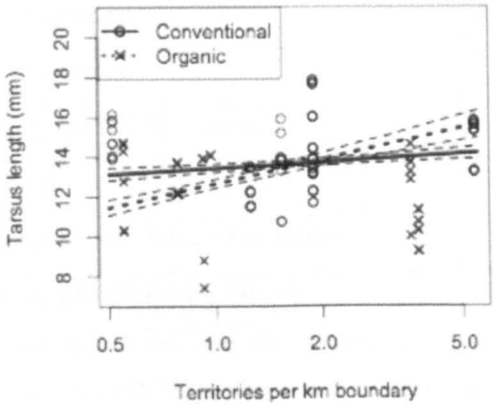


Figure 5. Chick growth was influenced by an association between territory density and farm management (Table 6). Points show raw data; lines are predicted from the MAM with mean values of 1st tarsus length (10.37 mm), hours between measurements (44.98 hours), corvid abundance (93.32 corvids), NND (298.7 m), Chick age (5.281 days), invertebrate abundance (46.04 invertebrates) and brood size (3.153 chicks) during 2007; dashed lines show ± 1 SE

Table 5. Results of an LME investigating variables influencing chick growth rate, in a model including interactions with NND. Terms remaining in the MAM are highlighted; estimates and SE are presented for significant terms. Nest ID was included as a random effect in all models to control for non-independence of chicks in the same nest. For non-significant terms, statistics presented are those from model comparisons to determine the influence of the term upon the fit of the model. Two-way interactions between log NND x Invertebrate abundance ($LRT_1<0.01$, p=0.95), log NND x Corvid abundance ($LRT_1=0.01$, p=0.93), log NND x Management and log NND x Brood size ($LRT_1=1.77$, p=0.18) neither significantly improved the fit of the model nor influenced the response variable and thus were removed.

Variable	**df**	**F**	**p**	**Estimate**	**SE**
1st tarsus measurement	**1, 110**	**235.452**	**<0.001**	**0.598**	**0.076**
Hours between measurements	**1, 110**	**14.471**	**<0.001**	**0.040**	**0.012**
Log NND	**1, 11**	**8.811**	**0.013**	**0.487**	**0.164**
Management	**1, 11**	**9.299**	**0.011**	**-0.688**	**0.305**
Chick age at 2nd measurement	**1, 110**	**5.165**	**0.025**	**0.550**	**0.190**
Log territories per km	**1, 11**	**4.712**	**0.053***	**0.457**	**0.210**
Variable	**df**	**F**	**p**		
Temperature^2	1	0.128	0.720		
Brood size	1	0.399	0.528		
Log corvid abundance	1	0.311	0.577		
Year	1	0.006	0.940		
Log invertebrate abundance	1	1.759	0.185		
Log provisioning rate+1	1	0.399	0.528		

* Likelihood ratio tests showed this term to significantly improve the fit of the model ($LRT_1=4.15$, p=0.042), and thus it remained in the MAM but is not considered to significantly influence the response variable.

Table 6. Results of an LME investigating factors influencing chick growth rate, in a model including farm scale territory density. Nest ID was included as a random effect in all models to control for non-independence of chicks in the same nest. Terms remaining in the MAM are highlighted; estimates and SE are presented for significant terms. For non-significant terms, statistics presented are those from model comparisons to determine the influence of the term upon the fit of the model. Two-way interactions between log Territory density x Invertebrate abundance ($LRT_1=1.38$, $p=0.24$) and log Territory density x Corvid abundance ($LRT_1=1.94$, $p=0.16$) neither significantly improved the fit of the model nor influenced the response variable and thus were removed.

Variable	**df**	**F**	**P**	**Estimate**	**SE**
1st tarsus measurement	**1, 107**	**541.045**	**<0.001**	**0.555**	**0.074**
Year	**1, 8**	**12.650**	**0.007**	**1.653**	**0.485**
Hours between measurements	**1, 107**	**3.808**	**0.054***	**0.037**	**0.013**
Corvid abundance	**1, 8**	**4.649**	**0.063***	**0.005**	**0.002**
Log NND	**1, 8**	**32.878**	**<0.001**	**1.174**	**0.262**
Age at second measurement	**1, 107**	**10.861**	**0.001**	**0.586**	**0.188**
Invertebrate abundance	**1, 107**	**9.170**	**0.003**	**0.025**	**0.007**
Log territory density	**1, 8**	**9.755**	**0.014**	**2.249**	**1.160**
Brood size	**1, 107**	**0.001**	**0.980**	**0.150**	**0.193**
Management	**1, 8**	**9.291**	**0.016**	**-0.784**	**0.232**
Log territory abundance x brood size	**1, 107**	**0.368**	**0.545***	**-0.576**	**0.336**
Log territory abundance x management	**1, 8**	**9.371**	**0.016**	**1.304**	**0.426**
Variable	**df**	**LRT**	**p**		
Temperature^2	1	0.032	0.858		
Log provisioning rate + 1	1	1.107	0.293		

* Likelihood ratio tests showed this term to significantly improve the fit of the model (Hours between measurements: $LRT_1=16.79$, $p<0.001$; Corvid abundance: $LRT_1=16.79$, $p<0.001$; Log territory abundance x brood size $LRT_1=16.79$, $p<0.001$), and thus it remained in the MAM but is not considered to significantly influence the response variable.

Discussion

Territory number

The number of Yellowhammer territories was positively associated with the length of available hedgerow and the length of fence associated with dense vegetation. This concurs with previous studies of Yellowhammer territory selection that indicate a preference within this species for territories containing suitable nesting habitat (Green et al. 1994; Kyrkos et al. 1998), as the majority of nests are found in hedgerows and dense herbaceous vegetation (Chapter 2) and hedgerow removal has been linked to the historic declines in Yellowhammer populations (Cornulier et al. in prep). Although territory numbers varied geographically, there were no clear north-south or east-west trends in abundance, consistent with BTO Breeding Atlas trends which show no geographical trends in abundance within the study region (Baillie et al. 2005).

Territory numbers almost halved between 2007 and 2008 on the farms in this study. This decline corresponds to country-wide declines of between 5 and 34% highlighted by the BTO's Breeding Bird Survey between 2007 and 2008 (Risely et al. 2009). The summer of 2007 was exceptionally wet (Mayes 2008), and consequently the breeding success of many species is likely to have been reduced, through a reduction in temperature, available foraging time, and invertebrate availability (Bradbury et al. 2003). Over-winter survival rates for adult and juvenile Yellowhammers are remarkably similar (Robinson 2005) and thus this species may suffer more from a reduced breeding output than other species that exhibit age-dependent survival as overall survival remains constant regardless of breeding success. By comparison, species exhibiting age-dependent survival, where adults are more likely to survive over-winter than juveniles, will have relatively higher survival following poor breeding seasons where the proportion of adults in the population is elevated.

Territory density showed no associations with nest success, and no associations were found between nest success and any of the variables investigated. The lack of association between nest visibility and nest success is surprising since corvids, considered the main predator of Yellowhammer nests (Bradbury et al. 2000) are visually oriented predators and are were thought more likely to predate more visible nests (Eggers et al. 2005). However, it is possible that behavioural compensation by adult birds may compensate for poorly concealed nests (Eggers et al. 2008).

Provisioning rate and chick growth

Large and small broods show contrasting relationships with local territory density in terms of provisioning rate. At high local territory densities, where territory quality is expected to be good and invertebrate availability is expected to be high (Davies and Lundberg 1984), parental provisioning rate to large broods was high compared to small broods, expected due to the lower food requirements of small broods of chicks. However, as local territory density decreases, provisioning rates to large broods deceases and that to small broods increases. It is possible that density-dependent competition for high quality food in areas of high local territory density leads to broods of all sizes being provisioned adequately, but food quality differing, explaining the increase in growth rate seen with decreasing local territory density. However, this does not explain the contrasting patterns in provisioning rates to large and small broods, unless small broods are of less reproductive value to their parents than large broods. This could explain the patterns observed, as parents of large broods may reduce their provisioning rate but increasing the time spent searching for high quality food as competition for high quality food is reduced at low territory densities, whereas parents of small broods increase the rate at which they provision poor quality food.

Provisioning rates were also higher on conventional farms than on organic, as were chick growth rates. This implies not only that food availability and accessibility is greater on conventional farms, which tend to have a simple habitat structure and more areas of bare ground such as within crop tramlines (pers. obs) but also that overall food quality may also be better leading to a higher overall growth rate of chicks. Growth rate also increases with increasing territory density at the farm scale – although this relationship is marginal on conventional farms and steeper on organic farms. Although not shown within my results, it is possible that there may be an interaction with nest predator abundance, especially on organic farms where a parallel study using the same sites demonstrated that the abundance of corvids was higher than on conventional farms (T. Benton, pers. comm). As a higher abundance of nest predators is known to depress parental provisioning rate (Eggers et al. 2005) with knock-on effects on chick growth and condition (Chapter 3), the management effects shown by the data may be top-down effects due to predation risk rather than bottom-up effects due to food availability or accessibility, with a dilution of risk effect at high farm-scale territory densities on organic farms allowing higher chick growth.

The provisioning data fit with a model of constant food availability (if not quality) across a range of territory densities, and the growth data suggests density-dependent competition for high quality food in areas of high territory density, contrary to expectations of the food maintenance model (Thresher, 1977 cited in Ebersole 1980). This implies that food availability during the breeding season does not influence territory choice in Yellowhammers and that territory choice is determined solely by available nesting habitat (Kyrkos et al. 1998; Bradbury et al. 2000; Cornulier et al. in prep). Whilst the reduction in available nesting habitat may be the factor limiting Yellowhammer population size and thus determining territory distribution and density (Cornulier et al. in prep), Whittingham et al (2005) suggest that breeding territory distribution is also linked to the availability of over-winter food resources (Whittingham et al. 2005). Thus, it is worth considering that there may be other explanations behind the lack of adherence to the food maintenance model. The availability of invertebrates in farmland habitats is highly variable due to anthropogenic disturbance and management: the application of pesticides and herbicides, along with physical management such as the mowing of margins all influence the abundance and accessibility of invertebrates (Morris et al. 2005; Hart et al. 2006; Douglas et al. 2009). It is possible that if Yellowhammers selected territories on the basis of habitat that might, at the onset of breeding, appear likely to provide a good source of invertebrate chick food, they may effectively fall into ecological traps as soon as pesticides are applied. This may be more likely for this species as their breeding season spans several months and therefore food availability during this time is unpredictable.

In conclusion, it appears that the availability of suitable nest sites is likely to be the limiting factor behind yellowhammer territory distribution. Data from provisioning adults suggests that the availability, although possibly not the quality, of food is relatively constant across territories, but that density-dependent competition may be occurring for high quality food in areas of high local territory density, leading to slower chick growth. I suggest that trends of higher provisioning rate and chick growth on conventionally managed farms may be a result of top-down effects from a higher abundance of nest predators on organic farms, rather than bottom-up effects of food availability.

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Appendix 1. Results of separate generalised linear mixed-effects models establishing whether the length of each boundary type (as defined in Table 1) differs between organic and conventional farms, when controlling for the total boundary length. Statistics presented are from likelihood ratio tests comparing models with and without the management term. Farm ID was included as a random factor within each model to control for repeated measures from the same farms across years.

Variable	**df**	**LRT**	**p**
Gappy hedge	1	0.128	0.721
Hedge with 10-50% trees	1	1.484	0.223
Fence with nettles	1	0.785	0.376
Fence or wall	1	0.001	0.971
Boundary with >50% trees	1	0.704	0.402
Hedge length	1	0.017	0.896

Chapter 5: Sex differences in behaviour around the nest during chick provisioning in Yellowhammers (*Emberiza citrinella*)

Abstract

Sex differences in provisioning to offspring are widespread, and have consequences for both reproductive success and survival. Females often suffer higher mortality than males and are thought more susceptible to the costs of reproduction, but males show an increased cost of parental care on survival. Here, I investigate sex differences in provisioning strategies and nest visitation behaviour in a declining farmland bird. As chick food availability is thought to be limiting in this species, females were expected to be working close to their ceiling of energetic expenditure during chick provisioning; consequently males were expected to increase their provisioning rate in response to an increase in chick age and larger brood size. Provisioning rates of females were consistently higher than those of males; however, males showed a greater degree of flexibility in their response to brood size and chick age. Females spent more time at the nest than males, and for females this time decreased with increasing chick age and brood size, probably due to a combination of the reduced risk of chilling and increased food demands of larger broods and older chicks. Parents responded differently to an increase in the activity of corvids, the main nest predator of the Yellowhammer: males increased the amount of time spent in the vicinity of the nest, possibly as a nest defence strategy, whereas females decreased the amount of time, possibly to reduce the levels of activity around the nest which have been linked to an increased risk of nest predation. I discuss potential reasons behind female-biased provisioning in this species, namely high levels of extra-pair paternity; I also discuss potential consequences of high work rates for sex-linked survival.

Introduction

Sexual conflict is present at many stages of reproduction, from fertilisation through to care of offspring, and is key to the evolution of mating systems (Krebs and Davies 1993). Socially monogamous mating systems, thought to have evolved in species where biparental care of young is a necessity, may seem harmonious; however, there is still conflict between the sexes over how much care to provide (Krebs and Davies 1993). Biparental care is the most common form of parental care in birds and occurs in over 90% of avian species (Wesolowski 1994).

Sex differences in food provisioning to offspring are widespread (Conrad and Robertson 1993; Hamer et al. 2006; English et al. 2008). Sex differences in avian provisioning behaviour were originally ascribed to differences in body size in sexually dimorphic species (Weimerskirch and Lys 2000), as the smaller sex tends to have reduced competitive ability and potentially poorer foraging efficiency (Weimerskirch and Lys 2000). However, the existence of differential provisioning strategies in sexually monomorphic species appears to contradict this (Lewis et al. 2002; Quillfeldt et al. 2004) and leads to the possibility that parents may respond differently to chick begging behaviour (Quillfeldt et al. 2004) in species where begging behaviour is an honest signal of nutritional need (Quillfeldt et al. 2006). Female Manx Shearwaters *Puffinus puffinus* adjust both their provisioned meal sizes and subsequent foraging trip duration according to the begging intensity of the chick; however males show no such adjustment (Quillfeldt et al. 2004). Differential responses to begging are also found in passerines: female Canaries *Serinus canaria* respond to both the height attained by nestlings during begging, and the intensity of the begging display, whereas males respond only to begging height (Kilner 2002), and responses to begging can also depend upon the actions of the other parent (Hinde and Kilner 2007).

Parents may differ in their foraging strategies in order to reduce intra-pair competition for food when foraging for young (Aho et al. 1997). As a consequence, parents may differ in foraging habitats (Aho et al. 1997; Krupa 2004), foraging strategies (Morse 1968; Lewis et al. 2002; Peck and Congdon 2006), or may forage at different distances from the nest (Robins 1971; Falconer et al. 2008) and bring back differing food items (Krupa 2004; Poulin and Todd 2006). This may be in part due to different roles in parental care: female passerines are more likely to brood nestlings in order to prevent chilling, especially when offspring are young (Morse 1968; Robins 1971; Grundel

1987; Markman et al. 1995; Lormee et al. 2005; Falconer et al. 2008; Budden and Beissinger 2009); however, males are more likely to guard or defend their nest against potential predators (Morse 1968; Robins 1971; Markman et al. 1995; Lessells et al. 1998) and may thus spend more time in the vicinity of the nest and not actively foraging for young. When faced with a model predator, males are more likely to risk their own survival for larger broods of older and better quality nestlings (Michl et al. 2000).

Provisioning behaviour also varies sex-specifically according to brood size and chick age. Feeding rates tend to be higher for large broods of chicks (Rauter et al. 2000; Wiebe and Elchuck 2003; but see also Moreno 1987) and food load size may also increase (Siikamäki et al. 1998), although in some species males increase provisioning more than females to larger broods (Grundel 1987; Carey 1990). Per-nestling feeding rates are not necessarily constant with increasing brood size: in some species, smaller broods may receive more food per-nestling (Grundel 1987): this may either be as a result of food-limitation in large broods, or lower energetic requirements of large broods due to decreased heat-loss. In other species, larger broods may receive more food per nestling, indicating that the demands of the brood increase disproportionately with increasing brood size (Falconer et al. 2008). However, this may be confounded by the size of food items, as indicated by a reduced provisioning rate to large broods showing no association with chick growth rate in Orange-Tufted Sunbirds *Nectarinia osea* (Markman et al. 1995), although experimentally increasing brood size in Fairy Martins *Petrochelidon ariel* decreases both per-capita food provisioning and growth rates (Magrath et al. 2007).

Provisioning rates, or the number and size of food items, also increase with increasing chick age (Grundel 1987; Moreno 1987; Wright 1998): in some species this happens in parallel for the sexes (Conrad and Robertson 1993); for some species males increase their provisioning for older chicks or fledglings more than females (Wiggins and Morris 1986; Carey 1990; Wheelwright et al. 2003) or females may even reduce provisioning (Bradley et al. 2002): in multi-brooded species this is may allow females to devote time to the next reproductive attempt (Wheelwright et al. 2003). Conversely, in other species, females increase their provisioning to older broods more than males, thought to be as a consequence of the reduced brooding requirements of older chicks (Falconer et al. 2008; Wiebe and Slagsvold 2009), or due to male birds spending time defending territories (Yasue and Dearden 2008) or nests (Hogstad 2005).

Experimentally increased brood size has species-specific effects, probably dependent on the ease of acquiring food and the ceiling to parental expenditure. The per-nestling provisioning rate of Eastern Phoebes *Sayornis phoebe* is unaffected by increasing brood size: both parents adjust their provisioning accordingly (Conrad and Robertson 1993), although the per-nestling provisioning rate of Fairy Martins declines with an experimentally increased brood size with knock on effects on chick growth (Magrath et al. 2007). Male American Kestrels *Falco sparverius* invest reproductive effort according to the number of young in the nest and can maintain this if the provisioning period is experimentally extended; females appeared unable to sustain their provisioning effort for the extended period of time (Dawson and Bortolotti 2008), suggesting that females are nearer to their ceiling of energy expenditure during the natural length of the chick rearing period than are males (Dawson and Bortolotti 2008). Male Pied Flycatchers *Ficedula hypoleuca* are able to increase provisioning to experimentally enlarged broods unlike females, which are thought unable to increase work rate any further (Siikamäki et al. 1998). Female work rate may be more crucial to chick survival than that of males in some species: the provisioning rate of female Macaroni Pnguins *Eudyptes chrysolophus* is associated with chick survival, whereas that of males relates to the growth and fledging mass of survivors (Barlow and Croxall 2002).

Temperature can influence provisioning in two ways: by increasing the amount of time that chicks require brooding, especially in small broods (Moreno 1987; Wiebe and Elchuck 2003), or by decreasing the availability of food for those species that rely upon a variable food supply such as invertebrates or fish with which to feed their young (Rauter et al. 2000; Low et al. 2008). Some species are able to compensate for a reduction in food availability, indicated by a lack of association between food availability and the number, size or weight of fledglings (Rauter et al. 2000); this may be because food availability still remains above the threshold at which the amount of food being brought to the chicks would decrease. Sex-specific differences in provisioning strategies between years may reflect contrasting annual food availability (Huin et al. 2000): for example, during bad food years, both Crested Auklet *Aethia cristatella* parents forage equally, however during good food years males brood the chick more in order to defend it from attack (Fraser et al. 2002).

Differences in parental expenditure between the sexes can lead to differential mortality. Females often have higher mortality than males (Liker and Székely 2005) and are thought more susceptible to the costs of reproduction (Dawson and Bortolotti 2008). However, males show a cost of increased parental care on survival (Liker and Székely 2005), so if environmental factors such as reduced food availability lead to a requirement for a higher male work rate, which in turn leads to a higher male mortality, a skewed sex ratio in a population is likely to have implications for future population reproductive success.

Here, I investigate sex differences in provisioning behaviour, factors influencing male singing behaviour, and sex differences in time budgets during chick provisioning in the Yellowhammer *Emberiza citrinella*, a declining farmland passerine. Food availability for chicks is known to be limiting in this species, and declines in invertebrate abundance have been linked to slower chick growth and reduced chick survival (Boatman et al. 2004; Morris et al. 2005; Hart et al. 2006). Adult and juvenile Yellowhammer survival is similar, (Siriwardena et al. 1998), suggesting that breeding adults may be improving the chances of survival of their offspring, with knock-on effects on their own survival. It is therefore thought that females are likely to be working at their maximum rate and that males will be required to absorb any shortfall in provisioning by females in order to reduce any impacts upon their chicks. Consequently, the following predictions are made:

1) Males are predicted to increase their provisioning rate more than females in response to increasing chick age and larger brood size.
2) Males are predicted to spend more time than females in the vicinity of the nest, and to decrease this time with increasing chick age and larger brood size.
3) Males are predicted to spend less time singing with increasing chick age and larger brood size.
4) Females are predicted to spend more time than males at the nest, especially when chicks are young.

Methods

Sites

Sites, territory and nest location and measurement of chick growth rate are as described in Chapter 3.

Provisioning and behavioural data

Observations of adult foraging behaviour were carried out when chicks were between 2 and 7 days old. Provisioning watches were carried out and provisioning rate calculated as detailed in Chapter 3. In addition, for each provisioning trip the sex of the parent was identified both on departure from and on return to the nest. Additional data collected during each provisioning watch consisted of the number of male song bursts, defined as either a complete song containing both the initial and final phrase, or just the initial phrase (Wonke and Wallschläger 2009).

The time of arrival to the vicinity of the nest after each foraging trip, time to return to the nest, time to leave the nest and time to leave the vicinity of the nest to forage was recorded for each provisioning trip and allowed the calculation of the time waiting on the hedge before and after each foraging trip, time foraging and time spent at the nest by each parent.

Statistical analyses

Statistical analyses were carried out in R (version 2.7.1 for Mac; http://www.R-project.org). Model comparisons using AIC values were used to determine whether terms significantly improved the fit of the model; those that didn't were removed in a stepwise fashion until only those terms that improved the fit of the model at $p<0.1$ remained; only terms that influenced the response variable at $p<0.05$ were considered to influence the response variable. Following model simplification, each term was reinserted into the minimum adequate model (MAM) in turn and compared with the MAM using AIC comparisons to ensure lack of association with the response variable. Statistics presented throughout are mean ± 1 SE.

Sex differences in provisioning

To determine whether the sexes differed in their provisioning behaviour in response to environmental variables, a generalised linear mixed-effects model with quasipoisson error distributions was constructed using the lmer function within the lme4 package (Bates and Maechler 2009) in R. The number of provisioning trips per parent was designated as the response variable, with two-way interactions of the sex of the parent with each of corvid activity, farm management, brood size, chick age, year, time of day, temperature and invertebrate abundance as predictor variables to determine whether male and female parents adjust their provisioning rate differentially in response to each variable. Quadratic terms for temperature and time of day were used as examination of the raw data suggested quadratic relationships between these two terms and provisioning rate. An interaction between brood size and invertebrate abundance was also considered in the maximal model as this interaction had been found to influence the model fit in a separate analysis examining factors influencing overall provisioning rate (Chapter 3). To control for between-provisioning watch and between-pair differences, provisioning watch ID nested within Nest ID within Farm were designated as random factors to control for the identity of parents as well as unmeasured variables such as chick hunger or begging behaviour that could not be controlled for but were assumed to be equal within the same provisioning watch.

Male song behaviour

A GLMM with binomial error distributions was constructed to determine which factors influenced whether or not a male sang during chick provisioning. Whether or not males sang was designated as the binomial response variable, and male provisioning rate, corvid activity, brood size, invertebrate abundance, farm-scale territory density, nearest neighbour distance, chick age, management and year were included as predictor variables, along with quadratic relationships with time of day and temperature. The maximal model also considered two-way interactions between farm-scale territory density and each of invertebrate abundance and corvid abundance as it was thought possible that corvid abundance and invertebrate abundance, which may constrain the time budgets of males in terms of foraging and chick provisioning behaviour, may interact with the density of male conspecifics in the area. Nest ID within Farm were designated as nested random factors to control for individual and local differences in song behaviour.

Sex differences in time budgets

Generalised linear mixed-effects models were constructed using the lmer function within the lme4 (Pinheiro et al. 2009) library in R (R Core Development Team 2006), to determine which factors influenced Yellowhammer time budgets whilst feeding chicks. Three different activities were identified: foraging, nest visitation, and spending time in the vicinity of the nest. Some birds were noted to only spend time foraging and visiting the nest; thus, two additional models were constructed to investigate firstly, which factors influenced whether or not a bird spent time in the vicinity of the nest, and secondly, for those that did, which factors influenced the amount of time spent. Binomial error distributions were fitted to the model investigated factors influencing whether or not a bird spent time in the vicinity of the nest; following the division of the other response variables (measured in seconds) to bring the dispersion parameter within acceptable limits (0.5 - 2), poisson error distributions were fitted to the other three models.

The maximal models contained corvid abundance, invertebrate abundance, management, year, chick age, brood size, and quadratic relationships with time of day and temperature, along with two-way interactions of each of these terms with the sex of the parent, to look for sex differences. The model of time spent foraging also contained the interaction between brood size and invertebrate abundance, as this term influenced provisioning rate and it was thus considered necessary to control for any effects in the foraging time model. Provisioning watch ID within Nest ID within Farm were included as nested random factors to control for individual differences and for unmeasured variables such as chick hunger, which was thought likely to differ within nests between provisioning watches.

Results

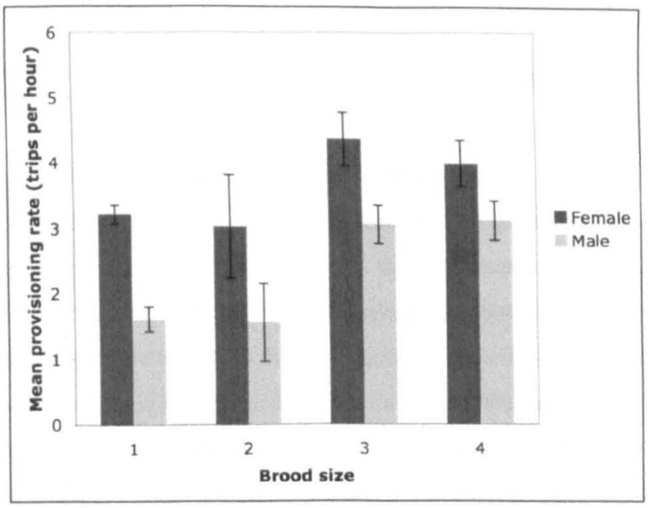


Figure 1. Males and females differed in their provisioning rates to differently sized broods (GLMM, $F_{1,42}$=4.95, p=0.03). Bars represent predicted mean provisioning rates; error bars depict standard error. Mean provisioning rates and SEs are predicted from the MAM (Table 1) with a chick age of 7 days, mean corvid abundance (6.696 corvids) and conventional management during 2007.

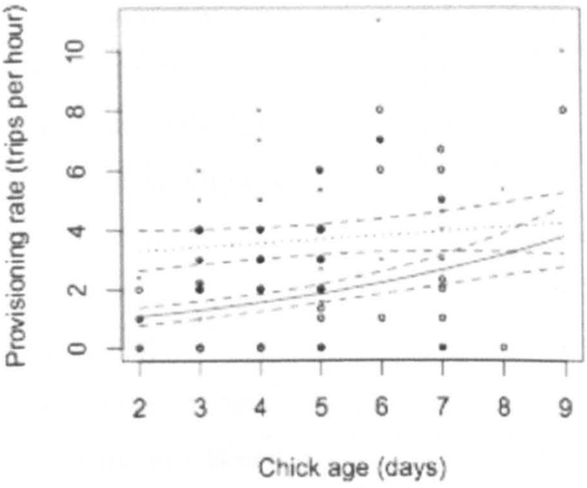


Figure 2. The change in provisioning rate with chick age differed between the sexes (GLMM, $F_{1,42}$=4.55, p=0.04). Points show raw data: crosses represent female provisioning rates; open circles depict male provisioning rates. Lines are predicted from the MAM (Table 1) with a brood size of three nestlings, mean corvid abundance (6.696 flying corvids), and conventional management during 2007: the solid line represents male provisioning; the dotted line shows female provisioning. Dashed lines represent SE.

Data were collected from 46 provisioning watches at 17 nests during 2007 and 2008. Nine nests were on organically managed farms and eight nests were on conventional farms.

Provisioning rate

Provisioning rates differed between the sexes, with a higher mean provisioning rate in females than males (Table 1; Males 2.62 ± 0.35 trips per hour, Females 3.88 ± 0.43 trips per hour). Male and female Yellowhammers also differed in their provisioning response to chick age, brood size and farm management (Table 1). Provisioning rates of both males and females increased with increasing brood size (Figure 1), although broods of 2 received no more food trips than broods of 1 and broods of 4 were provisioned at similar rates to broods of 3 by both parents (Figure 1).

Provisioning rates of both males and females increased with increasing chick age, although in females this increase was slight (Figure 2). Until chicks were 8 days old, females provisioned more frequently than males (Figure 2) but from 8 days of age males and females provisioned chicks more equally (Figure 2).

Table 1. Results from a GLMM to determine how the sexes differ in their provisioning behaviour. Significant interaction terms with parent indicate sex differences in response to the relevant variable; significant single terms indicate terms that the sexes respond to consistently. For significant terms, parameter estimates with SE are presented; for non-significant main effects, statistics are following reinsertion of the term into the minimum adequate model (MAM) and subsequent model comparison. All models contained nested random factors of provisioning watch ID within Nest ID within Farm to control for differences between pairs and within pairs between different provisioning watches when unmeasured factors such as chick hunger might differ. *This term approached significance in influencing the fit of the model (χ^2_1=3.69, p=0.05) and thus remains in the MAM but is not considered to significantly influence the response variable. Two way interactions of Sex of parent x corvid activity (χ^2_1=0.63, p=0.43), Sex of parent x year (χ^2_1=0.97, p=0.32), Sex of parent x invertebrate abundance (χ^2_1=0.63, p=0.43), Sex of parent x Temperature^2 (χ^2_1=1.33, p=0.25) and Sex of parent x time of day^2 (χ^2_1=1.29, p=0.26) neither significantly influenced the fit of the model nor significantly influenced the response variable and thus were removed from the MAM.

Variable	**df**	**z**	**p**	**Estimate**	**SE**
Insect abundance	1	2.479	0.013	0.011	0.004
Corvid activity	1	-2.824	0.005	-0.029	0.010
Sex of parent (Male)	1	-3.137	0.002	-2.298	0.733
Management (Organic)	1	-2.231	0.026	-0.405	0.182
Brood size	1	2.450	0.014	0.454	0.185
Chick age	1	0.725	0.468	0.038	0.052
Year (2008)	1	3.753	<0.001	0.602	0.160
Sex of parent x Management	1	1.905	0.057*	0.489	0.257
Sex of parent x Brood size	1	2.029	0.042	0.308	0.152
Sex of parent x Chick age	1	1.978	0.048	0.147	0.075
Insect abundance x Brood size	1	-2.176	0.030	-0.004	0.002
Variable	**df**	**χ^2**	**p**		
Temperature ^{2}	1	0.167	0.683		
Time ^{2}	1	0.283	0.595		

Male song behaviour

No terms influenced whether or not male birds sang during chick provisioning (Table 2).

Table 2. Results from a GLMM to determine which variables influence whether or not a male sings whilst provisioning nestlings. *This term approachaed significance in improving the fit of the model (χ^2_1=) and thus remains in the MAM but is not considered to significantly influence the response variable. For significant terms, parameter estimates with SE are presented; for non-significant main effects, statistics are following reinsertion of the term into the minimum adequate model (MAM) and subsequent model comparison. All models contained nested random factors of Nest ID within Farm to control for differences between males. Two-way interactions of Corvid activity x farm scale territory density (χ^2_1=0.08, p=0.78) and Invertebrate abundance x farm scale territory density (χ^2_1=0.11, p=0.74) neither significantly influenced the fit of the model nor significantly influenced the response variable and thus were removed from the MAM.

Variable	**df**	z	**p**	**Estimate**	**SE**
Chick age	1	-1.896	0.058*	-0.561	0.296
Variable	**df**	χ^2	**p**		
Male provisioning rate	1	0.021	0.885		
Temperature ^{2}	1	0.095	0.758		
Time of day ^{2}	1	0.130	0.719		
Brood size	1	2.078	0.149		
Management	1	0.007	0.933		
Year	1	0.124	0.724		
Farm scale territory density	1	0.326	0.568		
Invertebrate abundance	1	1.042	0.307		
Corvid activity	1	1.409	0.235		
Nearest neighbour distance	1	0.327	0.567		

Nest visitation behaviour

Time spent foraging

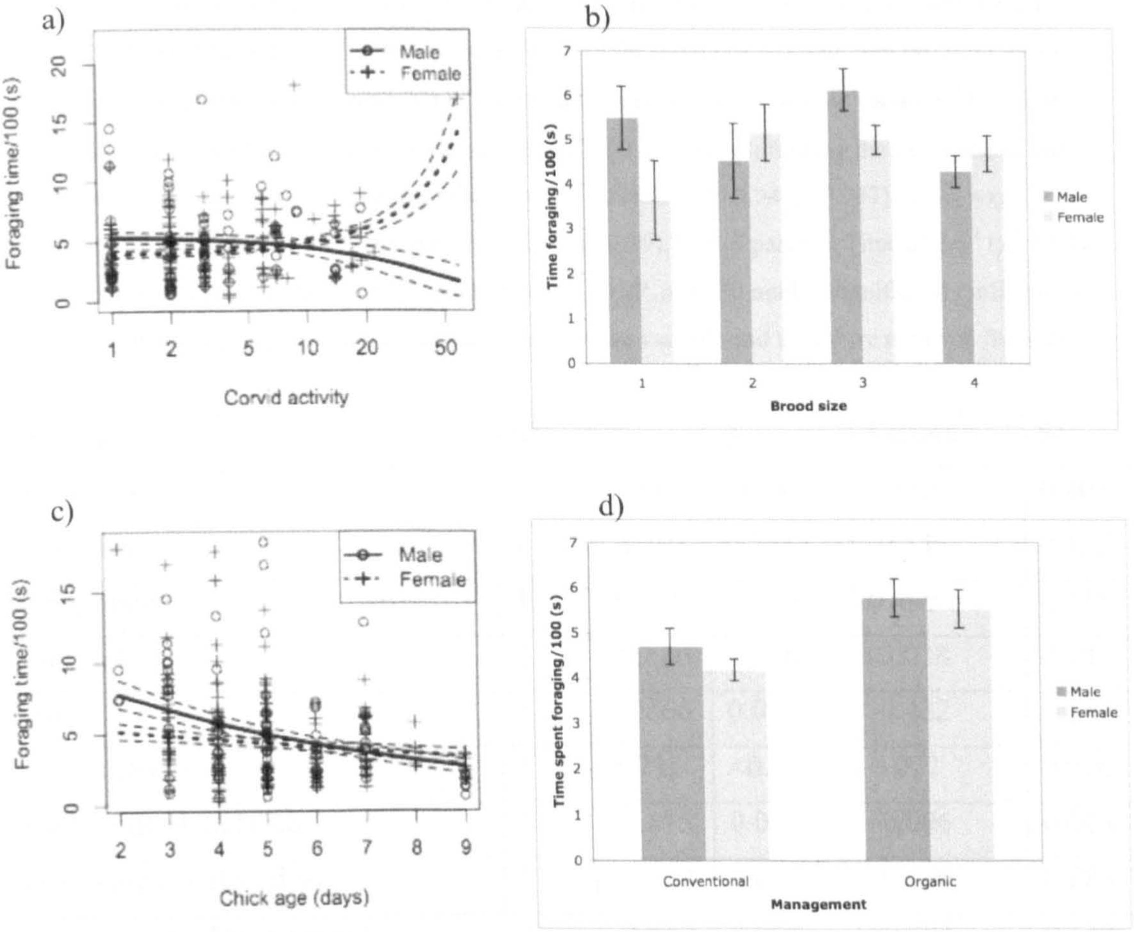


Figure 3. Parents differed in their time spent foraging with a) Corvid abundance, b) Brood size, c) Chick age and d) Farm management according to sex (Table 3.). For b) and d) bars represent mean ± SE. For a) and c), points represent raw data and lines are predicted from the MAM (Table 3) with mean values for brood size (2.959 chicks), chick age (5.051 days), invertebrate abundance (84.63 invertebrates) and corvid abundance (4.895 corvids) during 2007 and under conventional management. Dashed lines show SE.

The amount of time spent foraging was influenced by interactions between the sex of the parent and corvid activity, brood size, chick age and farm management. As corvid activity increased, male foraging time decreased whereas female foraging time increased (Figure 3a). The relationship between foraging time and brood size wasn't clear-cut; however, for broods of one chick, males spent more time foraging than females (Figure 3b). For young chicks (2-4 days old), males spent more time foraging than females; the amount of time spent foraging by both parents decreased with increasing chick age, but this relationship was steeper for males than for females and from 5 days old both sexes spent similar amounts of time foraging (Figure 3c). When nesting on organic farms, both sexes spent more time foraging than on conventional farms (Figure 3d).

Table 3. Results from a GLMM to determine which variables influence the amount of time a bird spends foraging. For significant terms, parameter estimates with SE are presented; for non-significant main effects, statistics are following reinsertion of the term into the minimum adequate model (MAM) and subsequent model comparison. All models contained nested random factors of Watch ID within Nest ID within Farm to control for individual differences, and for unmeasured variable such as chick hunger. *This term approached significance in improving the fit of the model ($\chi^2_1=3.480$, $p=0.062$) and thus is retained in the MAM but is not considered to significantly influence the response variable. ‡This term contained a point of high influence at corvid abundance = 59; however following the exclusion of this point the term still significantly influenced the response variable ($\chi^2_1=3.94$, $p=0.047$). Two-way interactions of Sex of parent x Temperature^2 ($\chi^2_1=1.73$, $p=0.19$), Sex of parent x Time of day^2 ($\chi^2_1=0.09$, $p=0.77$) and Sex of parent x invertebrate abundance ($\chi^2_1=0.27$, $p=0.60$) neither significantly influenced the fit of the model nor significantly influenced the response variable and thus were removed from the MAM.

Variable	**df**	**z**	**p**	**Estimate**	**SE**
Sex of parent	1	3.442	<0.001	1.385	0.402
Brood size	1	-1.101	0.271	-0.145	0.132
Management	1	3.414	<0.001	0.460	0.135
Chick age	1	-0.886	0.376	-0.038	0.043
Year	1	-2.866	0.004	-0.422	0.147
Corvid activity	1	3.791	<0.001	0.022	0.006
Invertebrate abundance	1	-1.815	0.070	-0.006	0.003
Sex of parent x Brood size	1	-2.358	0.018	-0.200	0.085
Sex of parent x Management	1	-2.652	0.008	-0.394	0.149
Sex of parent x Chick age	1	-2.010	0.044	-0.100	0.050
Sex of parent x Year	1	1.872	0.061*	0.347	0.185
Sex of parent x Corvid activity	1	-2.304	0.021‡	-0.037	0.016
Brood size x Invertebrate abundance	1	2.060	0.039	0.003	0.001
Variable	**df**	χ^2	**p**		
Temperature ^{2}	1	1.517	0.218		
Time of day ^{2}	1	0.818	0.366		

Time spent in vicinity of nest

Whether or not a parent waited in the vicinity of its nest was influenced only by invertebrate abundance (Table 4). Birds that waited had a higher invertebrate abundance in the vicinity of their nest than birds that didn't wait (Wait: 95.70 ± 3.64 insects; No wait: 66.41 ± 6.93).

Table 4. Results from a GLMM to determine which variables influence whether or not a bird spends time waiting in the vicinity of its nest. For significant terms, parameter estimates with SE are presented; for non-significant main effects, statistics are following reinsertion of the term into the minimum adequate model (MAM) and subsequent model comparison. All models contained nested random factors of Watch ID within Nest ID within Farm to control for individual differences, and for unmeasured variable such as chick hunger. *This term approached significance in influencing the fit of the model (χ^2_1=3.665, p=0.056) and thus remained in the MM but is not considered to significantly influence the response variable. Two-way interactions of Sex of parent x chick age (χ^2_1=0.17, p=0.68), Sex of parent x year (χ^2_1=0.10, p=0.75), Sex of parent x brood size (χ^2_1=0.18, p=0.67), Sex of parent x corvid activity (χ^2_1=0.52, p=0.47), Sex of parent x insect abundance (χ^2_1=0.58, p=0.28), Sex of parent x temperature^2 (χ^2_1=1.18, p=0.28), Sex of parent x management (χ^2_1=2.25, p=0.13), and Sex of parent x time of day^2 (χ^2_1=2.10, p=0.15) neither significantly influenced the fit of the model nor significantly influenced the response variable and thus were removed from the MAM.

Variable	**df**	z	p	**Estimate**	**SE**
Insect abundance	1	2.739	0.006	0.016	0.006
Temperature^2	1	1.853	0.063*	0.004	0.002
Variable	**df**	χ^2	p		
Brood size	1	1.583	0.208		
Time^2	1	1.231	0.267		
Management	1	1.160	0.282		
Chick age	1	0.001	0.995		
Year	1	0.105	0.746		
Corvid activity	1	0.272	0.602		

For birds that did wait, the amount of time spent waiting was influenced by an interaction between brood size and the sex of the parent, and by a quadratic relationship with temperature (Table 5). The amount of time spent waiting by females was consistently low across all brood sizes; however the amount of time that males spent waiting decreased with increasing brood size, until both parents spent similar amounts of time waiting for broods of four chicks (Figure 4a). The length of time spent waiting increased non-linearly with temperature (Figure 4b).

Table 5. Results from a GLMM to determine which variables influence the amount of time a bird spends waiting in the vicinity of its nest. For significant terms, parameter estimates with SE are presented; for non-significant main effects, statistics are following reinsertion of the term into the minimum adequate model (MAM) and subsequent model comparison. All models contained nested random factors of Watch ID within Nest ID within Farm to control for individual differences and for unmeasured variable such as chick hunger, which may differ within nests between provisioning watches. *This term approached significance in influencing the fit of the model (χ^2_1=2.72, p=0.099) and thus remained in the MAM but is not considered to significantly influence the response variable. Two-way interactions of Sex of parent x management (χ^2_1<0.01, p=0.99), Sex of parent x Time of day^2 (χ^2_1=0.08, p=0.78), Sex of parent x chick age (χ^2_1=0.43, p=0.51), Sex of parent x invertebrate abundance (χ^2_1=1.21, p=0.27), Sex of parent x year (χ^2_1=0.58, p=0.45), Sex of parent x temperature^2 (χ^2_1=1.14, p=0.34) and Sex of parent x corvid activity (χ^2_1=1.47, p=0.23) neither significantly influenced the fit of the model nor significantly influenced the response variable and thus were removed from the MAM.

Variable	**df**	**z**	**p**	**Estimate**	**SE**
Sex of parent (Male)	1	4.736	<0.001	2.310	0.488
Brood size	1	-1.057	0.291	-0.167	0.157
Temperature^2	1	2.427	0.015	0.002	0.001
Year	1	-1.842	0.066*	-0.561	0.304
Sex of parent x Brood size	1	-2.541	0.011	-0.421	0.166
Variable	**df**	**χ^2**	**p**		
Corvid activity	1	0.016	0.903		
Invertebrate abundance	1	0.006	0.936		
Chick age	1	0.921	0.337		
Time^2	1	2.518	0.113		
Management	1	0.186	0.667		

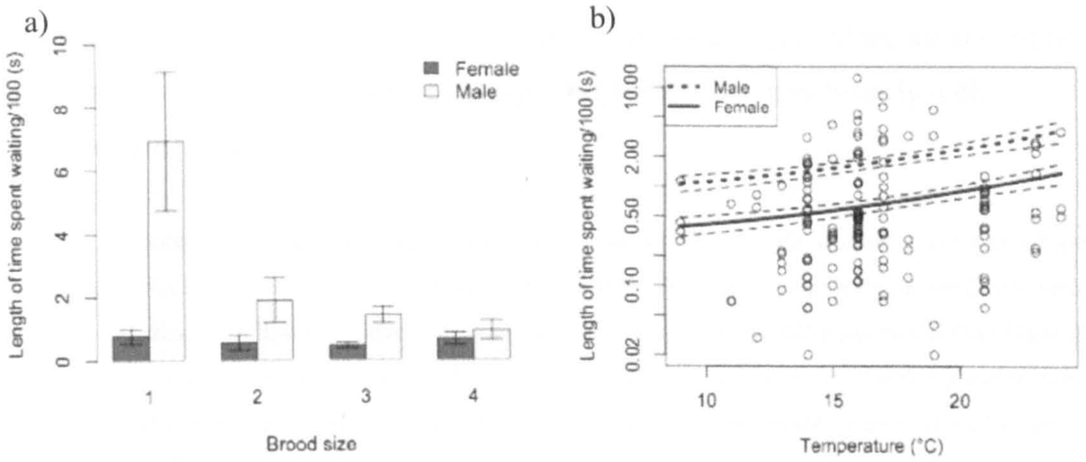
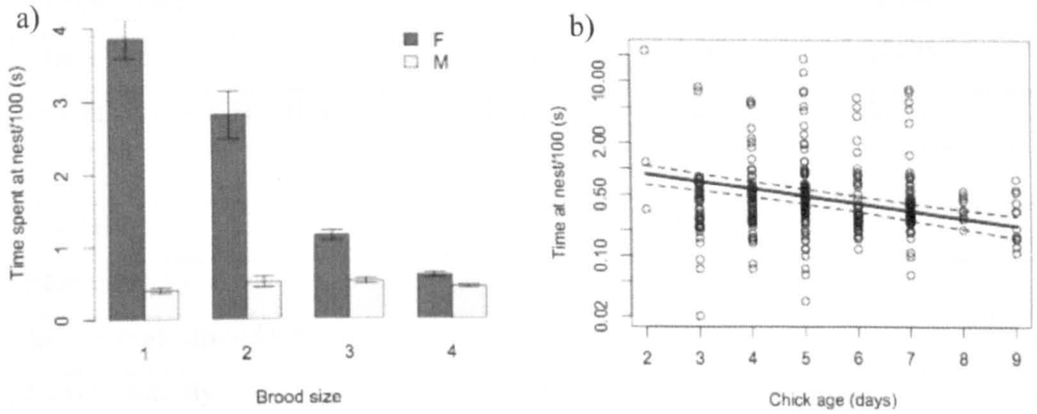


Figure 4. The length of time spent waiting in the vicinity of the nest was influenced by a) an interaction between brood size and the sex of the parent, and by b) a quadratic relationship with temperature (Table 5). For a), bars show mean values ± SE; for b), points show raw data; lines are predicted from the MAM (Table 5), with mean brood size (2.96 chicks) during 2007. Note log y-axis.

Time at nest

The time a bird spent at the nest was influenced by temperature, chick age, and an interaction between the sex of the parent and brood size (Table 6).



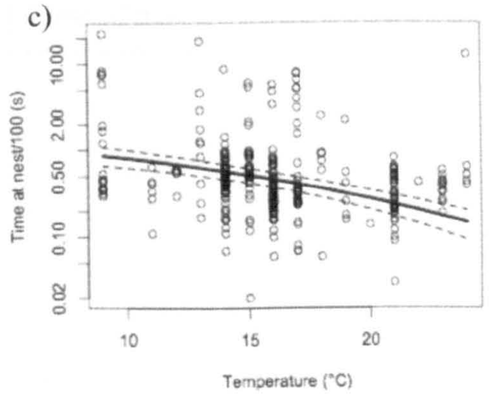


Figure 5. The time a bird spent at the nest was influenced by a) an interaction between brood size and the sex of the parent, b) chick age, and c) temperature. a) shows mean values ± 1 SE as predicted by the MAM (Table 6). For b) and c) points show raw data, and lines are predicted from the MAM (Table 6) with mean values of brood size (3.141 chicks), temperature (16.07 °C) and chick age (5.254 days) for the male parent. Note log y-axes.

Males spent the same amount of time at the nest for all brood sizes (Figure 5a); however females spent the most time at the nest with broods of one, decreasing the amount of time with increasing brood size (Figure 5a). Both sexes decreased the amount of time spent at the nest with increasing chick age (Figure 5b), and non-linearly with temperature (Figure 5c).

Table 6. Results from a GLMM to determine which variables influence the amount of time a bird spends at the nest. For significant terms, parameter estimates with SE are presented; for non-significant main effects, statistics are following reinsertion of the term into the minimum adequate model (MAM) and subsequent model comparison. All models contained nested random factors of Watch ID within Nest ID within Farm to control for individual differences and for unmeasured variable such as chick hunger, which may differ within nests between provisioning watches. Two-way interactions of sex of parent x insect abundance ($\chi^2_1<0.01$, p=0.98), sex of parent x management ($\chi^2_1=0.11$, p=0.74), sex of parent x temperature^2 ($\chi^2_1=0.01$, p=0.92), sex of parent x time of day^2 ($\chi^2_1=0.12$, p=0.73), sex of parent x corvid activity ($\chi^2_1=0.16$ p=0.69), sex of parent x year ($\chi^2_1=0.23$, p=0.63) and sex of parent x chick age ($\chi^2_1=2.51$ p=0.11) neither significantly influenced the fit of the model nor significantly influenced the response variable and thus were removed from the MAM.

Variable	**df**	z	p	**Estimate**	**SE**
Sex of parent (Male)	1	-3.046	0.002	-2.650	0.870
Brood size	1	-4.560	<0.001	-0.710	0.156
Temperature^2	1	-1.984	0.047	-0.002	0.001
Chick age	1	-2.039	0.041	-0.179	0.088
Sex of parent x Brood size	1	2.329	0.020	0.634	0.272
Variable	**df**	χ^2	p		
Management	1	2.184	0.139		
Invertebrate abundance	1	2.616	0.106		
Corvid activity	1	0.474	0.491		
Year	1	0.215	0.643		
Time of day^2	1	0.002	0.969		

Discussion

Female Yellowhammers consistently provision their young at higher rates than males. Females make more provisioning trips than males to small broods of one of two nestlings; however both parents provision broods of three and four nestlings at similar rates. Small broods require less food than large broods, and are also likely to require more brooding by the female to prevent chilling. That neither males nor females feed broods of four chicks at a higher rate than broods of three implies that either both parents have reached the upper limit of their energy expenditure (Siikamäki et al. 1998), or that parents are able to increase the amount of food brought back per trip so that per-nestling food provisioning remains the same (Markman et al. 1995).

Both parents increase their provisioning rate to older chicks, consistent with other studies of passerines (Wright et al. 1998; Rauter et al. 2000; Nordlund and Barber 2005; Falconer et al. 2008): females increase their provisioning rate only slightly, possibly as older chicks require less brooding (Falconer et al. 2008). Males increase their provisioning rate dramatically: male provisioning rates to two-day-old chicks are less than half that of females, whereas male provisioning rates to chicks that are ready to fledge are equal to that of females, a pattern that has been found in other studies (Wiggins and Morris 1986; Carey 1990; Wheelwright et al. 2003). This fits with the increased nutritional requirements of older nestlings and may imply that males may be compensating for the fact that females are unable to increase their provisioning rates (Siikamäki et al. 1998). That males increase their investment for older chicks and larger broods concurs with evidence from Collared Flycatchers *Ficedula albicollis* that males are more likely to risk their own survival for larger broods of older nestlings (Michl et al. 2000).

Whether or not a male sang during chick provisioning was influenced only by chick age, with males with younger chicks being more likely to sing. This fits with previous results as males with younger chicks spend less time provisioning than those with older chicks and therefore have more time available for territorial activities. It is also possible that once a territory is established and a pair is breeding that only infrequent territorial song is necessary to stave off potential intruders.

As chick age increased, the foraging trip duration of both parents decreased. This correlates with an increased provisioning rate and suggests that as the food demands of the chicks increase, parents are forced to forage closer to the nest and can consequently make trips of a shorter duration (Wright et al. 1998). It is possible that foraging further from the nest may be an anti-predation strategy, in that it reduces the level of activity in the area local to the nest and consequently reduces the risk of nest predation (Eggers et al. 2005; Remes 2005): this is supported by the increase in foraging trip length with increasing corvid activity shown by females. It is also possible that young chicks require high quality food, which requires longer provisioning trips to acquire, but as chicks age and their food demands increase, the quality of food provided declines as parents are forced to increase their provisioning rates (Wright et al. 1998). Males reduce their foraging trip length with increasing corvid activity, possibly to increase the amount of time that can be spent in nest guarding. Both sexes spend longer on foraging trips on organic farms than on conventional, implying that food may not be as abundant or as accessible on organic farms necessitating a longer search time.

It is possible that waiting in the vicinity of the nest is a nest guarding or a nest defence strategy, and that if a bird is able to watch for nest predators they may be able to ward off a potential predator or, using an alarm call, warn the chicks to prevent them begging to a predator and thus reduce their risk of predation, as has been found in other species (Platzen and Magrath 2005). Males wait for longer with increasing temperature, whereas temperature does not influence the amount of time spent waiting prior to provisioning by females. It is likely that with increasing temperature, the abundance of prey increases (Low et al. 2008) and consequently load size may increase, meaning that birds may be able to bring more food back to the nest with each visit and increase the amount of time available to guard the nest without risking starvation of the chicks. Increasing temperature will also decrease the food requirements of chicks as lower temperatures require a higher metabolic rate for thermoregulation and maintenance (Siikamäki 1996). It therefore seems that birds are more able to relax their foraging effort when chicks require less food and food is more abundant, and thus spend more time waiting in the vicinity of the nest.

Males spend more time waiting than females, and the amount of time that males spend waiting decreases with increasing brood size. Larger broods have greater nutritional requirements and therefore both parents are required to work hard in order to ensure that large broods receive sufficient food (Wright et al. 1998).

Females spend more time at the nest than males, unsurprising since only female Yellowhammers brood nestlings. The time females spend at the nest decreases with increasing brood size, and that of both parents decreases with increasing chick age, likely to be due to the reduced likelihood of chilling of larger broods and older chicks (Falconer et al. 2008), or possibly due to older chicks taking less time to ingest food provided by the parents. This is supported by a decreased time spent at the nest with increasing temperature, indicating that thermal constraints restrict the amount of time the female can spend provisioning (Wiebe and Elchuck 2003).

Overall, females show relatively little flexibility in their provisioning behaviour or time budgets during chick provisioning, indicating that they are maximising their work rate, possibly due to limited food availability, and may be unable to further increase their energetic expenditure (Siikamäki et al. 1998). Conversely, males are more flexible in their provisioning behaviour and possibly more able to assess need (Carey 1990), possibly by assessing chick begging behaviour (Kilner 2002). It seems likely that where a higher work rate is required than that which the female can provide, males can compensate for any shortfall. This is similar to dynamics in other systems (Siikamäki et al. 1998); for example, the provisioning rate of female Macaroni Penguins is associated with whether or not chicks survive, whereas male provisioning rate is associated with the growth and fledging mass of surviving offspring (Barlow and Croxall 2002).

Yellowhammers have relatively high levels of extra-pair paternity (Sundberg and Dixon 1996), which may explain why biparental care is not equal in this species: whilst egg dumping in Yellowhammers is unknown and consequently females can be sure of the relatedness of their nestlings, one study showed 69% of nests to contain extra-pair young (Sundberg and Dixon 1996) and therefore it pays for males to invest less in nestlings than females as they cannot be certain of their relatedness.

It appears likely that female Yellowhammers are working at the ceiling of possible energy expenditure during chick provisioning: as females are thought more susceptible to the costs of reproduction (Dawson and Bortolotti 2008), this may lead to a high female-biased over-winter mortality. Conversely, the requirement from large broods and older chicks for a higher work rate from males may lead to a high male-biased mortality, as males can show a cost of increased parental care on survival (Liker and Székely 2005). It remains unclear whether this would lead to a skewed sex ratio, or just to a high overall adult mortality. A brood manipulation experiment would be able to confirm these results experimentally, and an intensive population study linking breeding work-rate and over-winter survival would be necessary in order to establish both whether a link exists and the implications that increased breeding work rates may have for Yellowhammer population dynamics.

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Chapter 6. Morphological associations with haemoparasitism: cause or consequence?

Abstract

Avian haemoparasites are found worldwide at high prevalence and yet sub-clinical consequences for their hosts are rarely reported. Here I investigate parasite prevalence, abundance and associations with host and environmental variables in a population of Yellowhammer, *Emberiza citrinella* over-winter (November-May). Two lineages of *Haemoproteus* spp. and a novel *Leucocytozoon* lineage were identified from sequence data, with an overall prevalence of 50%. *Haemoproteus* infection varied temporally, with a peak prevalence during mid-December during one year but not the next; *Leucocytozoon* infection showed no clear peak. I discuss possible reasons behind the peak of *Haemoproteus* infection, including stress response associated with a reduction in food availability. Infection rates did not differ between age classes or between the sexes but were higher during the colder winter of 2008/09 than during the winter of 2007/08. Nearly double the numbers of birds were caught during 2007/08 despite similar sampling effort. I found temporally variable associations between infection with *Haemoproteus* and wing and tail lengths: wing lengths were shorter in infected birds than in uninfected birds during 2007/08 but not during 2008/09; tail lengths were shorter in infected birds during all months except January (data from this month were only available during 2008/09). Although temporal variability clouds these relationships, I use these data to test two hypotheses: 1) Parasite infection influenced tail length, and conversely, 2) Smaller birds were more likely to be infected, or more likely to suffer from patent infection if infected. I found no support for hypothesis 2, as none of tarsus length, head-beak length, or the interactions of either with month or year were related to parasite status, suggesting that parasites influence feather growth during moult, but that this relationship can be influenced by mortality induced by severe weather conditions. Finally, I detected parasite infection in 60% of seven-day-old nestlings, indicating that the nestling stage may be when most birds become infected with haemoparasites. To my knowledge, this is the youngest age at which parasite infection has been detected in wild birds.

Introduction

Avian haemoparasites are widely distributed and found at high prevalence within many species (Schueurlein and Ricklefs 2004; 2005). As parasites compete with their hosts for resources they are generally detrimental: the lethal consequences of avian malaria where it has been introduced to naïve host species are well-documented (e.g. Warner 1968). However, research on the impacts of sub-clinical avian malaria infections has been largely restricted to impacts on sexually-selected traits, after Hamilton and Zuk (1982) proposed the 'good genes' hypothesis. They proposed that birds with brighter plumage were more resistant to parasites, and thus that plumage colouration and other sexually selected traits could be used reliably as a mate choice cue to allow females to select for males with genes conferring parasite resistance (Hamilton and Zuk 1982). Much evidence has been found in support of this hypothesis: for example, yellow plumage colouration in both the Cirl Bunting *Emberiza cirlus* and the Yellowhammer *Emberiza citrinella* are reliable indicators of health status (Sundberg 1995; Figuerola et al. 1999), and haemoparasitic infection of White-Crowned Sparrows *Zonotrichia leucophrys* and Canaries *Serinus canaria* is associated with reduced song performance (Spencer et al. 2005; Gilman et al. 2007). However, evidence is not entirely conclusive (e.g. Read and Harvey 1989) and the results of some studies are contradictory: for example, Red-Backed Shrikes *Lanius collurio* infected by haematozoa have larger tail colour patterns (a sexually-selected trait) than uninfected males (Votypka et al. 2003).

More recent work has focussed on the possible implications of haemoparasitisic associations with sexually selected traits in terms of reproduction and life-history. Haemoparasites have been associated with a delay in the onset of breeding (Allander and Bennett 1995), reduced clutch size (Korpimaki et al. 1993), egg volume and hatching success (Dufva 1996), lower provisioning rate (Tomas et al. 2005), reduced chick condition and size (Dufva 1996) and reduced fledging success (Sundberg 1995; Dyrcz et al. 2005); again, some studies are contradictory: for example Davidar and Morton (1993) found a higher breeding success in Purple Martins *Progne subis* infected with *Haemoproteus* spp. Experimental work involving brood manipulation indicates a trade-off between parental effort and immune defence against parasites, with parents of experimentally enlarged broods across a range of species generally showing a higher prevalence and higher intensity of parasitic infection (Richner et al. 1995; Allander 1997; Siikamäki et al. 1997; Nordling et al. 1998; Wiehn et al. 1999; Knowles et al. *In press*). Parasite infection is not necessarily causal in this relationship: increased stress due to an increased reproductive output may render an individual more likely to become infected, or less able to suppress a chronic infection. For example, Dawson and Bortolotti (2001) found that male American Kestrels *Falco sparverius* whose mates had high reproductive outputs were more likely to become parasitized or remain parasitized, and were subject to higher intensity infections than those males whose mates had lower reproductive outputs.

Haemoparasite infections vary temporally (Bensch and Åkesson 2003; Cosgrove et al. 2008) and the relapse of chronic infections generally coincides with the onset of the breeding season when infections are found at high prevalence (Sundberg 1995; Allander and Sundberg 1997; Cosgrove et al. 2008). These relapses are associated with an increased day length and are thought to be caused by hormones and stress associated with the onset of breeding (Valkiunas et al. 2004). Prevalence tends to decrease throughout the breeding season (Hasselquist et al. 2007; Cosgrove et al. 2008) but is followed by another peak of infection post-breeding (Cosgrove et al. 2008), thought to be due to infection of newly fledged naïve individuals (Beaudoin et al. 1971). However, little work has been carried out on the impacts that blood parasites may have on their hosts outside the breeding season (Allander and Sundberg 1997).

Associations between haemoparasites and the morphology of their hosts have been occasionally reported. Infected birds often have a reduced body condition (Figuerola et al. 1999; Schrader et al. 2003) and a lower mass than uninfected individuals (Schrader et al. 2003; Dyrcz et al. 2005), supported by an experimental infection of Blackcaps *Sylvia atricapilla* (Valkiunas et al. 2006; but see also Bennett et al. 1988). These effects on mass do not generally appear to impact upon survival (Weatherhead 1990; Schrader et al. 2003; but see also Davidar and Morton 1993). Some studies have also shown parasitized birds to have shorter wing and tail lengths compared to uninfected birds (Rätti et al. 1993; Hatchwell et al. 2001; but see also Votypka et al. 2003) with impacts upon arrival date in a migratory species (Rätti et al. 1993). Although parasitism is not associated with differential timing of moult (Allander and Sundberg 1997) it is possible that parasites may compete for host resources post-breeding, thus restricting moult (Rätti et al. 1993; Hatchwell et al. 2001); conversely it may be that smaller birds are somehow more susceptible to parasitism (Weatherhead 1990; Rätti et al. 1993). It is important to establish this causality: if the former is true and parasites impact upon feather growth then they could cause important population-level consequences for their hosts which may previously have been underestimated. However, if the latter is true and smaller birds are more susceptible to parasitism, effects of parasites on host populations may conversely have been over-estimated: smaller individuals tend to have lower dominance rankings (Lindström et al. 2005), reduced survival (Braasch et al. 2009) and consequently a reduced reproductive output. If parasitized birds tend to be smaller then this may confound previous studies investigating life-history implications of parasitism.

Here I investigate parasite prevalence, identity and association of infection with host and environmental variables. I investigate morphological associations with parasite infection and test two contrasting hypotheses regarding the causality of the predicted associations with morphological variables: firstly, that parasites affect feather growth (feather length measured through both wing length and tail length) and secondly, conversely, that smaller birds are more likely to be infected by parasites (body size measured through both tarsus length and head-beak length).

Methods

Study population and blood sampling

Work was carried out within an individually marked population of Yellowhammers near Tadcaster, North Yorkshire (lat. 53° 53'N, long. 1° 15'W). Birds were caught in static mist nets and whoosh nets at an established supplementary feeding site baited with wheat and weed seeds, within an experimental agroforestry block surrounded by arable farmland. 203 birds were caught on 30 sampling occasions between November 2007 and April 2009. Sixteen birds were caught and sampled on two occasions within this period and three birds were caught and sampled on three separate occasions (these occasions were more than two months apart, as required by the terms of the HO licence).

Blood was taken through venipuncture of the brachial vein and stored with EDTA prior to freezing. Blood samples were also collected from 10 seven-day-old nestlings from four broods (three broods of three nestlings and one brood of one nestling) from other sites in Gloucestershire, Wiltshire and Hampshire used as part of a separate project during June and July 2008.

Morphometrics

Birds were aged and sexed according to plumage variation (Svensson 1992; Dunn and Wright In press). Morphometrics were taken as detailed by Dunn and Wright (In press): wing length and tail length were used as measures of feather growth, and head-beak length and tarsus length as measures of size. Measurements of wing length were taken using a standard metal wing rule and rounded up to the nearest mm; other measurements were taken using digital callipers (± 0.1 mm).

DNA Extraction and detection of blood parasites

DNA was extracted from 30μl of whole blood using a standard phenol-chloroform extraction followed by ethanol precipitation (Sambrook et al. 1989). Successful DNA extraction was confirmed by using a Nanodrop ND-1000 Spectrophotometer (Nanodrop Technologies Inc., Wilmington, DE) and diluted to a working concentration of 25 – 100 ng/μl.

Blood parasite presence or absence was determined through PCR using established protocols. The presence of *Plasmodium* and *Haemoproteus* was established using primers HaemNF and HaemNR2 nested within HaemF and HaemR2 (Waldenström et al. 2004), and *Leucocytozoon* spp. were detected using primers HaemFL and HaemR2L nested within primers HaemNFI and HaemNR3 (Hellgren et al. 2004). All protocols were carried out in a working volume of 25µl containing 50 – 200 ng template DNA, 1.25mM dNTPs, 3mM $MgCl_2$, 0.4µM of each primer, 1 x GoTaq Flexi Buffer (Promega, Madison, WI) and 1 U GoTaq Flexi (Promega, Madison, WI); a positive control of DNA from a bird with known infection and a negative control containing deionised water in place of DNA were included with each PCR reaction to ensure successful amplification and lack of contamination respectively.

The PCR protocol for first round reactions consisted of a denaturation step of 94°C for 3 minutes followed by 20 cycles of 94°C for 30 seconds, 50°C for 30 seconds and 72°C for 45 seconds, with a terminal extension step of 72°C for 10 minutes; the protocol for second round reactions contained 35 cycles but otherwise consisted of an identical thermal profile. PCR protocols were carried out on a GeneAmp PCR System 9700 (Applied Biosystems).

As non-target DNA can be amplified with nested PCR methods (Szöllösi et al. 2008) a subsample of positive samples were sequenced using an ABI sequencer at the Core Genomic Facility, Sheffield University, to confirm the identity of parasites.

Statistical analyses

All analyses were carried out in R version 4.2.1 (www.R-project.org). Chi-squared tests were used to determine whether expected numbers of infected and non-infected individuals differed from observed numbers between the sexes, age classes, or between years. General linear models with binomial error structures and infection status (with each parasite separately) as the response variable were used for each of known age, day and month as the chi-squared test assumptions of expected values greater than 5 were not met for these variables. Data were then grouped into three time groups according to season (Nov – Dec 2007; Jan – May 2008; Jan – May 2009) in order to determine whether visible differences according to time were statistically significant (Crawley 2007).

To determine whether feather length was associated with infection by either *Haemoproteus* spp. or *Leucocytozoon* spp, four general linear models with gaussian error distributions were constructed with either wing length or tail length as the response variable. Age, sex, month, year and infection status (two separate models were constructed for each parasite) were designated as response variables along with two-way interactions between age and sex, and between infections status and each of age, sex, month and year to determine whether any associations differed between age classes, sexes, months or years. Data from only one sampling occasion was included where birds had been samples more than once, in order to avoid pseudoreplication. These models were repeated for *Haemoproteus* spp. only, with head-beak length and tarsus length as response variables to determine whether any associations with parasitism were with size or with feather length. Model comparisons using AIC values were used to determine whether terms significantly improved the fit of the model; those that didn't were removed in a stepwise fashion until only those terms that improved the fit of the model at $p<0.1$ remained; only terms that influenced the response variable at $p<0.05$ were considered to influence the response variable. Following model simplification, each term was reinserted into the minimum adequate model (MAM) in turn and compared with the MAM using AIC comparisons to ensure lack of association with the response variable. Statistics presented throughout are mean ± 1 SE.

For recaptured birds, associations between parasite status and feather length were tested using generalised linear mixed effect models with either wing length or tail length as the response variable, and infection by *Haemoproteus* spp. as the predictor variable, designating bird ID as a random factor. The infection by *Haemoproteus* term was then removed from the maximal model and the two models with and without the term compared to deduce the significance of the term.

Results

Parasite prevalence and identity

225 blood samples from 203 birds were screened for the presence of *Plasmodium* spp., *Haemoproteus* spp. and *Leucocytozoon* spp. Using the protocol of Waldenstrom *et al* (2004), for detection of *Plasmodium* spp. and *Haemoproteus* spp., 105 of 225 samples (47%) tested positive for parasites. A subset of samples were tested using the protocol of Hellgren *et al* (2004), for detection of *Leucocytozoon* spp., and 52 of 195 samples (27%) were found to contain parasites. Of the 52 birds testing positive for *Leucocytozoon* spp., only 7 were uninfected with *Haemoproteus* spp. giving an overall parasite prevalence of 50%.

Thirty-eight sequences were obtained from 34 birds. Of these, one sequence was identified as a novel *Leucocytozoon* lineage and the remainder were identified as *Haemoproteus* lineages DUNNO01 and EMRUT01 (Genbank accession numbers DQ991080 and EF380192). The *Leucocytozoon* lineage was amplified using Hellgren et al (2004) and all the *Haemoproteus* lineages were amplified using Waldenström et al (2004).

Associations with host and environmental variables

Haemoproteus infection showed no association with age (χ^2=0.02, df=1, p=0.90), known age (GLM, $Dev_{1,148}$=0.01, p=0.94) or sex (χ^2=1.02, df=1, p=0.31). *Leucocytozoon* infection showed no association with age (χ^2=0.85, df=1, p=0.36), known age (GLM, $Dev_{1,125}$=0.01, p=0.93) or sex (χ^2=0.01, df=1, p=0.90).

After removing data from days where fewer than five birds were caught, prevalence of *Haemoproteus* and *Leucocytozoon* both varied with day (*Haemoproteus*: GLM, $Dev_{12,134}$=25.16, p=0.01; *Leucocytozoon*: GLM, $Dev_{12,115}$=30.27, p<0.01). Infection rates of both parasites also varied with month (*Haemoproteus*: GLM, $Dev_{5,197}$=14.47, p=0.01; *Leucocytozoon*: GLM, $Dev_{5,168}$=11.90, p=0.04), and between years (*Haemoproteus*: χ^2=11.78, df=1, p<0.01; *Leucocytozoon*: χ^2=10.42, df=1, p<0.01), with prevalence of *Haemoproteus* increasing from 40% in the winter of 2007/08 to 68% in the winter of 2008/09, and *Leucocytozoon* prevalence rising from 20% in the winter of 2007/08 to 50% in the winter of 2008/09.

Haemoproteus showed a peak of infection in mid-December 2007, with over 50% of birds infected: prevalence then declined to 10% in April 2008. No clear pattern was shown during 2008/09 (Figure 1a), although only three sampling days yielded more than five birds. No clear peak was shown for *Leucocytozoon* infection during 2007/08, although infections with this parasite were detected throughout December and into February, but were not found after mid-February during 2007/08 (Figure 2b); during 2008/09 the parasite was found into April (Figure 2b). To confirm the statistical significance of these patterns, data were grouped into three time periods: November - December 2007; January - May 2009; and January 2009 – April 2009. Days on which fewer than five birds had been captured were reincluded in this analysis. *Haemoproteus* infection differed in prevalence between the three time periods (GLM, $F_{2,196}=9.07$, $p<0.01$), with the second (GLM, $z=2.44$, $p=0.02$) and third (GLM, $z=-2.10$, $p=0.04$) time periods differing from the first, and from each other (GLM, $z=4.074$, $p<0.01$) confirming a winter peak of infection between November and December 2007, followed by a period of lower prevalence between January and May 2008, and a higher prevalence between January and May 2009. This trend was slightly different for *Leucocytozoon* infection (GLM, $F_{2,168}=4.61$,

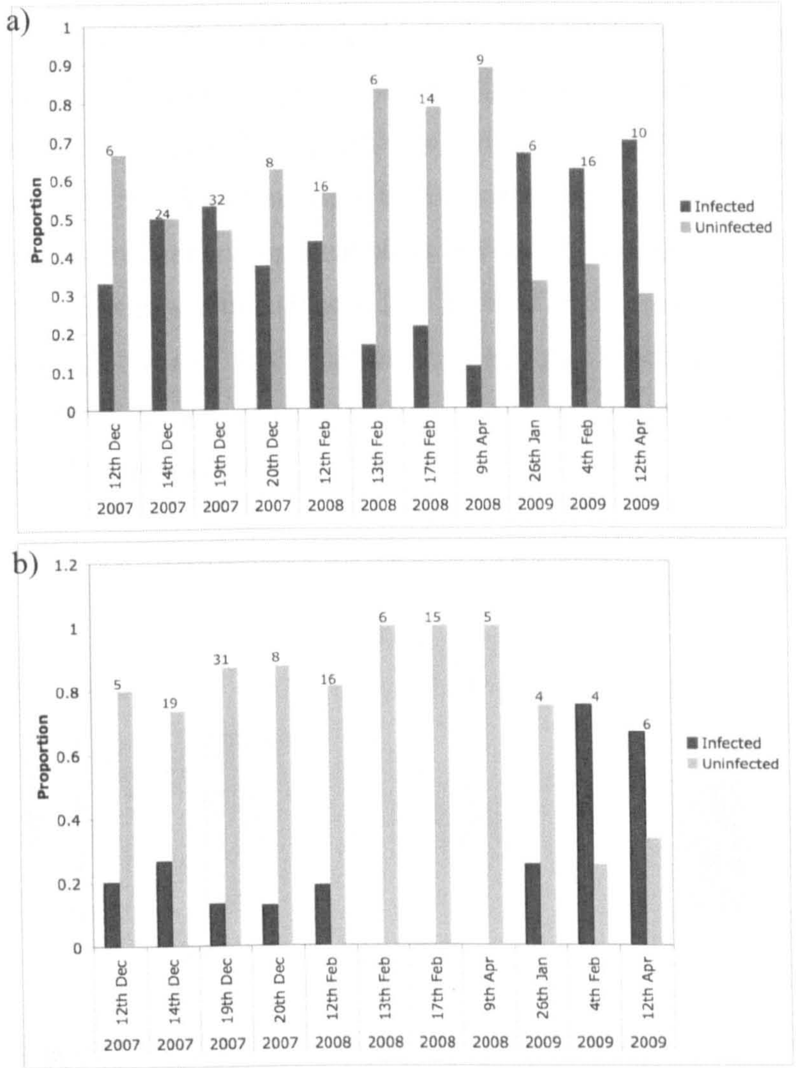

Figure 1. Prevalence of a) *Haemoproteus* (GLM, $Dev_{12,134}=25.16$, $p=0.01$) and b) *Leucocytozoon* (GLM, $Dev_{12,115}=30.27$, $p<0.01$) varied with day. Prevalence of both parasites was higher during 2008/09 than during 2007/08. Bars show proportions of infected and uninfected birds; numbers above bars show sample size

p<0.01) with the second time period showing no difference in prevalence from the first (GLM, t=0.53, p=0.59); however, prevalence was higher during the third time period than both the first (GLM, t=-2.58, p<0.01) and second (GLM, t=2.89, p<0.01) time periods.

Morphological associations with parasitism

Wing length was associated with both an interaction between age and sex, and an interaction between infection with *Haemoproteus* infection status and year (Table 1; Figure 2a). Males had longer wings than females and adult birds had longer wings than juveniles (Figure 2b). In the winter of 2007/08, birds infected with *Haemoproteus* had shorter wings than uninfected birds; however, in the winter of 2008/09, this was not the case and the wing lengths of infected birds were slightly longer than those of uninfected birds (Figure 2a). Tail length was influenced by interactions between age and year, and between month and infection by *Haemoproteus* (Table 3; Figure 3). During all months apart from January, infected birds had shorter tails than uninfected; however in January the opposite was true (Figure 3a). Tails of adult birds were longer in 2008 than in 2007; however tails of first year birds were shorter (Figure 2b). Neither *Leucocytozoon* infection nor any of its interactions were associated with wing length (Table 2) or tail length (Table 4).

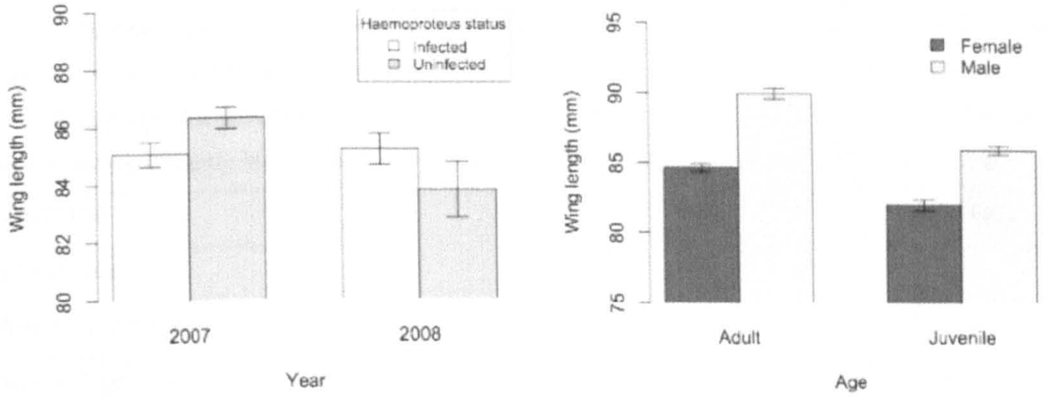

Figure 2. Wing length was influenced by interactions between a) *Haemoproteus* infection status and year, and b) Age and Sex (Table 1). Bars show mean ± 1 SE.

Table 1. Results from a GLM to determine whether infection by *Haemoproteus*, or any interactions therewith, are associated with wing length. For significant terms, parameter estimates with SE are presented; for non-significant main effects, statistics are following reinsertion of the term into the minimum adequate model (MAM) and subsequent model comparison. Two-way interactions of sex x infection status (F_1=0.97, p=0.33) and month x infection status (F_5=1.42, p=0.22) neither significantly influenced the fit of the model nor significantly influenced the response variable and thus were removed from the MAM.

Variable	**df**	**F**	**p**	**Estimate**	**SE**
Sex (Male)	1, 200	10.236	<0.001	5.231	0.511
Age (Juvenile)	1, 200	-5.214	<0.001	-2.580	0.495
Haemoproteus infection (uninfected)	1, 200	2.057	0.041	0.807	0.393
Year (2008)	1, 200	0.904	0.367	0.434	0.480
Sex x Age	1, 200	-2.184	0.030	-1.455	0.666
Haemoproteus infection x Year	1, 200	-2.143	0.033	-1.638	0.764
Variable	**df**	**F**	**p**		
Month	5, 189	0.545	0.742		

Table 2. Results from a GLM to determine whether infection by *Leucocytozoon*, or any interactions therewith, are associated with wing length. For significant terms, parameter estimates with SE are presented; for non-significant main effects, statistics are following reinsertion of the term into the minimum adequate model (MAM) and subsequent model comparison. *This term approached significance in influencing the fit of the model (F_1=3.09, p=0.08); thus, this term remains in the MAM but is not considered to significantly influence the response variable. Two-way interactions of sex x infection status (F_1=0.91, p=0.34), age x infection status (F_1=1.32, p=0.25), year x infection status (F_1=0.24, p=0.63) and month x infection status (F_4=1.18, p=0.32) neither significantly influenced the fit of the model nor significantly influenced the response variable and thus were removed from the MAM.

Variable	**df**	**F**	**p**	**Estimate**	**SE**
Sex (Male)	1, 171	123.174	<0.001	5.119	0.528
Age (Juvenile)	1, 170	99.639	<0.001	-2.768	0.547
Sex x Age	1, 169	3.089	0.081*	-1.254	0.714
Variable	**df**	**F**	**p**		
Month	5, 164	0.996	0.422		
Leucocytozoon infection	1, 168	0.333	0.565		
Year	1, 168	0.083	0.773		

Table 3. Results from a GLM to determine whether infection by *Haemoproteus*, or any interactions therewith, are associated with tail length. For significant terms, parameter estimates with SE are presented (contrasts for Month are against the mean, contrasts for factors with two levels are for the level stated and compared to the other level); for non-significant main effects, statistics are following reinsertion of the term into the minimum adequate model (MAM) and subsequent model comparison. Two-way interactions of sex x infection status (F_1=0.97, p=0.33) and month x infection status (F_5=1.42, p=0.22) neither significantly influenced the fit of the model nor significantly influenced the response variable and thus were removed from the MAM.

Variable	**df**	**F**	**p**	**Estimate**	**SE**
Month (Dec)	4, 146	1.752	0.142	0.171	0.419
Month (Jan)				-1.078	0.688
Month (Feb)				0.088	0.397
Month (Mar)				0.366	0.492
Month (Apr)				0.483	0.463
Haemoproteus infection (uninfected)	1, 145	3.497	0.064	-0.150	0.961
Sex (Male)	1, 144	65.287	<0.001	4.582	0.653
Age (Juvenile)	1, 143	56.908	<0.001	-2.505	0.605
Month (Dec) x *Haemoproteus* infection	4, 149	2.450	0.049	0.055	0.412
Month (Jan) x *Haemoproteus* infection				1.381	0.678
Month (Feb) x *Haemoproteus* infection				-1.032	0.395
Month (Mar) x *Haemoproteus* infection				-0.376	0.487
Month (Apr) x *Haemoproteus* infection				-0.028	0.462
Sex x Age	1, 138	4.178	0.043	-1.762	0.862
Variable	**df**	**F**	**p**		
Year	1, 137	0.808	0.370		

Table 4. Results from a GLM to determine whether infection by *Leucocytozoon*, or any interactions therewith, are associated with tail length. For significant terms, parameter estimates with SE are presented; for non-significant main effects, statistics are following reinsertion of the term into the minimum adequate model (MAM) and subsequent model comparison. Two-way interactions of sex x infection status (F_1=0.91, p=0.34), year x infection status (F_1=0.05, p=0.82), age x infection status (F_1=0.01, p=0.93) and month x infection status (F_4=0.80, p=0.53) neither significantly influenced the fit of the model nor significantly influenced the response variable and thus were removed from the MAM.

Variable	**df**	**F**	**p**	**Estimate**	**SE**
Sex (Male)	1, 122	46.112	<0.001	4.079	0.459
Age (Juvenile	1, 121	79.036	<0.001	-3.659	0.452
Variable	**df**	**F**	**p**		
Year	1, 120	0.307	0.581		
Month	4, 117	0.437	0.782		
Leucocytozoon infection	1, 120	0.118	0.731		

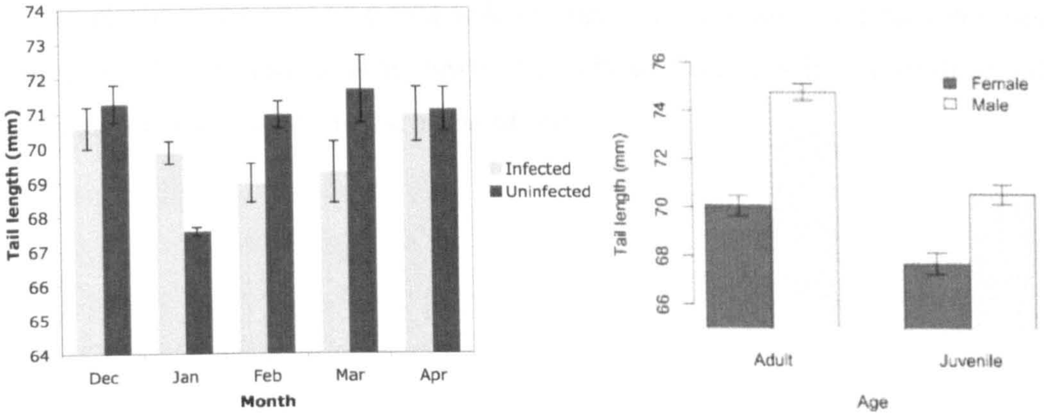

Figure 3. Tail length was influenced by interactions between a) Month and *Haemoproteus* infection status, and b) Age and sex (Table 3). Bars show mean values ± 1 SE.

To determine whether the associations between year, *Haemoproteus* infection status and wing length were a consequence of body size, further analyses were carried out to determine whether these associations were consistent with an association with body size generally, or specifically with feather length. No associations with either head-beak length ($F_{1,109}$=0.31, p=0.58; Appendix 1) or tarsus length ($F_{1,150}$=0.68, p=0.41; Appendix 2) were found (Figure 4).

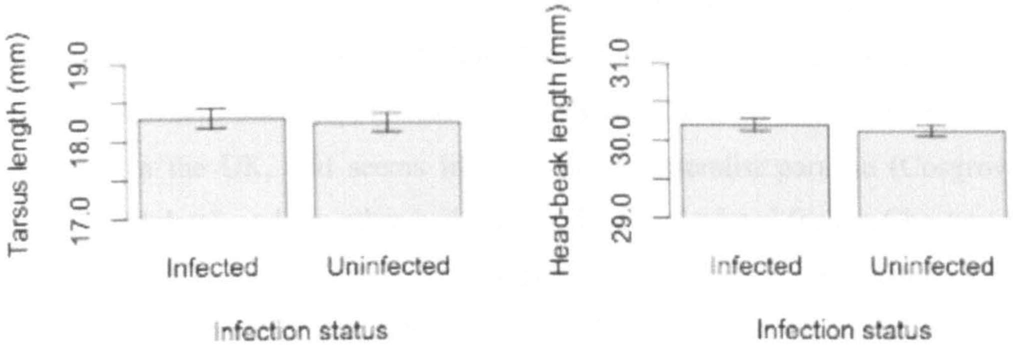

Figure 4. No difference in a) tarsus length or b) head-beak length was found between birds infected or uninfected by *Haemoproteus* spp.

Within recaptured birds, infection by *Haemoproteus* spp. had no effect upon either wing length (χ^2_1=0.11, p=0.74) or tail length (χ^2_1=0.16, p=0.69).

Infection in Yellowhammer nestlings

Of 10 chicks from four broods (three broods of three chicks and one brood of one chick) from which blood samples were obtained, 7 samples tested positive for parasites using the protocol of Waldenström et al (2004). Two chicks from each broods of three tested positive, as did the chick from the brood of one.

Discussion

Parasite prevalence, identity and association with environmental variables

Multiple sequences were obtained from three distinct haemoparasite lineages. Of the two *Haemoproteus* lineages, one had previously been isolated from a Dunnock *Prunella modularis* in the UK, and seems likely to be a generalist parasite (Cosgrove et al. Unpublished data), and the other had previously been isolated from a Chestnut Bunting *Emberiza rutila* in South Korea, and may be an *Emberiza* specialist (Ishtiaq et al. 2007). The *Leucocytozoon* sequence was from a novel lineage and more work is required to determine whether this parasite is a specialist or a more generalist parasite.

The haemoparasite prevalence of 50% found here is low when compared to a previous study of Yellowhammers sampled during the breeding season, which found 70% of birds to be infected by *Haemoproteus coatneyi*, but high when compared to other species sampled during the winter months where the prevalence of patent infections (infections where parasites remain circulating in the blood) approaches 0% (Schrader et al. 2003; Cosgrove et al. 2008). Infection of Blue Tits *Parus caeruleus* by *Plasmodium* spp. shows an increase in prevalence from February through to the start of the breeding season (Cosgrove et al. 2008), thought to be a relapse of current infection caused by stress due to the onset of breeding (Applegate 1971; Beaudoin et al. 1971; Allander and Sundberg 1997). This is in contrast to our results, which show the lowest detected prevalence on the latest sampling date during 2007 (9th April); however, it must be considered that Yellowhammers commence breeding later than Blue Tits and a previous study of Yellowhammers indicated that parasite intensity was low at the beginning of April and peaked at the beginning of May, outside our sampling period and coincidental with the onset of the breeding season (Allander and Sundberg 1997).

Our data appear to show a novel peak of *Haemoproteus* prevalence between mid-December 2007 and mid-February 2008; *Leucocytozoon* prevalence showed no clear peak but was not detected beyond mid-February in 2007. This peak is not apparent from other studies of haemoparasitism in temperate species (Schrader et al. 2003; Cosgrove et al. 2008; but see also Klei and DeGiusti 1975). Transmission of malaria parasites in temperate regions is thought to be negligible throughout the winter due to a cessation of vector activity (Cosgrove et al. 2008) but parasites remain dormant in host tissues (Valkiunas 2005) and are activated by stress hormones, usually at the onset of breeding (Applegate 1971; Allander and Sundberg 1997). Two hypotheses are proposed for this winter peak in prevalence of circulating parasites. Firstly, host immunity can be lowered during the winter (Hasselquist et al. 1999; Møller et al. 2003; Hasselquist 2007), which may allow a relapse of existing infections as reduced immune function is associated with increased parasite prevalence (Ots and Hõrak 1998). However a multi-species study that included yellowhammers provided unconvincing evidence for a reduction in winter immunity for this species, although the sample size was small (Møller et al. 2003). The second possibility is that a reduction in over-winter food availability may trigger a relapse of infection through increased circulating corticosterone levels. A reduction in over-winter food availability has been linked to population declines in many farmland bird species, including Yellowhammers (Peach et al. 1999; Robinson and Sutherland 1999; Bradbury et al. 2000) and corticosterone levels have been shown to increase at times of low food availability (Clinchy et al. 2004). Increased corticosterone levels have been experimentally linked to both an increased parasite prevalence and an increased intensity of infection (Applegate 1970) so it appears plausible that a reduced food supply may induce relapses of haemoparasite infection, resulting in the observed peak in prevalence during winter. The potential implications of this require further exploration.

Parasite prevalence was higher during 2008 than during 2007, coincidental with lower bird numbers despite similar sampling effort. This may be due to an early cold spell during the autumn of 2008 (National Climate Information Centre 2008), which is likely to have caused high mortality and may have caused increased stress causing a relapse of infection as described previously.

Our data provide no evidence for sex or age differences in parasite infection. During the breeding season, difference in parasite prevalence between the sexes are frequently seen, with a higher prevalence and intensity of infection in females (Norris et al. 1994; Hasselquist et al. 2007), although other studies indicate that the relative prevalence between the sexes varies temporally, with a peak in males when territories are being established, and a peak in females when chicks have hatched (Applegate 1971; Allander and Sundberg 1997). In flocking situations and competitive interactions, males are usually more dominant (Domenech and Senar 1999; Seibert and Crowell-Davis 2001) and monopolise preferred roosting habitat (Mezquida et al. 2005). In American Kestrels, where size dimorphism is reversed, the smaller males suffer energetic consequences as a result of exclusion from preferred habitat by females (Ardia 2002).

However, yellowhammers form mixed age and sex flocks over-winter and size differences between the ages and sexes are restricted to feather length and not body size (Dunn and Wright *In press*), which may explain the lack of association with parasitism over-winter found here.

Morphological associations with parasitism

I demonstrate associations between *Haemoproteus* infection and wing and tail length, which differ between years and months. Previous studies have also shown associations between feather length and haemoparasites (Rätti et al. 1993; Hatchwell et al. 2001; Votypka et al. 2003): of these, Hatchwell et al. (2001) analyse data from only one year, and Votypka et al. (2003) do not appear to consider the potential influence of inter-year variation upon their analyses. Whilst Rätti et al. (1993) found an interactive effect of year and age on arrival date in a model containing parasite status and suggest that the interaction between all three terms may be significant (although they do not test for this), they did not consider the potential effect of year upon their associations between parasite status and wing and tail length (Rätti et al. 1993).

Whilst the association between *Haemoproteus* infection and feather length does not appear straightforward, no association was found between parasitism and measures of size, indicating that smaller birds are no more likely to be parasitized, and suggesting an effect of parasitism on feather growth during moult, as proposed by Rätti et al. (1993). However, this effect may well be complicated by environmental factors that differ between years, and consequently may be less exaggerated, or even entirely absent, in some years. In this case it is possible that the relatively mild autumn of 2007 (National Climate Information Centre 2008) led to a relatively high yellowhammer survival rate, and that birds susceptible to the effects of parasitism during moult survived over-winter, at least during early winter when the majority of birds sampled were caught. The autumn of 2008 was quite severe (National Climate Information Centre 2008) and it could be that birds that were susceptible to the effects of parasitism suffered high mortality prior to the sampling period, explaining both the observed year-dependent association between parasite infection and wing length, and the decreased sample size during the second winter of the study.

Infection in Yellowhammer nestlings

Parasite infection was found in 60% of yellowhammer nestlings screened. Sample size was only ten chicks and thus little can be read into the prevalence of infection; however, that infections were found at all in seven-day-old nestlings is worthy of note. Cosgrove et al (2006) found no evidence of infection by either *Plasmodium* or *Haemoproteus* in 195 fourteen-day-old nestling blue tits, although they did find evidence of one infection with *Leucocytozoon*. Indeed, prior to Cosgrove et al. (2006), only one study had found evidence of haemoparasitic infection in passerine nestlings, this being in ten-day-old Red-Winged Blackbird *Agelaius phoeniceus* nestlings (Weatherhead and Bennett 1991). This had led to the question of whether the absence of infection was due to birds being infected only following fledging, or whether birds were infected in the nest but that the prepatent period of the parasites was too long to allow the infection to reach patency prior to fledging (Cosgrove et al. 2006). Whilst it must be noted that many avian haemosporidia are species-specific (Valkiunas 2005) and that there is a wide variety in the prepatent period of haemosporidians, it is possible that the difference in detection of parasites between the studies of Cosgrove et al. (2006), Weatherhead and Bennett (1991), and this study may be due to the ecology of the avian species, rather than their parasites. The Blue Tits screened within the study of Cosgrove et al. (2006) are a box and hole-nesting species which may lead to a reduced accessibility of chicks to the vectors. Conversely, both Yellowhammers and Red-Winged Blackbirds are open-nesting species, which may increase the accessibility of nestlings to the vectors of haemosporidians.

I show a novel winter peak of infection in Yellowhammers, suggesting that the effects of blood parasites in avian life-history may not just be restricted to the breeding season. I find time-specific associations of *Haemoproteus* spp. with feather length, but not size, which suggest associations with environmental stressors. Finally, I detect blood parasite infection in 7-day-old nestlings, suggesting that haemoparasites may play a part in the ecology of very young birds, potentially playing a role in post-fledging survival or condition. This work highlights the importance of blood parasites in the ecology of their hosts, and emphasises the need for a greater understanding of the associations between haemoparasites and their hosts, especially in species under environmental pressures, where the effects of parasitism may be emphasised.

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Appendix 1. Results from a GLM to determine whether infection by *Haemoproteus*, or any interactions therewith, is associated with head-beak length. For significant terms, parameter estimates with SE are presented; for non-significant main effects, statistics are following reinsertion of the term into the minimum adequate model (MAM) and subsequent model comparison. Two-way interactions of sex x infection status (F_1=0.77, p=0.38), age x infection status (F_1=0.61, p=0.43), year x infection status (F_1=1.23, p=0.27), month x infection status (F_4=0.39, p=0.82), and sex x age (F_1=0.61, p=0.43) neither significantly influenced the fit of the model nor significantly influenced the response variable and thus were removed from the MAM.

Variable	**df**	**F**	**P**	**Estimate**	**SE**
Age (Juvenile)	1, 151	6.211	0.014	-0.256	0.103
Variable	**df**	**F**	**p**		
Month	4, 147	0.383	0.821		
Year	1, 150	0.026	0.870		
Haemoproteus infection status	1, 150	0.682	0.410		
Sex	1, 150	0.821	0.366		

Appendix 2. Results from a GLM to determine whether infection by *Haemoproteus*, or any interactions therewith, is associated with head-beak length. For significant terms, parameter estimates with SE are presented (contrasts for Month are against the mean, contrasts for factors with two levels are for the level stated and compared to the other level); for non-significant main effects, statistics are following reinsertion of the term into the minimum adequate model (MAM) and subsequent model comparison. Two-way interactions of sex x infection status ($F_1=0.28$, $p=0.60$), age x infection status ($F_1=0.01$, $p=0.91$), year x infection status ($F_1<0.01$, $p=0.97$) and month x infection status ($F_4=0.44$, $p=0.78$) neither significantly influenced the fit of the model nor significantly influenced the response variable and thus were removed from the MAM.

Variable	**df**	**F**	**p**	**Estimate**	**SE**
Sex (Male)	1, 116	1.939	0.167	0.691	0.281
Age (Juvenile)	1, 115	0.063	0.802	0.430	0.247
Month (December)	1, 111	2.735	0.032	-0.652	0.235
Month (January)				-0.038	0.196
Month (February)				-0.081	0.138
Month (March)				0.670	0.183
Month (April)				0.101	0.162
Age x Sex	1, 110	5.028	0.027	-0.795	0.355
Variable	**df**	**F**	**p**		
Year	1, 109	1.905	0.170		
Haemoproteus infection	1, 109	0.305	0.582		

Chapter 7. Survival analysis and population dynamics of an individually marked yellowhammer population

Abstract

The understanding of factors influencing survival is crucial in the study of population dynamics; demographic and morphological shifts can occur within populations over relatively short time frames as a result of differential survival, influencing population structure. Here I determine the effect of demographic and size variables on survival over four winters in a population of yellowhammers (*Emberiza citrinella*) from North Yorkshire, UK. I also analyse capture data from 21 years since 1986 to determine whether sex ratio, age ratio, or size vary over time. The probability of a bird being recaptured decreased through time, but was unaffected by age, sex or wing length. Survival probability was influenced by sex and wing length, with males having a higher survival probability than females, and survival probability increasing with increasing wing length. Sex ratio did not differ significantly between years, although populations tended to be slightly male biased. Age ratios differed between years but not between months, implying high variation of breeding success resulting in low proportions of first year birds following a poor breeding season; the four most recent winters had a higher proportion of adult birds in the population than previously. Mean wing length, when controlling for the effects of age and sex on wing length, decreased with time. The apparent paradox between wing length decreasing over time, and an increased wing length increasing survival may be explained by smaller wing lengths in first year birds as habitat quality or food availability during the breeding season has declined, leading to a gradual reduction in mean population wing length.

Introduction

The understanding of factors influencing survival is vital in population biology; reproductive success and survival are the two main factors contributing to population trends and are themselves interlinked. Many animals do not survive to reproduce and consequently have an intrinsically reduced fitness. An understanding of the genotypic, phenotypic and environmental issues influencing survival is crucial to the understanding of population dynamics, and is especially important in declining populations where variation in survival may be linked to population decline (Siriwardena et al. 1998).

Survival is often related to age, with animals that have survived one year being more likely to survive to the next (Clobert et al. 1988) due to improved experience and social status increasing the ability of the individual to acquire the necessary resources (Newton et al. 1996). This phenomenon is widespread across many avian species (Clobert et al. 1988); however, in other bird species survival decreases continually from the year of first breeding (Loery et al. 1987).

Survival may also be sex-linked and can frequently be associated with dominance status: in the more common scenario where females are the smaller sex (Domènech and Senar 1999), females are subordinate to males. Subordinate individuals tend to be more vigilant than dominant individuals and consequently spend less time foraging (Domènech and Senar 1999). Thus, competition between the sexes has the potential to lead to a reduction in female survival and consequently a male-biased sex ratio (Clobert et al. 1988; Benkman 1997); this can be reversed in species where female social-dominance is seen (Hogstad 2006). Females can also suffer a peak in mortality following their first breeding season (Smith 1995). A skewed sex ratio in a population with a monogamous mating system reduces the proportion of birds able to breed and is likely to affect the reproductive success of the population as a whole.

A study in 1998 by Siriwardina et al. investigated whether farmland bird population trends could be predicted by age or sex-linked survival across species (Siriwardena et al. 1998). They estimated survival rates of 0.44 – 0.56 for yellowhammers, with no evidence for any significant effect of age or sex on survival probability, although females tended to have higher survival than males (Siriwardena et al. 1998) and no difference in adult or first year survival between 1962 and 1994. Since this study was carried out, yellowhammer populations have continued to decline in the UK (Eaton et al. 2008) and survival rates may have changed, as may the factors influencing survival.

This chapter aims firstly, to determine whether age, sex or size (wing length) are linked to survival probability in a population of yellowhammers, and secondly, to use ringing data from the same site from the past 21 years to determine whether long term temporal fluctuations or trends in sex ratio, ratio of adults to first year birds, or size are present within this population.

Methods

Study site

Yellowhammers were caught and ringed at Headley Hall Farm near Tadcaster, West Yorkshire, UK (lat. 53° 53'N, long. 1° 15'W). Birds were caught between October and May during the winters of 2005/6 – 2008/09 using mist nets, whoosh nets and cage traps at established supplementary feeding sites. Feeding sites were baited with wheat and weed seed, situated within an experimental agroforestry block surrounded by arable farmland. Birds had been caught and ringed at this site since 1986, with data absent from only two winters: sample sizes per winter ranged from 3 to 205 (Mean 50 ± 13.96). All data were used to analyse temporal changes in yellowhammer populations and the potential for fluctuations in sex ratio, age ratio, and size. Data from 2005 – 2009 were used to analyse factors influencing survival.

Biometric data

Following capture, birds were aged and sexed by examination of plumage (Svensson 1992; Dunn and Wright *in press*) and categorised as either adult or first-year birds. Birds were weighed using a digital pocket scale (± 0.1g; Satrue, Taiwan), and measurements of wing length, measured as the maximum wing chord (Redfern and Clark 2001) were taken using a standard metal wing rule and rounded up to the nearest mm.

Statistical Analyses

Temporal changes in yellowhammer populations

To determine whether populations showed significant fluctuations in sex ratio, the ratio of adults to juveniles, and size, data from 1986 to 2009 were analysed using R version 2.4.1 for Mac (www.R-project.org). Two binomial generalised linear models were constructed, with each of age (first year or adult) and sex (male or female) as the response variable, and winter (as a categorical variable) and month (to control for temporal trapping variability between years) as the predictor variables. As age ratio, and not number of individuals, was being examined, it was not necessary to control for trapping effort. Error structures were adjusted to quasi-binomial where the dispersion parameter indicated that this was necessary. In order to control for the fact that age and sex both influence wing length in yellowhammers (Svensson 1992; Dunn and Wright *in press*), a generalised linear model was constructed with wing length as the response variable, and age, sex, winter (as a continuous variable) and all interactions as predictor variables to determine whether trends in wing length were evident over time. Model comparisons using AIC values were used to determine whether terms significantly improved the fit of the model; those that didn't were removed in a stepwise fashion until only those terms that improved the fit of the model at $p<0.1$ remained; only terms that influenced the response variable at $p<0.05$ were considered to influence the response variable. Following model simplification, each term was reinserted into the minimum adequate model (MAM) in turn and compared with the MAM using AIC comparisons to ensure lack of association with the response variable. Statistics presented throughout are mean ± 1 SE.

Survival analysis

To estimate annual survival, the encounter histories of 321 individual colour-marked yellowhammers captured between December 2005 and May 2009 were analysed using Cormack-Jolly-Seber mark-recapture models. Analysis was carried out in R version 2.8.0 (www.R-project.org) using the package RMark (Laake and Rexstad 2009) to construct models from program MARK (White and Burnham 1999). This allows the calculation of survival probability and recapture probability separately (Grüebler et al. 2008), taking into account the fact that individuals may survive but not be recaptured. Encounter histories of birds were pooled into four time categories, comprising October – May during 2005/06, 2006/07, 2007/08 and 2008/09. Birds were grouped according to sex (male or female) and age (first winter or adult); wing length was also included as a covariate to determine whether survival or recapture probability may be size-dependent.

Firstly, the probability of recapture (p) was examined. The probability of survival (Φ) was set at a constant, and it was hypothesised that the probability of recapture might be dependent upon 1) Age, 2) Sex, 3) Time, and 4) Wing length. As age and sex both influence wing length, the combinations of age and wing length, sex and wing length, and age, sex and wing length were also used to construct models. The $\hat{c}$ variance inflation factor was calculated and adjusted to control for over-dispersion of data, as is common within capture-recapture datasets (Lebreton et al. 1992). This correction did not alter the model selection results.

Models were selected on the basis of ΔQAICc values, with models differing in QAICc from the 'best' model by more than 2 considered to have a real difference from the best model (Burnham and Anderson 1998); thus, only models differing in QAICc from the best model by less than 2 are considered further.

The best recapture model was used to build survival models. The same factors as were thought to influence the probability of recapture were also considered the most likely to influence survival, with the exception of time. Thus, a further seven models were considered here. Models that did not differ from the best model (i.e. with a ΔQAICc of less than 2) were averaged to provide weighted estimates of the effects of important parameters on survival.

Results

Temporal changes in yellowhammer populations

Data from 994 captures between 1986/87 and 2008/09 were analysed to determine whether variation in sex and age ratios between years was evident, and whether there were any temporal trends in wing length. Sex ratio varied from 31% to 55% female birds, with an overall sex ratio of 47% female birds; however there were no significant differences between years (GLM, $F_{18,956}=1.17$, $p=0.28$), or between months ($F_{7,974}=1.41$, $p=0.20$). Age ratio varied from 0 – 50% of adults in the population, with an average of 25.90 ± 3.03% adults. Age ratio differed significantly between years (GLM, $F_{18,943}=3.53$, $p<0.01$; Figure 1); upon further investigation using contrasts, 2005 – 2009 differed in age ratio from earlier years (GLM, $F_{1,943}=29.23$, $p<0.01$), with a higher proportion of adult birds in the population (Figure 1). Age ratios did not differ between months (GLM, $F_{7,936}=0.56$, $p=0.79$).

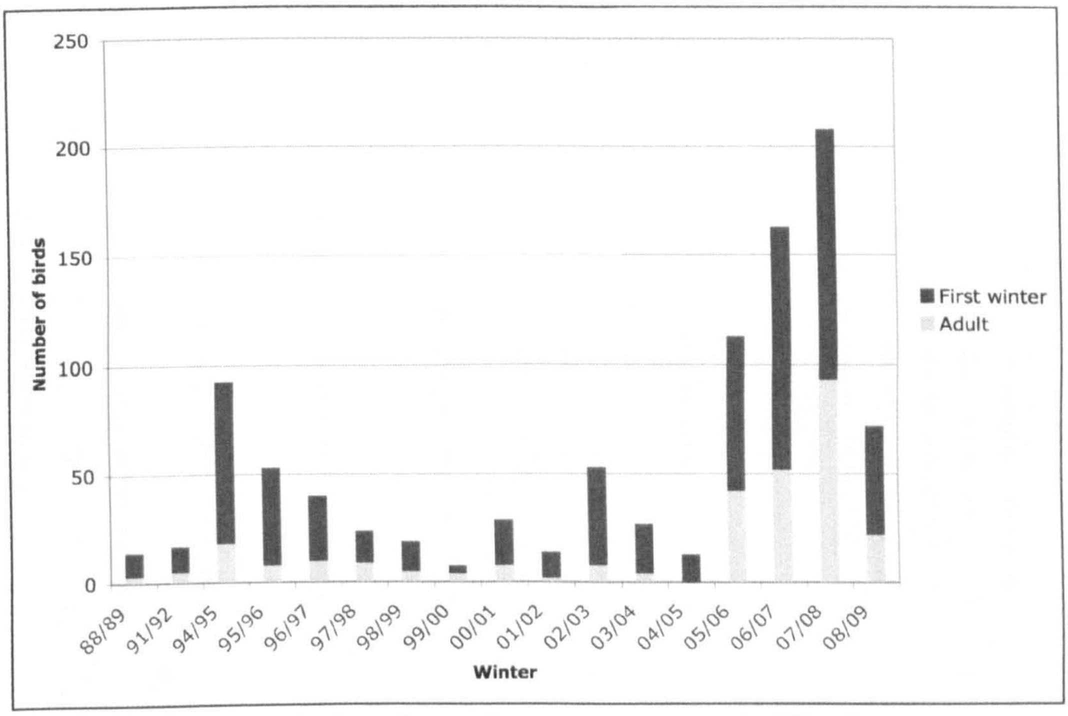

Figure 1. Variation in sample size and age ratio across years. Age ratio differed between years (GLM, $F_{18,946}=3.60$, $p<0.01$) with a higher proportion of adult birds in the population between 2005-2009 than earlier (GLM, $F_{1,963}=29.23$, $p<0.01$)

Table 1. Results of a GLM determining whether temporal trends in wing length were present in a population of yellowhammers. For significant terms, parameter estimates with SE are presented. Two-way interactions of Winter x Age (F_1=2.14, p=0.14) and Winter x Sex (F_1=1.80, p=0.18) neither significantly influenced the fit of the model nor significantly influenced the response variable and thus were removed from the MAM.

Variable	**df**	**F**	**P**	**Estimate**	**SE**
Age (Juvenile)	1, 828	337.030	<0.001	-2.660	0.215
Sex (Male)	1, 827	1054.898	<0.001	4.935	0.244
Winter	1, 826	39.880	<0.001	-0.090	0.014
Age * Sex	1, 825	4.504	0.034	-0.631	0.297

When controlling for age and sex, wing length changed over time (Table 1). A trend towards shorter wings over time can be seen within both the raw data (Figure 2), and in lines predicted from the MAM (Figure 3).

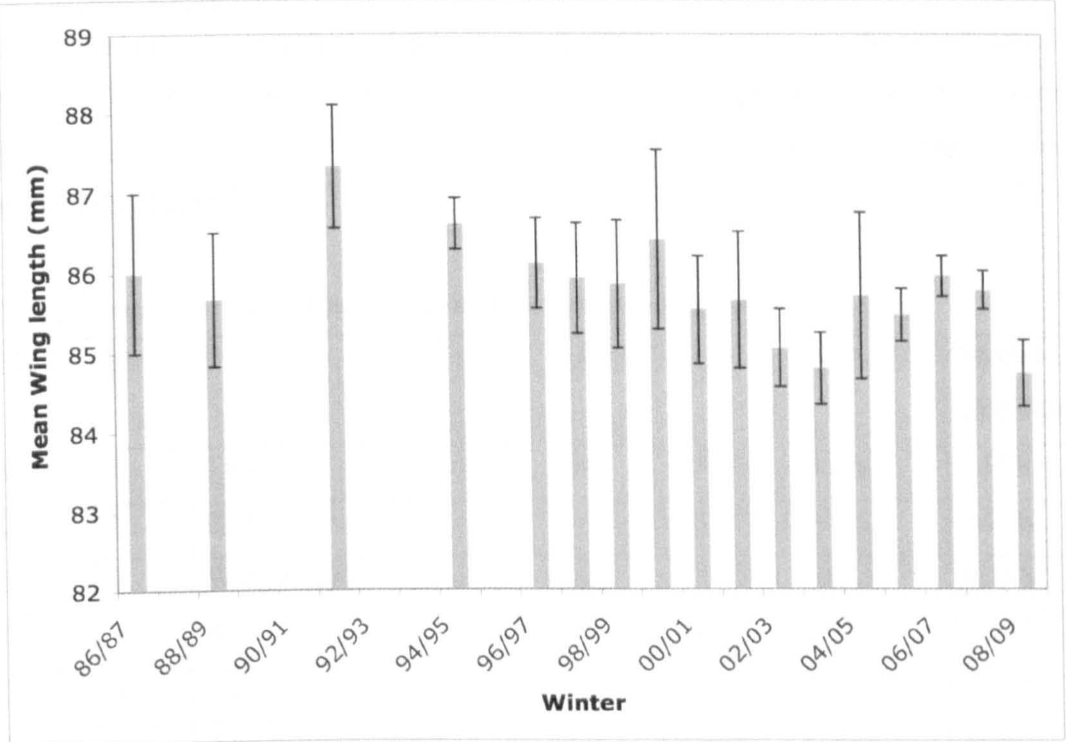

Figure 2. Mean wing length ± SE over time. Years with no bars are years for which no data are available

Survival analysis

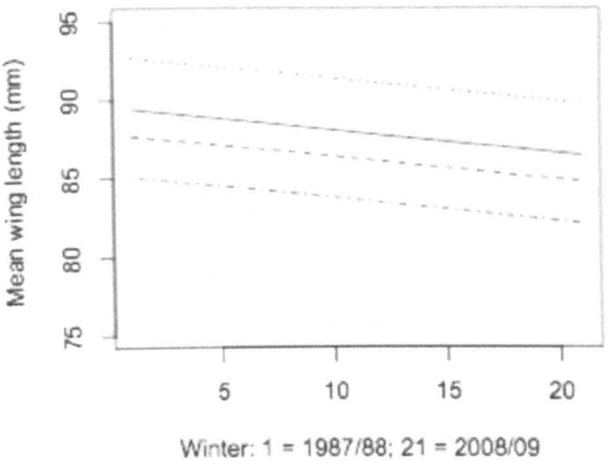

Figure 3. Predicted trends in mean wing length over time from the minimum adequate model (Table 1) for adult males (dotted line) first-winter males (solid line), adult females (dashed line) and first winter females (dot-dash line)

Data from 321 birds captured across four winters were analysed to determine which factors affected survival. Of the eight candidate models generated to predict the probability of a bird being recaptured, ΔQAICc identified model 1 (Table 2) as the most parsimonious. As ΔQAICc is greater then 2 between models 1 and 2, model 1 can be selected above any other model in the candidate set. This was used to construct models predicting survival probability (Table 3).

Table 2. Summary of the candidate models predicting the probability of recapture (p)

Model	Φ	P	npar	QAICc	ΔQAICc	Model likelihood
1	1	Time	4	164.52	0.000	1.000
2	1	Constant	2	167.10	2.572	0.276
3	1	Wing length	3	168.34	3.821	0.148
4	1	Sex	3	168.42	3.895	0.143
5	1	Age	3	169.10	4.578	0.101
6	1	Age + Wing length	4	170.26	5.738	0.057
7	1	Sex + Wing length	4	170.29	5.764	0.056
8	1	Age + Sex + Wing length	5	172.25	7.723	0.021

As ΔQAICc between the top three models is less than 2, it can be said that these models are closely linked and that survival estimates can not be taken from any one model. Therefore the relative weights of each of these three models were used in constructing model estimates (Table 4).

Table 3. Summary of the candidate models predicting the probability of survival (Φ)

Model	Φ	p	npar	QAICc	ΔQAICc	Model likelihood
1	Constant	Time	4	163.68	0.000	1.000
2	Wing length	Time	5	163.86	0.185	0.911
3	Sex	Time	5	164.67	0.995	0.608
4	Age	Time	5	165.71	2.034	0.361
5	Age + Wing length	Time	6	165.85	2.176	0.337
6	Sex + Wing length	Time	6	165.92	2.243	0.326
7	Age + Sex + Wing length	Time	7	167.93	4.257	0.119

The averaged model estimates indicate a positive effect of increased wing length on survival (Table 4; Figure 4), and a reduced female survival compared to males (Table 4). Probability of recapture decreased with increasing time, although not linearly (Table 4).

Table 4. Averaged model estimates predicting survival (Φ) and recapture (p) probabilities for yellowhammers.

	Estimate	SE	LCL	UCL
Φ				
Wing length (75 mm)	0.434	0.058	0.374	0.595
Wing length (95 mm)	0.686	0.058	0.447	0.722
Sex Male	0.632	0.170	0.322	0.920
Sex Female	0.588	0.141	0.263	0.767
p				
Time 2 (2006/07)	0.206	0.069	0.102	0.372
Time 3 (2007/08)	0.160	0.108	0.038	0.478
Time 4 (2008/09)	0.150	0.204	0.008	0.801

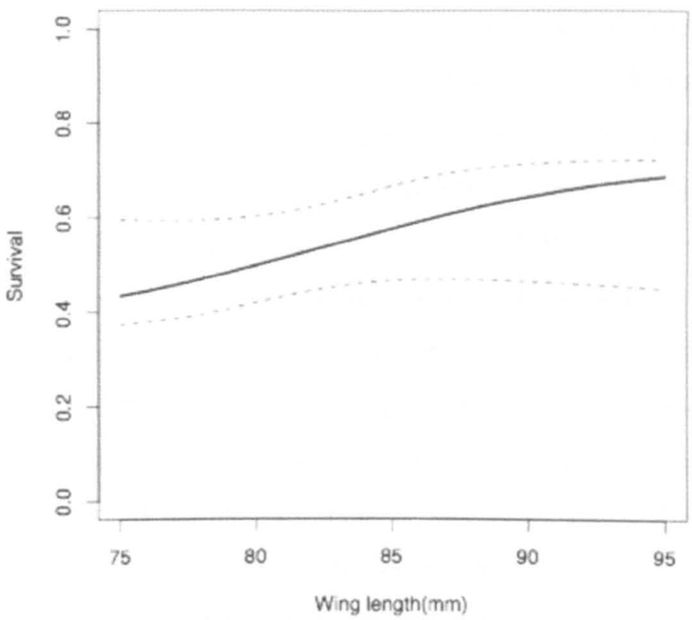

Figure 4. Predictions of the influence of wing length on survival using model estimates averaged from the three best models (Table 4)

Discussion

No evidence was found for skewed sex ratios in any year, although the sex ratio was consistently biased towards males. Sex was also found to influence survival, with females showing lower survival rates. This could be due to male social dominance: male yellowhammers are the larger sex and are therefore likely to be dominant over females in the feeding hierarchy (Domènech and Senar 1999) possibly resulting in female biased mortality as found in great tits and crossbills (Clobert et al. 1988; Benkman 1997). Alternatively, sex-linked mortality may be occurring post-breeding, corresponding to differential effort during reproduction (e.g. Smith 1995). Chapter 5 suggests that females may be working at the upper ceiling of effort during chick provisioning, whilst males vary their reproductive effort according to the requirements of chicks (Chapter 5). This is supported by a similar pattern in great tits, where handicapped females maintained a similar work rate during chick provisioning to non-handicapped females, whereas handicapped males reduced their work rate (Sanz et al. 2000). An increased work rate during the breeding season can result in increased mortality and thus in this species may result in female biased mortality post-breeding. A male-biased population also allows sexual selection to maintain sexually selected traits within the population, as a proportion of males will remain non-breeding 'floaters' each breeding season.

Age ratio varied between years, with large fluctuations in the proportions of juveniles in the population: this ratio can be used to assess the health of the population, in terms of recruitment success (Newton 1999) and has been validated as an effective way of monitoring changes in reproductive success (Peery et al. 2007). Whilst Newton (1999) used the adult: juvenile ratio in October as a measure of annual productivity, survival rates of first year and adult yellowhammers do not differ (Siriwardena et al. 1998; Robinson 2005; this study) and the adult:juvenile ratio did not differ between months in this study; thus the use of data from entire winters is unlikely to cause any bias in this measure. Whilst different trapping methods may also influence the proportion of adults captured (Domènech and Senar 1997), mist netting was used for the majority of captures during this study: cage traps were used on only three successful capture occasions, and whoosh nets on one successful capture occasion during years of high capture effort. Therefore, fluctuations in adult: juvenile ratio are likely to be an accurate representation of either breeding success or post-fledging survival, resulting in differential recruitment to the breeding population between years (Newton 1999), and the higher ratio of adults in the population during the latter four winters indicates either that breeding or fledging success has been reduced, or that post-fledging survival has decreased since 2005. It would be useful to see whether this variation is due to environmental effects such as mean summer temperature or number of rain days during the breeding season, as rain and temperature influence nestling growth and condition (Bradbury et al. 2003), which in turn have the potential to influence future survival and reproductive success (Lindström 1999; Metcalfe and Monaghan 2001; Lummaa and Clutton-Brock 2002; Taborsky 2006). Demonstrating a direct link between poor growth and condition in the nest and lower survival in wild birds would provide an important demographic mechanism behind population changes through reduced juvenile recruitment.

Wing length was also found to differ between years, with a trend for decreasing wing length since 1986 within this population. Wing feathers finish growing post-fledging (after leaving the nest) in first years and are moulted and re-grown post-breeding in adults. A decreasing wing length could be due to three mechanisms: 1) Decreased survival of birds with longer wing lengths; 2) Decreasing wing lengths in individual adult birds between years, or 3) Reduced wing length in first year birds leading to a reduced population average. The survival analysis showed that birds with longer wings had a higher survival and directly contradicts hypothesis 1. Unpublished data from this study indicates that wing length can increase slightly within individuals between years, but only rarely decreases (J. Dunn, unpubl. data), supported by another study which found tail length to be stable within individuals following re-growth (De La Hera et al. 2009). Food availability and other environmental stressors can influence feather growth rate, with slower growth rates where food is limiting or conditions are harsher (Swaddle and Witter 1997; Carlson 1998; Talloen et al. 2008). Dominance hierarchies may also influence feather growth (Hogstad 2003) with subordinates growing feathers more slowly than dominant individuals, probably as a result of differential food availabilities through competition for favourable foraging habitats (Grubb 1989). Extending the feather growth period can compensate for slower growth rates (White et al. 1991); however, in temperate species with extended breeding seasons, adverse weather may limit the time available for moult and a slower feather growth rate may potentially result in shorter feathers, or feathers of lower quality which may impact on thermal maintenance. Evidence that feather length can be influenced by habitat quality in young birds (Grubb et al. 1998) lends support to hypothesis 3, whereby habitat quality and food availability have declined leading to reductions in juvenile feather length and an overall reduction in mean wing length within the population.

This work provides support for changing demography and morphology in a population of a declining farmland bird, impacting on survival, and temporally correlated with changing habitat quality through decreasing invertebrate abundance. This work has implications for other species influenced by environmental change and suggests that long-term physiological changes within populations can result. A physiological mechanism behind the trend is suggested for this species, although further work is necessary to confirm this.

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Chapter 8: Conclusions

Chapter 2: Nesting and foraging ecology

Yellowhammer clutch size and fledging success were similar to that found in other studies, both recent and historical (Peakall 1960; Bradbury et al. 2000), indicating that no change has occurred in fledging success since the start of the yellowhammer population decline. This is supported by other studies reporting that breeding productivity has in fact increased since the onset of the decline (Bradbury et al. 2000; Cornulier et al. 2009), implying that the quality, not quantity of fledglings may have lessened leading to a reduction in over-winter survival.

Nest predation was the cause of most nest failures, consistent with previous studies (Crick et al. 1994; Bradbury et al. 2000; Hart et al. 2006) and suggesting that yellowhammer populations may be susceptible to increased populations of nest predators such as corvids, whose populations have increased concurrently with the yellowhammer population decline (Gregory and Marchant 1995).

Comparison of current data with a dataset from 1960 (Peakall 1960) suggests that the height of yellowhammer nests above ground has increased. This may be due to the availability and structure of available nesting habitat: hedge height may have increased, or the availability of herbaceous vegetation associated with hedgerows may have decreased due to pesticide usage and consequent habitat simplification (Boatman et al. 1994), forcing birds to select nest sites with a higher level of vegetation cover to reduce the risk of nest predation.

Yellowhammers appear to select foraging sites on the basis of habitat structure, choosing sites with lower vegetation densities and less vegetation cover than control sites, probably due to the increased accessibility to food and visibility of predators that these habitats provide (Whittingham and Evans 2004; Douglas et al. 2009). However, foraging sites had higher invertebrate abundances than control sites with the same vegetation height and vegetation cover, suggesting that birds may also be selecting sites on the basis of food availability.

Where invertebrates at foraging sites were abundant, the rate at which adults provision their chicks decreases with increasing vegetation cover, probably as perceived predation risk (mediated by habitat structure) increases and the amount of time spent scanning for predators increases, reducing the time available to forage in visually obstructed habitats. Conversely where food availability is low, provisioning rate increases with increasing vegetation cover, probably as food availability and vegetation cover are positively correlated and implying that where food is scarce, parents are forced to take more risks when foraging for their young.

Chapter 3: Food availability and nest predation risk

Food availability and corvid abundance were not found to differ between organic and conventional farms, although a larger scale study that included the farms in the current study found a higher abundance of both corvids and invertebrates on organic farms (T. Benton, pers comm.; D. Gabriel, pers. comm.). However, organic farms often have a more complex habitat structure, so an increased abundance of invertebrates does not necessarily mean that food is more available as accessibility may be reduced.

An increase in corvid activity decreased the rate at which adult birds provisioned their young. No relationship was found with corvid abundance, indicating that adult birds are able to accurately assess the risk to their nest and adjust their provisioning rate accordingly. This is consistent with other studies investigating behavioural compensation for predation risk (e.g. Eggers et al. 2005) and is to my knowledge the first time that this has been demonstrated in a farmland environment. Invertebrate abundance was unrelated to provisioning rate, suggesting that reducing the risk of nest predation is more important that ensuring nestlings are well provisioned.

Interactions between nest predation risk, food abundance and brood size influenced chick condition and growth. An increased corvid abundance led to a reduction in chick condition and growth in large broods, suggesting that parents are unable to compensate fully for the effects of increased corvid activity on provisioning rate; however an increased invertebrate abundance was positively associated with both condition and growth, as has been found previously in this species (Boatman et al. 2004; Hart et al. 2006). Where food availability was low, chick growth and condition were negatively associated with increasing corvid abundance, again suggesting that parents cannot compensate for behavioural changes induced by increased nest predation risk. Conversely, where food availability was high, chick growth and condition both showed slight increases with increased predation risk, suggesting that parents were either able to increase their provisioning rate when corvid activity was reduced, or were able to increase the amount of food brought back to the nest per foraging trip, thus maximising the food intake of the brood. This may be an adaptive mechanism to ensure that chicks fledge as early as possible in order to reduce their risk of predation in the nest. To my knowledge, this is the first study to demonstrate indirect effects of nest predator abundance on nestlings through changing parental behaviour.

No differences in fledging success were evident between chicks raised in high or low corvid and high or low invertebrate environments; however, there is increasing evidence that conditions encountered whilst growing can influence future survival and future reproductive success through delayed life history effects (Lindström 1999; Metcalfe and Monaghan 2001; Beckerman et al. 2002; Taborsky 2006). There is evidence that yellowhammer breeding productivity has increased since the start of the population decline (Bradbury et al. 2000; Cornulier et al. 2009), indicating a reduction in fledgling quality, rather than quantity. The yellowhammer population decline is coincidental with, if slightly behind that of the corvid population increase (Gregory and Marchant 1995; Baillie et al. 2009). It is conceivable that as corvid abundance has increased (Gregory and Marchant 1995) and invertebrate abundance has decreased (Boatman et al. 2004), nestling growth and condition may have declined, leading to a reduction in the quality of fledglings. If yellowhammer territories are restricted by the availability of suitable nesting habitat (Cornulier et al. Under review), territories within high corvid areas may act as ecological traps and result in population sinks.

Chapter 4: Territory density and bird behaviour

Numbers of yellowhammer territories were strongly associated with the length of hedgerow and the length of fence with dense herbaceous vegetation, the two habitats where yellowhammer nests were found within this study, and in concordance with previous studies (Green et al. 1994; Kyrkos et al. 1998). The number of territories declined sharply between the two years of the study, with a 42% decline on the same farms. Only nest concealment was important in determining the likelihood of predation, and it appeared that more visible nests were predated prior to hatching.

Local territory density (nearest neighbour distance) and brood size interacted to influence both parental provisioning rate and chick growth rate. At high local territory densities, large broods were associated with a high parental provisioning rate, but slower growth whereas small broods were associated with lower provisioning rates and faster, suggesting differential food quality to large and small broods (Wright et al. 1998), possibly as a result of density-dependent competition for high quality food. At low local territory densities, large broods show fast growth, consistent with a reduction in competition and an adequate supply of high quality food. This suggests that the availability of suitable nesting habitat, not food availability, influences territory density in yellowhammers, and that density dependent competitive effects may limit productivity and reduce chick quality in large broods in areas of high territory density.

Chapter 5: Sex differences in parental behaviour around the nest

Differences in parental behaviour when feeding young were found, with females showing a consistently higher provisioning rate than males. Females showed much less flexibility than males when provisioning: males increased their provisioning rate with both an increasing chick age, and with larger broods. Females also increased their rate of provisioning, but to a much lesser extent. Analysis of time budgets showed that in males, the increase in time spent provisioning with increasing chick age or brood size came about from a reduction in the amount of time spent in the vicinity of the nest prior to and post-provisioning (likely to be time spent in territory guarding and nest defence). Females spent little time in the vicinity of the nest pre- or post-provisioning, but spent more time at the nest, probably brooding chicks: the amount of time females spent at the nest decreased with increasing chick age and brood size as the food demands of chicks increase and their thermal requirements decrease.

Parents differed in their response to an increase in the activity of corvids: previously I showed that parents decreased their rate of chick provisioning (Chapter 3), but males increased the amount of time spent in the vicinity of the nest, probably as a nest defence strategy, whereas females decreased the amount of time spent in the vicinity of the nest, possibly to reduce the levels of activity around the nest and reduce the likelihood of nest predation.

The relatively inflexible behaviour of females suggests that they may either be working at their limit of energy expenditure, or at a set limit to enhance their own survival. Males appear to take up any extra demand from chicks and increase their work rate where necessary. Female-biased provisioning in this species is likely to be due to high levels of extra-par paternity (Sundberg and Dixon 1996) and may have implications for sex-linked survival.

Chapter 6: Blood parasite prevalence and association with morphological variables

Three blood parasites were found within a yellowhammer population over-winter, with an overall prevalence of 41%. A novel peak of infection was found during mid-winter, possibly as increased food stress leads to relapses of existing infections via the same hormonal mechanism as documented for other species prior to the onset of breeding as circulating corticosterone levels increase. A high prevalence of infection may be linked to harsh weather, which decreases the available food supply through cold temperatures reducing penetrability of soil to foraging birds: this corresponds to a higher prevalence of infection during the second winter of this study, when conditions were harsher.

Temporally variable associations were found between wing and tail lengths and parasitism. No association was found between head-beak or tarsus length and parasitism, implying that parasite infection affects feather growth. This relationship was only found during the mild winter of 2007/08 and not during the harsher winter of 2008/09, suggesting that birds susceptible to the effects of parasites on feather length during moult are less likely to survive a harsh winter, corresponding with the reduced number of birds caught during 2008/09 despite a similar trapping effort.

60% of 7-day old nestlings sampled were found to be infected by blood parasites: to my knowledge this is the youngest age at which infection has been detected in a wild bird, and implies that many individuals become infected by blood parasites whilst in the nest.

Overall, these data suggest that blood parasites and sub-clinical disease may be an overlooked factor in the health of farmland bird populations, and may constitute yet another stressor upon already pressurised populations.

Chapter 7: Survival and long-term morphological trends

Survival probability in a yellowhammer population was influenced by both sex and wing length. Survival was male-biased, and increased with increasing wing length. The population was found to be male biased, although the sex ratio was not extreme, and did not differ significantly between years. Age ratios differed significantly between years, with an increased proportion of adult birds in the population during the past four years, indicating a decline in recent breeding success.

Mean wing length, when controlling for the effects of age and sex, was found to have decreased since 1986. The apparent paradox between a decreasing mean population wing length and increased survival of birds with longer wings can be explained by a reduction in wing length of juvenile birds recruited into the population, implying a decrease in quality of fledglings due to poorer habitat quality or reduced food availability during the growth period, both factors that have previously been linked to reduced feather growth (Grubb 1989; Grubb et al. 1998).

Conclusions

This study contributes further knowledge to the demographic and mechanistic factors affecting bird populations in farmland, both during the breeding and the non-breeding seasons. Using the yellowhammer as a model species, I demonstrate that breeding success per pair appears unchanged since the start of the population decline, implying that fledgling quality and not quantity has changed, as suggested previously (Cornulier et al. 2009). I propose a mechanism by which this may have occurred, through an increase in corvid abundance impacting on the growth and condition of chicks in the nest through behavioural compensation by provisioning adults. This decrease in growth and condition is especially marked in areas where food availability is low, implying a synergistic effect of food availability and predation risk (Krebs et al. 1995; Zanette et al. 2003; Clinchy et al. 2004). Both corvid increases and decreasing invertebrate populations occurred simultaneously prior to the onset of the yellowhammer population decline (Gregory and Marchant 1995; Boatman et al. 2004). This effect may be further compounded by the reliance of yellowhammers upon suitable nesting habitat for territories: in patches of good nesting habitat with high territory densities, apparent density-dependent competition for high quality food reduces chick growth and may reduce fledgling quality, potentially leading to population sinks in areas of good nesting habitat, or areas with high corvid population densities. Low food availability for chicks may also force adults into taking more risks when foraging for food for their young, as invertebrates are more abundant where vegetation cover is greater despite higher perceived predation risk for birds foraging in visually obstructed habitats.

Yellowhammer survival is male-biased, possibly due to higher work rates of females during the breeding season, although population sex-ratios are not extreme. The high prevalence of blood parasite infection in yellowhammers over-winter implies that infection may compound food stress or vice-versa: as two stressors can have synergistic effects (Krebs et al. 1995; Zanette et al. 2003; Clinchy et al. 2004; Sih et al. 2004) the reduction of food availability during harsh winters may be compounded by sub-clinical parasite infection. Parasites are also associated with reductions in feather growth: as an increased wing length increases survival probability, parasites may have indirect effects on survival. Mean population wing length, when controlling for the effects of age and sex, shows a long-term decline. This is likely to be due to a reduction in the quality of first-year birds recruiting into the population leading to a reduction in mean population wing length.

Although this study focussed on yellowhammers, the mechanisms outlined in this study are likely to be present in other species, and the synergistic effects of multiple stressors may be alleviated to some extent by reducing the impact of just one. For example, the effects of corvid abundance on chick growth are considerably reduced where food is more abundant.

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Appendix 1: Ringing and Migration 24: 240-252 (2009)

Ageing and sexing the Yellowhammer *Emberiza citrinella caliginosa* during the non-breeding season

JENNY C. DUNN[1]* and CHRIS WRIGHT[2]

[1] *Institute of Integrative and Comparative Biology, L. C. Miall Building, University of Leeds, Leeds. LS2 9JT, UK.*

[2] *Field Research Unit, Leeds University Farms, Headley Hall, Tadcaster. LS24 9NT, UK.*

* Correspondence author

Email: J.C.Dunn01@leeds.ac.uk

Short title: Ageing and sexing the Yellowhammer

Abstract

Individual or population-level analyses using ringing data require accurate identification of the age and sex of birds in the hand. Many species are difficult to age and sex: work on known age and sex birds is essential if we are to increase the value of ringing data for these species. In this study we have used molecular sexing techniques and known-age birds to characterise plumage characteristics useful in distinguishing the age and sex of Yellowhammers *Emberiza citrinella caliginosa.* Tail feather shape was useful in ageing both adult and first year birds, supporting current ageing criteria; other features were associated with first year birds but not with adults. Most, but not all, birds could be sexed using the amount of yellow visible on the side of head and crown. The amount of black on the longest tail covert shaft and the amount of white colouration on the fifth and sixth tail feathers were useful for identifying both sexes. The rump-feather shaft colour and under-tail covert colouration may be useful for sexing ambiguous birds. Our results provide additional ageing and sexing criteria for *E. c. caliginosa* and can be used to improve the accuracy of ringing data for this declining subspecies.

Introduction

Knowledge of the age and sex of a bird is crucial when undertaking any analysis of condition, reproductive success (Kokko 1998) or survival (Tavecchia *et al* 2001). The sex of a bird intrinsically influences its reproductive success, especially in species with high levels of extra-pair copulation (Sundberg & Dixon 1996), and factors such as immunocompetence and susceptibility to disease are frequently sex-linked (e.g. Roulin *et al* 2007). The age, and thus breeding experience, of birds influences sexually-selected traits and reproductive success in many avian species (Sundberg & Dixon 1996, Komdeur *et al* 2005) and age may also influence the frequency or intensity of breeding strategies such as mate guarding (Johnsen *et al* 2003). Survival may be sex-linked (Tavecchia, et al. 2001, Eeva *et al* 2006) and frequently the probability of surviving until the next year is higher for older birds (Martin 1995, Tavecchia, et al. 2001).

Around 50% of avian species exhibit sexual dimorphism (Griffiths *et al* 1996), allowing easy identification of the sex of a bird in the field or in the hand. Age in small passerines is largely categorised as birds either hatched during the previous breeding season (first/second year birds, herein referred to as first years) or birds born before this (adults). In many species this is identified by observing a contrast in wing covert colour in first year birds that have undergone a partial post-juvenile moult (Svensson 1992). Other species, such as those in the bunting family, frequently moult all their greater coverts, and sometimes the carpal covert, tertials and alula (Jenni & Winkler 1994, Blasco-Zumeta 2008). As a result, no contrast within wing coverts is visible and assessing age in these species is largely dependent on an assessment of the wear and bleaching on primary feathers and tail feathers grown in the nest (first-year birds) in comparison with recently-moulted feathers on adult birds (Svensson 1992, Jenni & Winkler 1994). However, as winter progresses the wear on adult feathers increases and differences between the age classes are less obvious: late-hatched birds may have similar amounts of wear to adults that have undergone post-breeding moult, so this criterion can often be inaccurate, as has been found within known-age reed buntings (Baker 1986).

The Yellowhammer (*Emberiza citrinella*) is a temperate bunting species that exhibits marked plumage variation. The most marked differences are between adult males and first-year females, adult male birds having a high proportion of intense yellow colouration on their head and breast, and first-year female birds being markedly dull with very little yellow on their head and pale yellow on their breast.

Males of this species acquire the breeding plumage on their head by abrasion in spring, with black and brown feather tips during the non-breeding season obscuring the yellow head colour of a breeding bird. This makes the differences between first-year males and adult females at this time of year less clear-cut and consequently many birds cannot be aged reliably using known criteria in the non-breeding season (e.g. Thompson 1987), reducing the reliability of data collected by ringers.

Previous studies have attempted to find reliable methods of accurately determining age and sex in Yellowhammers: most have relied upon shape and wear of tail feathers (e.g. Svensson 1992) which can be unreliable as some first year birds will moult some, if not all of their tail feathers (Blasco-Zumeta 2008). Skull ossification is also a recommended technique for ageing this species (Svensson 1992); however this technique takes more time than is often available (e.g. Cobb 1997). Whilst some studies have examined additional plumage-colouration criteria, including crown feathers (Svensson 1992), tail feather colour (Norman 1992) and head and breast colouration (Blasco-Zumeta 2008), considerable confusion remains and results are not always consistent (Svensson 1996), which may be due to regional geographic variation or variation between subspecies.

The subspecies of Yellowhammer found in north and west Britain, *E. c. caliginosa* (Clancey), is slightly darker and more streaked than the more widespread *E. c. citrinella* subspecies found in southern England and into continental northern and central Europe (Svensson 1992). Crown feather markings are used to determine sex in *E. c. citrinella* (Svensson 1992); however, these are inaccurate when applied to *E. c caliginosa*. For example, males of the latter subspecies frequently possess a prominent black shaft streak restricted to females of the former subspecies (e.g. Fig 1).

Yellowhammers in Britain have undergone significant population declines since the beginning of the 1980s with an estimated population decrease of 25% between 1980 and 1994 (Siriwardena *et al* 1998), and a further significant decline of 19% between 1994 and 2007 (Risely *et al* 2008). Whilst still relatively widespread, it is important that population analyses of this species utilise accurate age and sex data to identify any sex or age-related variation in survival.

In this paper we describe a study of a population of *Emberiza citrinella caliginosa* from North Yorkshire during the non-breeding season. We have categorised plumage characteristics showing marked variation; using molecular techniques to establish sex, and a subset of birds of known age, we have assessed whether variation in these plumage characteristics, along with morphometric variables, is related to age or sex and can thus be used as a reliable technique to identify the age or sex of an unknown bird of this subspecies in the hand.

METHODS

Study sites

Yellowhammers were caught and ringed at Leeds University Farms near Tadcaster, West Yorkshire, UK (lat. 53° 53'N, long. 1° 15'W). Birds were caught between December 2007 and April 2008 in static mist nets at established supplementary feeding sites, baited with wheat and weed seed, situated within an experimental agroforestry habitat surrounded by arable farmland.

Biometric data collection

Full morphometrics of a subset of birds (n = 111) were taken as shown in Fig. 2. If an individual was captured more than once, only the first set of measurements was included in the analysis to avoid pseudoreplication; to ensure consistency, all measurements were taken by the same person (JCD). The following measurements were recorded for each individual (see also Fig. 2): wing length, measured as the maximum wing chord; head and beak length (HB), measured from the tip of the bill to the centre of the back of the skull (Redfern & Clark 2001); tail length (TL), measured from the tail base to the tip of the longest outer retrix; beak length (BL), measured from the feathering to the tip of the beak; beak depth (BD), measured at the point of feathering (Svensson 1992); and tarsus length (TSL), measured as the minimum tarsus length from the foot to the inside of the knee. Measurements of wing length were taken using a standard metal wing rule and rounded up to the nearest mm; other measurements were taken using digital callipers (± 0.1 mm).

Age

The age of birds was assessed in the hand by considering the shape and colour of the central tail feathers, along with an examination of the amount of wear and bleaching on the tail, tertials, and primaries, and classified as either adult or first-year birds (Svensson 1992). Birds that were definitely adult (ringed before the previous breeding season) were noted, along with birds that were almost certainly first years: if a bird had a fault bar present in its tail along with three of either pointed, narrow, bleached or worn rectrices, it was considered to be almost certainly a first-year bird. A fault bar alone was not considered sufficient to indicate a first-year bird, as adults that lose their tail may re-grow rectrices simultaneously, potentially producing a fault bar. These birds were then used to confirm the accuracy of criteria identified as potentially useful through analysis of the entire dataset and are herein referred to as "known adults" and "known first-years" although it should be noted that birds in the latter category could not be aged with the same absolute certainty as the ringed adults.

Sex

Sex of birds was assessed in the hand using the amount of colour on the head, along with wing length and age (as above) to differentiate between adult female and first-year male birds (Svensson 1992).

Molecular determination of sex

DNA was extracted from 30 μl of whole blood using a standard phenol-chloroform extraction technique and diluted to a working concentration of 25 – 100 ng μl^{-1}. Sex was determined using the polymerase chain reaction (PCR) technique with the P2 and P8 primers described by Griffiths *et al* (1998) to amplify sections of the CHD-Z and CHD-W genes. Sexes are differentiated on the basis that both sexes possess the CHD-Z gene, whereas the CHD-W gene is unique to females (Fig 3). The PCR was carried out in a total reaction volume of 10 μl, containing 0.8 mM deoxynucleotide triphosphates, 1 μM of each primer, 2 μl of 5X GoTaq Flexi buffer (Promega, Southampton, UK), 2 mM $MgCl_2$, 0.25 U GoTaq Flexi DNA polymerase (Promega) and 25 – 100 ng template DNA. No positive control was used as all samples were expected to produce bands; a negative control containing deionised water in place of template DNA was included with each PCR reaction to ensure lack of contamination. The PCR amplification protocol consisted of a denaturation step at 94°C for 2 min, 40 cycles of 94°C for 45 s, 48°C for 45 s and 72°C for 45 s, with a terminal extension step of 72°C for 5 min. PCR protocols were carried out on a GeneAmp PCR System 9700 (Applied Biosystems, Warrington, UK). PCR products were separated by electrophoresis through a 3% agarose gel in standard Tris/borate/EDTA buffer, stained with ethidium bromide and visualised under UV light.

Photographic analysis of plumage characteristics

A series of digital photographs were taken of the crown, side of head, wing, breast, rump and tertials, wing coverts and tail of each bird in order to minimise the processing time for each bird in the hand. Photographs were taken using a Nikon CoolPix p5000 digital camera and analysed 'blind' with respect to molecularly-determined sex and assessment of age and sex using plumage criteria. Features that were analysed to determine whether they showed any correlation with the age or sex of a bird, along with category classifications, are described in Table 1. Not all photographs were of sufficient quality to distinguish the necessary features and the number of birds for which each feature was analysed is given in the results in Tables 2 and 3.

The intensity of colour of a bird can frequently be used to determine sex in sexually dimorphic species (e.g. Molina-Borja & Avila 2006). However, the use of colour-intensity criteria to assess a bird whilst in the hand is dependent upon ambient light conditions and is often highly subjective. In this study, male birds with pale colouration and female birds with intense colouration were observed (Authors, pers. obs.), implying that other environmental determinants of colour intensity, for example haemoparasites (Sundberg 1995), may be important in this species. Thus, colour intensity is not considered further here.

Statistical analyses

Statistical analyses were conducted in R version 4.2.1 (www.R-project.org). For analyses of sex, molecular sex was used as the response variable. For significant terms, the association and percentage accuracy were calculated for each category classification. In addition, the data for birds misidentified in the hand (n=10: 5 males, 5 females) were examined to determine whether characteristics that were significant from the statistical analysis could have been used to sex these individuals correctly. Whilst the sample size of misidentified birds was small, examination of these data may point towards criteria that might be useful in sexing ambiguous birds. For age analyses, age as established in the hand according to Svensson (1992) was used as the response variable for initial analysis. For significant terms, the association and % accuracy were calculated for each category classification. Consistency was then checked using a subset of data from birds of known age (adults ringed during previous years, n = 31; first years as previously defined in the "Age" section, n = 10) as consistent misidentification of age in the hand would otherwise lead to inevitable biases in data.

Analysis of plumage data

Plumage analysis was conducted separately for age and sex. Generalised linear models with binomial error structure were constructed for each feature separately with either age or sex as the binary response variable, to determine whether significant differences in frequency distribution were present between age classes, or between sexes, and thus whether this feature could be used reliably to determine age or sex.

Analysis of morphometric data

For morphometric data, generalised linear models were constructed for each morphometric variable separately, with the morphometric variable in question as the response variable and age, sex and age*sex interaction as fixed factors, to determine whether each morphometric variable was influenced by age and/or sex. Where necessary, models were fitted with quasi-gaussian error distributions to control for overdispersion of data. Non-significant terms were removed from the model in a stepwise fashion until only terms significant at $p<0.05$ remained.

Results

Plumage data

Plumage data were collected from 151 Yellowhammers between December 2007 and April 2008. Whilst there were many significant associations between age/sex and plumage characteristics (Table 2: age; Table 3: sex), only those which had an accuracy of greater than 80% are described and discussed as only these will be sufficiently reliable for determining the age and sex of unknown Yellowhammers. Characteristics that were examined but were not associated with age or sex are summarised in Appendices 2 (age) and 3 (sex).

Age

Head: No significant associations with age were found for any plumage features of the head (Appendix 2).

Wing: Tertial markings showed a significant relationship with age: 89% of birds with distinct demarcation on the tertial feathers (Fig1ai) were identified as first year, supported by 90% of known-age first years (Table 2). The amount of wear and bleaching on the tertials also differed with age, although reliability across the entire dataset was below 80%. First-year birds tended to have worn and bleached tertials, supported by 80% of known-age first years (Table 2). Secondary feather shape also differed with age, although the accuracy within the entire dataset was below 80% (Table 2): first-year birds tended to have a notched end to their secondaries (Figure 4di) and this feature was present in 88% of known first years. In contrast, adult birds tended to have a flat tip to their secondaries (Table 2; Figure 4dii), but this was not supported by the sample of known adults. Whilst primary-tip shape and primary-covert wear and shape differed significantly between adult and first-year birds, associations were neither clear, nor supported within the subset of known-age birds (Table 2).

Tail: Tail feather shape, width, colour and wear differed according to age. It was not possible to categorise the tail morphology of 11% of birds due to tails either being missing or dampened prior to processing (n=16). Rounded central feather tips were associated with adult birds, whereas worn and bleached central feathers were associated with first year birds, as were sharply angled or pointed outer tail feathers (Table 2). All birds with white colouration reaching the shaft on both sides of the outermost tail feathers were first years, although this was relatively rare (Table 2).

Coverts and body feathers: The extent of black on the upper tail coverts, along with the colour of the under-tail covert shafts had significant associations with first years, but not adult birds. 87% of birds with no black on the longest upper tail covert were first years, as were 82% of birds with chestnut colouration on the shaft of the under-tail coverts.

Sex

141 birds were successfully sexed using molecular techniques. 10 birds (5 males, 5 females) had been incorrectly sexed in the hand: these were used to determine which features that show significant differences between the sexes may be most useful in identifying ambiguous birds. The results of statistical analyses showing the features which may be useful in determining sex are shown in Table 3; plumage features that had no association with sex are summarised in Appendix 3.

Head: All plumage features of the head that were examined showed significant and accurate associations with sex (Table 3). 84% of birds with >20% of the crown showing visible yellow colouration were identified as male on the basis of molecular evidence, and 89% of birds with <10% visible yellow colour on the crown were confirmed as female on the basis of molecular evidence. However, this criterion only accurately sexed the misidentified male birds, not the females (Table 3). Birds with yellow or chestnut malar stripes tended to be male, as did birds with a distinct bright yellow region above and behind the eye (Fig 2b). Birds without this region tended to be female, and this trend was consistent within ambiguous birds (Table 3).

Wing: Tertial feather markings showed significant differences between the sexes; however, the association was neither clear nor reliable. Thus, no plumage characteristics of the wing proved to be significantly and accurately associated with sex (Table 3; Appendix 3).

Tail: The amount of white on the tail showed significant and reliable associations with sex for a small number of birds: all birds with white colouration reaching the shaft on both sides of the outer tail feather were male, as were all birds with white colouration reaching the shaft on one side of the fifth tail feathers (Table 3). 80% of birds with a very small patch of white on the fifth tail feather when compared to the amount on the sixth tail feather (Fig 4bi) were female and all birds with similarly sized white patches on the fifth and sixth tail feathers (Fig 4biv) were male (Table 3).

Coverts and body feathers: The colour of the shaft of the under- and upper-tail coverts proved useful in identifying male and female birds (Table 3). 95% of birds with no black on the longest upper-tail covert shaft were male and 86% and 95% of birds with half and all the shaft black, respectively, were identified as female on the basis of molecular evidence. 95% of birds with chestnut under tail covert shafts were male. Although not highly accurate for the entire dataset, the colour of the rump feather shaft could correctly identify 100% of misidentified birds (although the sample size was small), with females having a black shaft and male shafts blending with the rest of the feather (Table 2).

Morphometric data

Significant differences were found between males and females in terms of wing length, tail length, beak length and beak depth, but not for head-beak length or tarsus length, with males having on average longer wings and tails than females, but females having longer and deeper beaks (Table 4). Age differences were found for wing length, tail length and beak depth, with adult birds having longer wings and tails, and deeper beaks than first year birds (Table 4). Mean values, along with standard deviations and range are displayed in Table 5.

Frequency distributions for wing length are shown for first years and adults in Figure 5. Male and female wing lengths overlap in both first years (Figure 5a) and adults (Figure 5b). However, on removal of the top 20% of female wing lengths and the bottom 20% of male wing lengths, the remaining adults could be sexed reliably using this measurement, with wing lengths below 87mm being from female birds and wing lengths above 87mm being from male birds. First-year birds could not be sexed reliably using wing length: with removal of 20% of overlapping wing lengths as before, 11% of male and 13% of female wing lengths still overlapped. However, birds with wing lengths of less than 80mm could be aged and sexed unambiguously as first year females (n=6; 4% of total birds); birds with wing lengths greater than 92mm were adult males (n=12; 8%), and birds with wing lengths greater than 90mm were male (n=22; 15%).

Birds with short tail lengths could not be aged or sexed reliably; however all birds with tail lengths greater than 75mm were male (n=12; 11%)

Discussion

Ageing

Current criteria used to age Yellowhammers involve the examination of abrasion and shape of the tail feathers along with an assessment of wear on primary tips (Svensson 1992). Here we assess the reliability of these criteria, as well as examining alternatives that may prove useful in increasing the accuracy of ageing this species, particularly the subspecies present in northern Britain, *Emberiza citrinella caliginosa*.

The shape of outer and central tail feathers had a high accuracy for ageing first-year and adult birds respectively, in agreement with existing ageing criteria (Svensson 1992). Whilst it must be taken into consideration that these criteria were initially used to age unknown birds in the hand, this relationship was consistent with birds of a known age so it is concluded that these criteria are reliable for ageing circa 80% of birds. The amount of wear and bleaching on central tail feathers proved reliable as the majority of birds with feathers classified as worn and bleached were first years (although it must be noted that this characteristic was used to identify first year birds in the first instance and that many known adults also had worn and bleached central tail feathers). However, many first years also had fresh feathers, probably due to a later hatching date, or a partial or full moult of tail feathers as seen in some first-year Reed Buntings (Baker 1986); therefore, ageing birds with fresh central tail feathers was less reliable. Central tail-feather width showed significant differences between adults and first years and this was also consistent with known-age birds; however the accuracy of this criterion was low, so it is not considered to be reliable in identifying unknown Yellowhammers. In view of this, and the fact it was not possible to categorise the tail morphology of 11% of birds due to tails either being missing or dampened prior to processing, it is desirable to have other features that are known to change reliably with the age of a bird.

Three novel criteria showed significant differences between adult and first-year birds, with a high degree of accuracy for at least one category within each. The majority of birds with no black on the shaft of the longest upper-tail covert were first years, although no relationship was found with other amounts of black. Interestingly, this relationship was also associated with male birds, suggesting that the vast majority of birds with this feature can be identified as first-year males. All birds with white on both sides of the shaft of the outermost tail feather were first years, although the sample size here was relatively small which may explain the inconsistency of this result with known-age birds. The majority of birds with a chestnut shaft on the under-tail coverts were first years, although less than half of the known-age first years exhibited this characteristic. However, no novel criteria had reliable associations with adult birds.

Whilst the shape of the primary tips differed significantly between adults and first years, there were no clear associations. Primary-covert shape and width both differed between age classes; however the associations here were not clear and this was not supported within the sub-sample of known-age birds. The shape of secondary feathers also differed between adults and first years, with adult secondaries tending to have a flat edge, and first year birds tending to have strongly notched edges to their secondaries. This association was upheld within the sub-sample of known-age birds; however, the associations were not strong enough to be reliable as a single criterion for ageing this species, but may be useful when considered in conjunction with other plumage characteristics and morphological measurements.

Sexing

Current criteria used to sex the Yellowhammer involve the examination of the colour of the crown feathers, with males having more than half of their crown feathers yellow with no prominent black distal streak, and females with virtually no yellow on their crown feathers. However, this is inaccurate with the subspecies in question (e.g. Fig 1) and so new criteria are needed in order to allow accurate sexing of this subspecies in the hand.

Three criteria involving examination of the head of birds had a high accuracy for identifying both male and female birds. The majority of birds with more than 20% yellow visible on their crown were male and the majority of birds with less than 10% visible were female. This could be used to identify accurately the majority of males misidentified as females in the hand, but less than half of females misidentified as males, indicating that old female Yellowhammers may be misidentified frequently as males due to increased yellow colouration (Blackburn 2006). Malar stripe colour seems to be a useful criterion in identifying male birds, with the majority of birds with chestnut flecks, or a solid chestnut malar stripe, and most birds with a pure yellow malar stripe identified as male on the basis of molecular evidence. However, less than half of the misidentified males could be successfully sexed using this method, suggesting that male birds with increased yellow or chestnut colouration are older and more easy to sex (Sundberg & Dixon 1996). Although only 77% of birds with brown flecks or a solid brown malar stripe were identified as female on the basis of molecular evidence, all misidentified female birds could have been accurately sexed this way and thus this may be useful in identifying ambiguous female birds in conjunction with other criteria. The presence of a distinct yellow region above and behind the eye of a bird (Fig. 2b) could be used with high accuracy with both sexes, as male birds tended to possess this region and females tended not to. This could be used to identify 80% of both males and females previously misidentified in the hand.

Five novel criteria were found to differ significantly in their association with sex, with a high level of accuracy for at least one category within each. Most birds with only very small white patches on their fifth tail feathers were identified as female on the basis of molecular evidence, and all birds with white patches on their fifth tail feathers equivalent in size to the patches on the sixth were identified as male, although sample sizes within these two categories were relatively small and all misidentified birds possessed either small or medium white patches which show no significant association with either sex. The extent of the white colouration on the sixth and fifth tail feathers may be useful in sexing small numbers of birds: all birds with white colour reaching the shaft of the sixth tail feather on both sides were male, as were all birds with white colouration reaching the shaft of the fifth tail feather. The extent of black on the shaft of the longest upper-tail coverts may be useful in identifying both sexes: most birds with no black were male, nearly all birds with a completely black feather shaft were female, and the majority of birds with more than a third of the feather shaft black were also female. Whilst only 77% of birds with less than a third of the feather shaft black were male, there is a clear trend for females possessing more black on this feather shaft than males. However, less than half of misidentified birds could be sexed successfully using this criterion alone. Nearly all birds with a chestnut shaft on the short under-tail coverts were identified as male; however a large number of males, together with females, possessed a black shaft on these feathers.

The colour of the shaft of the rump feathers may be useful in sexing Yellowhammers, although accuracy was below 80%: female birds tended to have a black feather shaft, and male birds tended to have the shaft the same colour as the rest of the feather. All misidentified birds fitted this trend, so this criterion may be useful for sexing ambiguous birds.

Whilst tertial markings showed a significant differential association between sexes, the association was not clear, or accurate enough to be useful in determining sex. The longest under-tail covert colour showed a significant association although accuracy was below 80%, with 68% of birds with black only identified as female and most birds with black and chestnut colouration identified as male. However, all male birds misidentified as female possessed black and chestnut colouration, so this may be a useful aid in identifying ambiguous males, but not females.

Morphometrics

Wing length and tail length both differed significantly between sexes and between age classes. Although there was a significant degree of overlap, over 80% of adults could be sexed accurately using wing length, provided they had been aged by other means; 80% of female wing lengths were below 87mm and 80% of male wing lengths were above this value. However, first years could, in general, not be sexed reliably using wing length alone except at the extremes, although this measurement could still be useful when considered in conjunction with other criteria.

Whilst tail length, beak length and depth differed between ages and sexes, these differences were small and thus could not be reliably used to differentiate between sexes or age classes.

Conclusion

The shape of outer and central tail feathers proved useful in ageing adult and first year birds respectively. Birds with worn and bleached central tail feathers tended to be first years; however first years often had fresh feathers so ageing birds with fresh central tail feathers was inaccurate. Birds possessing no black on the longest upper-tail covert tended to be first years, as did birds with white on both sides of their outermost tail feather shaft and birds with a chestnut shaft on the under-tail coverts.

The majority of birds could be sexed accurately using the amount of yellow visible on the crown and side of head. Chestnut and yellow malar stripe colour also proved useful in sexing some males. The amount of white on the outermost two tail feathers may be useful in identifying both sexes, with females tending to have less white on the fifth tail feather than males, and birds with white on both sides of the shaft of the outermost tail feather being male. The extent of black on the shaft of the longest upper-tail covert showed a clear relationship with sex, with females having a much larger amount of black than males, which tended to have very little or none. A chestnut shaft on the shorter under-tail coverts proved useful for identifying some males. The shaft colour of the rump feathers and presence of black and chestnut colouration on the under-tail coverts may be useful in identifying ambiguous birds.

Birds with extremes of wing length could be identified as first year females and adult males and birds with long tails could be identified as males; the majority of adults, but not first years, could be sexed using wing length providing they had first been aged. No other morphometric variable considered here is likely to prove useful in ageing or sexing this species.

Criteria found to be useful for ageing and sexing this species are summarised in Appendix 1.

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Table 1. Features considered as likely predictors of age or sex, along with criteria used for each feature.

Feature	Criteria
Head	
% of visible yellow on crown	Less than 10% More than 20%
Malar stripe colour	Completely yellow (Yellow) Chestnut or chestnut flecks (Chestnut) Black or black flecks (Black) Brown or brown flecks (Brown)
Distinct bright yellow above and behind eye (region c in Figure 2b)	Yes No
Wing	
Shape of primary tips	Square Pointed Rounded Intermediate
Shape of primary coverts	Rounded Pointed
Width of primary coverts	Narrow Wide
Shape of secondary tips (Figure 4	Flat Notched
Wear and bleaching on tertial feathers	Fresh Worn and bleached
Markings on tertial feathers (Figure 4a)	Distinct demarcation between light and dark colouration (Distinct) Blurred boundary between light and dark colouration (Diffuse)
Shape of 2nd alula	Rounded Pointed
Shape of 3rd alula	Rounded Pointed
Yellow/white edging on median coverts	Yes No
Tail	
Shape of central tail feather tip	Pointed Rounded
Width of central tail feather	Narrow Wide
Central feather wear and bleaching	Worn and bleached Fresh
Angle/shape of outer tail feather (Svensson 1992)	Sharp Shallow
Extent of white on sixth (outer) tail feather	Reaches shaft Does not reach shaft
Extent of white on fifth tail feather	Reaches shaft Does not reach shaft
Size of white patch on fifth tail feather (Figure 4b)	Very small Small Medium Same as white patch on sixth tail feather
White on fourth tail feather	Present Absent
Coverts and body feathers	
Colour of shaft of rump feathers level with middle tertial	Black Chestnut (Blended)
Extent of black on shaft of longest tail covert (Figure 4c)	No black Short (less than 1/3 of shaft) black

	Half (1/3 – 2/3) of shaft black Entire feather shaft black
Colour of longest under-tail covert (in addition to yellow)	Black Black and chestnut
Colour of shaft of shorter under-tail coverts	Black Chestnut

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Table 2. Significant results of statistical analyses showing features that differ between age classes.

Feature	**Resid. Dev**	**df**	**p**	**n**	**Association and % accuracy (n)**	**Consistent with known age birds? (n)**
Wing						
Shape of primary tips	174.73	3, 139	**<0.0001**	143	Round: 76% first year (45)	In 60% first years (10)
					Pointed: 51% first year (57)	
					Square: 68% adult (31)	In 27% adults (30)
					Intermediate: 89% adult (9)	
Shape of primary coverts	194.67	1, 143	**0.039**	144	Pointed: 61% first year (84)	In 70% first years (10)
					Rounded: 57% adult (60)	In 40% adults (30)
Width of primary coverts	194.15	1, 142	**0.029**	144	Narrow: 59% first year (98)	In 70% first years (10)
					Wide: 60% adult (47)	In 33% adults (30)
Shape of secondary tips	150.97	2, 116	**0.001**	119	Flat: 64% adult (58)	In 67% adults (27)
					Notched: 69% first year (58)	**In 88% first years (8)**
					Mixed: 100% first year (1)	
Wear and bleaching on tertial feathers	155.45	1, 126	**<0.0001**	128	Worn and bleached: 72% first year (75)	**In 80% first years (10)**
					Fresh: 68% adult (53)	In 63% adults (24)
Markings on tertial feathers	125.06	1, 126	**<0.0001**	128	Diffuse: 71% adult (72)	**In 84% adults (25)**
					Distinct: 89% first year (56)	**In 90% first years (10)**
Tail						
Shape of central tail feather tips	127.69	1, 131	**<0.0001**	135	**Rounded: 84% adult (49)**	In 63% adults (24)
					Pointed: 78% first year (80)	**In 100% first years (9)**
					Intermediate: 100% first year (5)	

Width of central tail feathers	177.06	1, 135	**0.002**	138	Narrow: 71% first year (62) Wide: 57% adult (75)	**In 89% first years (9)** In 67% adults (24)
Central tail feather wear and bleaching	137.94	1, 130	**<0.0001**	133	**Worn and bleached: 88% first year (57)** Fresh: 67% adult (75)	**In 100% first years (10)** In 78% adults (18)
Angle/shape of outer tail feathers	149.54	1, 133	**<0.0001**	135	**Sharp: 83% first year (60)** Shallow: 67% adult (75)	In 67% first years (9) **In 83% adults (24)**
Sixth tail feather white to shaft	159.00	2, 123	**0.001**	126	**Yes both sides: 100% first year (5)** Yes: 60% first year (86) No: 69% adult (35)	**In 100% first years (1)** In 71% first years (7) In 29% adults (24)
Coverts and body feathers						
Extent of black on longest upper-tail covert	144.44	4, 110	**0.011**	115	**No black: 87% first year (23)** < 1/3 black: 53% adult (53) 1/3 – 2/3 black: 53% adult (15) All black: 54% first year (24)	In 44% first years (9)
Other under tail covert shaft colour	162.23	1, 122	**0.006**	125	Black: 51% adult (102) **Chestnut: 82% first year (22)**	**In 88% adults (25)** In 44% first years (9)

Statistics presented are the residual deviance (Resid. Dev.), degrees of freedom (df), p value (p) and sample size (n). For significant features the association and % accuracy across the entire dataset is given, along with sample size (n) and whether or not the feature is significant across the reduced dataset of known age birds. Features with accuracy higher than 80% are shown in bold.

Table 3. Results of statistical analyses to determine which features differ between sexes.

Feature	**Resid. Dev**	**df**	**p**	**n**	**Association and % accuracy (n)**	**Consistent with misidentified birds?**
Head						
% of visible yellow on crown	92.322	1, 113	**<0.0001**	115	**>20%: 84% male (76)** **<10%: 89% female (37)**	**In 80% males (5)** In 25% females (4)
Malar stripe colour	124.99	3, 133	**<0.0001**	140	**Chestnut: 93% male (30)** Black: 59% male (34) Brown: 77% female (52) **Yellow: 95% male (21)**	In 20% males (5) In 60% males (5) **In 100% females (5)**
Distinct bright yellow above and behind eye	92.87	1, 135	**<0.0001**	137	**Yes: 92% male (77)** **No: 85% female (59)**	**In 80% males** **In 80% females**
Wing						
Markings on tertial feathers	158.68	1, 120	**0.027**	122	Distinct: 72% male (53) Diffuse: 52% male (69)	In 60% males
Tail						
Sixth tf white to shaft	145.10	2, 115	**0.0004**	118	**Yes both sides: 100% male (4)** Yes: 66% male (80) No: 68% female (34)	No misidentified birds In 60% males (5) In 25% females (4)
Fifth tf white to shaft	152.35	1, 114	**0.017**	116	**Yes: 100% male (5)** No: 56% male (111)	no misidentified birds
Size of white patch on	153.06	3, 166	**0.019**	120	**Very small: 80% female (5)**	No misidentified birds

fifth tail feather					Small: 51% female (41) Medium: 64% male (70) **Same as sixth tf: 100% male (4)**	In 50% females (4) **In 80% males (5)** No misidentified birds
Coverts and body feathers						
Rump feather shaft	135.92	1, 124	**<0.0001**	126	Black: 78% female (45) Blended: 76% male (81)	**In 100% females (5)** **In 100% males (5)**
Extent of black on longest upper-tail covert	88.02	4, 104	**<0.0001**	109	**No black: 95% male (21)** Short black: 77% male (52) **Half black: 86% female (14)** **All black: 95% female (21)**	In 25% males (4) In 50% males (4) No misidentified birds In 33% females (3)
Longest under tail covert shaft colour	136.89	1, 116	**<0.0001**	118	Black: 68% female (50) Black and chestnut: 76% male (68)	In 40% females (5) **In 100% males (5)**
Other under tail covert shaft colour	141.08	2, 115	**<0.0001**	118	Black: 52% female (95) **Chestnut: 95% male (21)**	**In 100% females (5)** In 25% males (4)

Statistics presented are the residual deviance (Resid. Dev.), degrees of freedom (df), p value (p) and sample size (n). For significant features the association and % accuracy are shown, along with sample size in each category (n) and level of consistency among misidentified birds. Features with accuracy 80% or higher are in bold.

Table 4. Showing statistical significance of age and sex in influencing morphological variables.

	Age			Sex		
Variable	df	F	p	df	F	p
Wing length	1, 136	47.044	**<0.0001**	1, 137	76.619	**<0.0001**
Tail length	1, 96	18.720	**<0.0001**	1, 97	33.397	**<0.0001**
Head-beak length	1, 98	2.148	0.15	1, 99	1.039	0.31
Beak length	1, 98	0.014	0.91	1, 99	6.660	**0.01**
Beak depth	1, 98	4.028	**0.047**	1, 99	4.094	**0.046**
Tarsus	1, 59	0.039	0.845	1, 60	0.019	0.892

Statistics presented are the test statistic (F), degrees of freedom (df) and p value (p). The age*sex interaction term was not significant for any morphological variable and thus was removed from all models. Significant terms are represented in bold.

Table 5. Data summary for morphometric variables showing significant differences between age classes and/or sexes.

Variable	Statistics	
Wing length	Adult F	84.79 +/- 1.75 (81 – 88)
	Juv F	82.62 +/- 2.74 (76 – 90)
	Adult M	89.53 +/- 2.61 (84 – 95)
	Juv M	86.02 +/- 2.63 (80 – 92)
Tail length	Adult F	69.71 +/- 2.29 (65.1 – 74.3)
	Juv F	67.81 +/- 2.88 (62.7 – 73.9)
	Adult M	73.80 +/- 2.29 (68.2 – 77.1)
	Juv M	70.94 +/- 3.33 (62.8 – 76.8)
Beak length	F	10.91 +/- 0.50 (9.93 – 12.00)
	M	10.65 +/- 0.50 (9.26 – 11.80)
Beak depth	Adult F	6.78 +/- 0.29 (6.2 – 7.3)
	Juv F	6.62 +/- 0.32 (6.1 – 7.1)
	Adult M	6.64 +/- 0.21 (6.2 – 7.1)
	Juv M	6.56 +/- 0.30 (6.0 – 7.3)

For each variable, statistics presented are mean +/- sd (range); measurements are all in mm.

Legends to Figures

Figure 1. Photograph of the crown of an adult Yellowhammer wrongly identified as a female in the hand by the authors and subsequently identified as male following molecular sexing (captured and sexed in the hand during February). Note the prominent black shaft that in *E. c. citrinella* is restricted to females (Svensson 1992).

Figure 2. Morphometrics taken from each individual and some aspects of plumage colouration: a) Head-beak length (HB), Beak depth (BD), Tarsus length (TSL) and Tail length (TL); b) Beak length (BL), region c (see Table 1) and malar stripe (MS).

Figure 3. PCR products of *Emberiza citrinella* CHD genes amplified using primers P2 and P8 (Griffiths, et al. 1998). Lane 1 contains 100bp ladder with the top band of 500bp; Lane 2 shows a section of CHD-Z gene only as found in males; Lane 3 shows both CHD-Z and CHD-W genes as found in females.

Figure 4. Illustrating categories described in Table 1. a) Tertial markings: i) Distinct and ii) Diffuse; b) Size of white patch on fifth tail feather i) Very small, ii) Small, iii) Medium and iv) Same as patch on sixth tail feather; and c) Extent of black on shaft of longest upper-tail covert i) No black, ii) Short black, iii) Half black and iv) All black; d) Secondary tips i) Notched and ii) Flat.

Figure 5. Frequency distribution of wing lengths for a) 48 male and 29 female first year and b) 34 male and 28 female adult Yellowhammers.

Figure 1.

Figure 2.

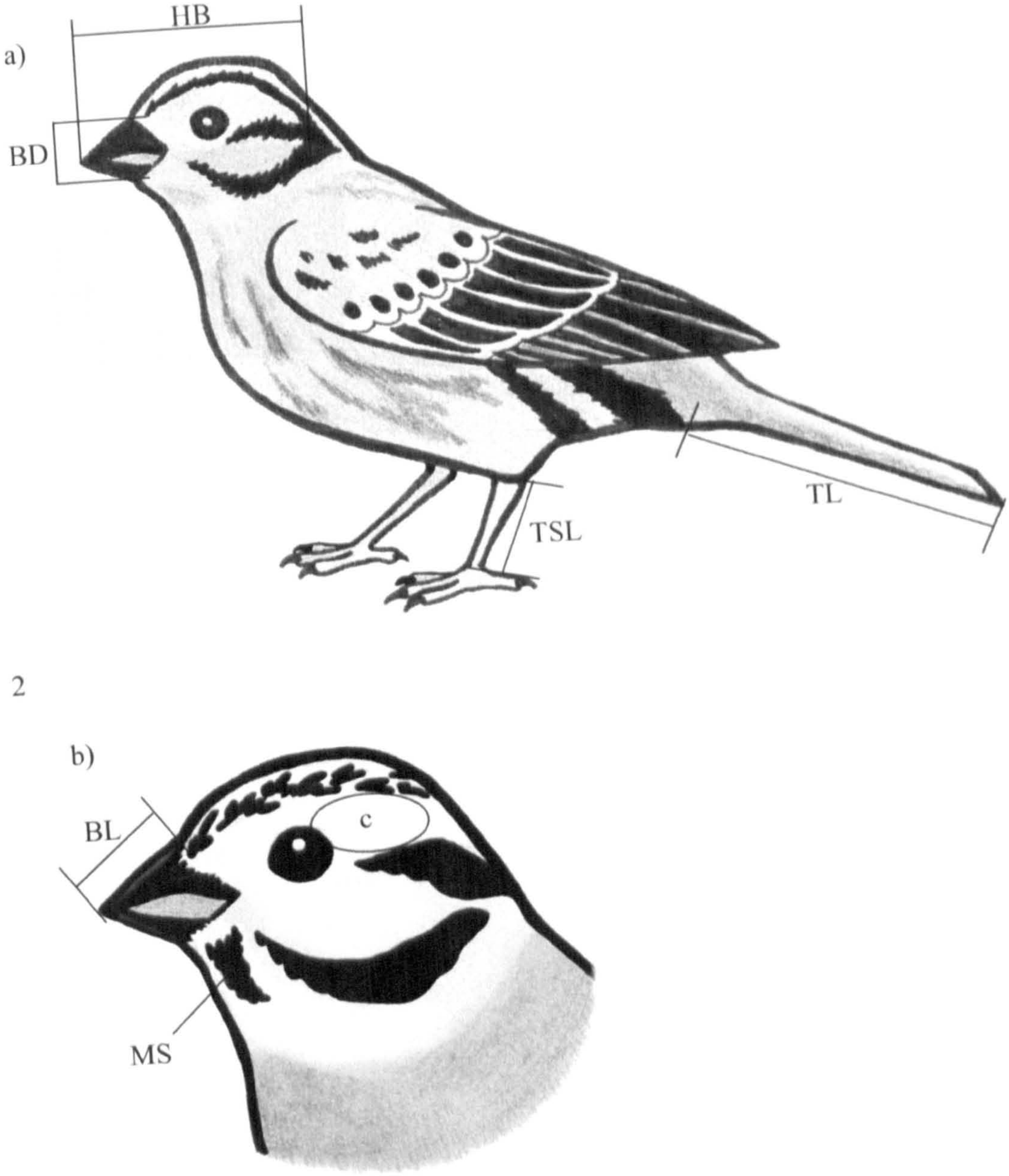


Figure 3.

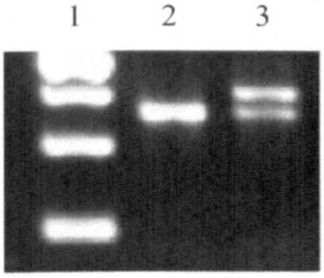
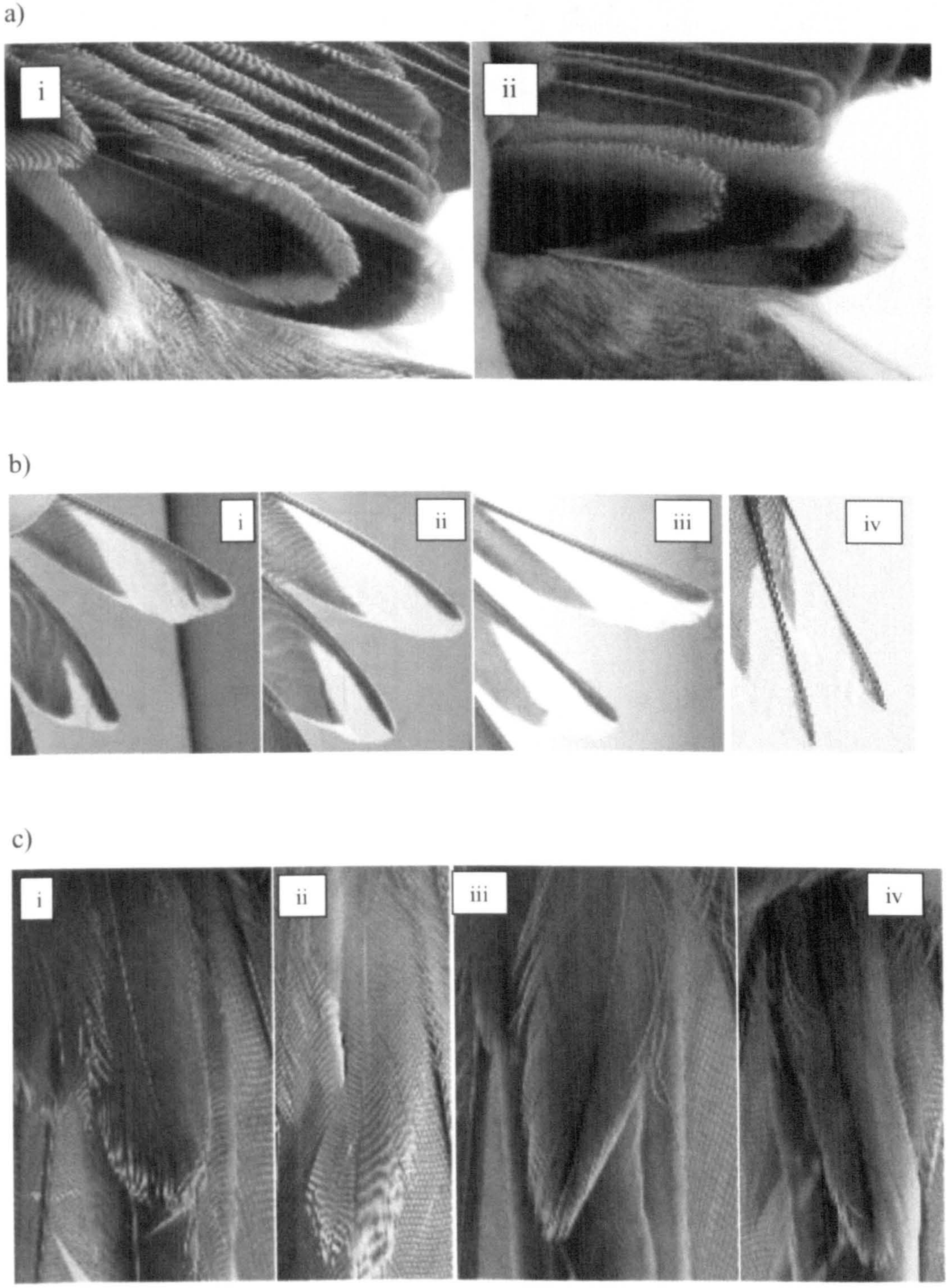


Figure 4.



d)

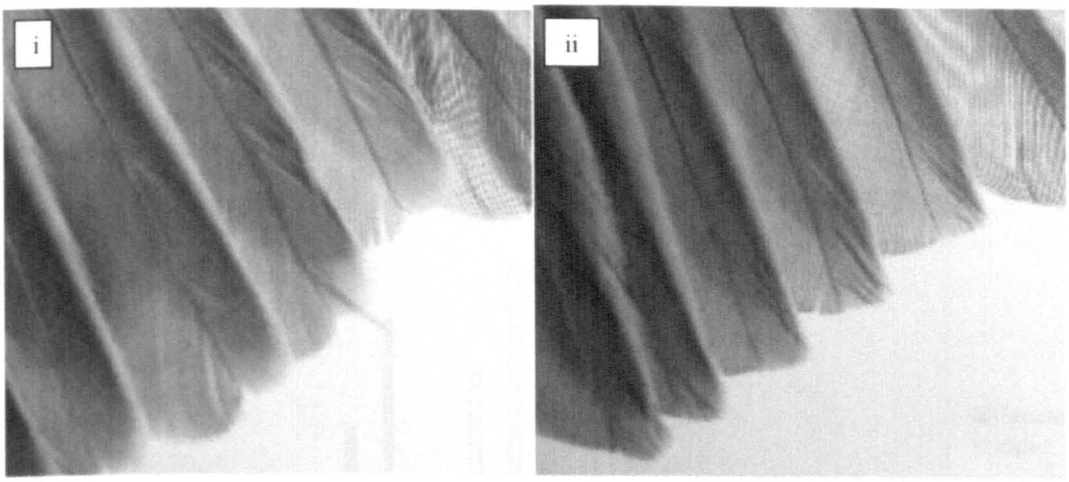
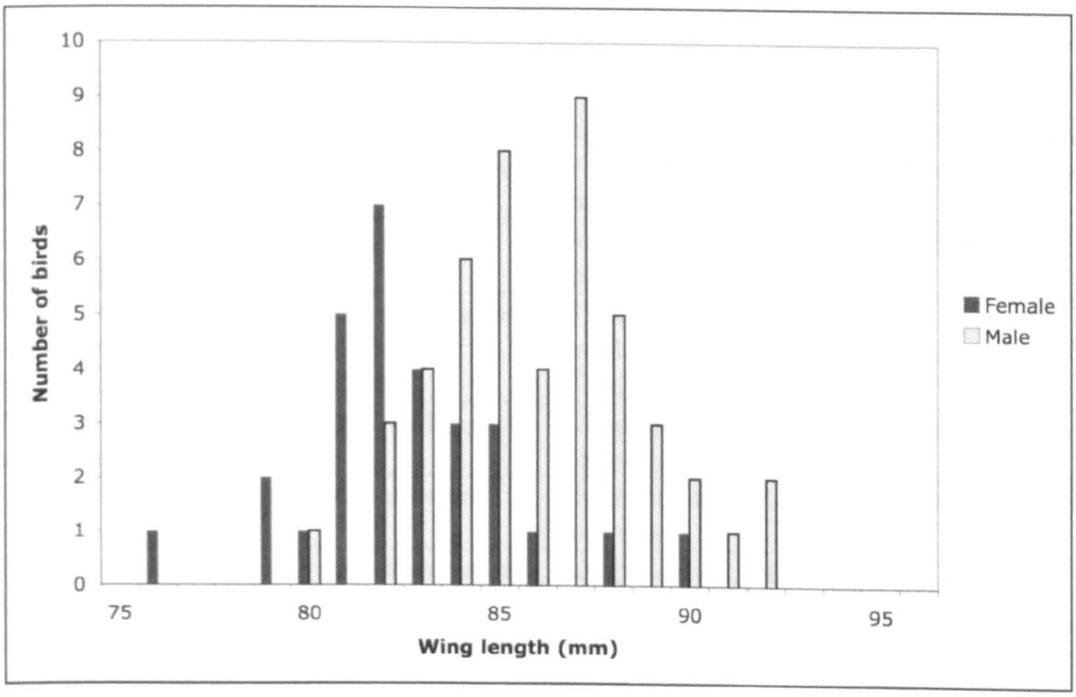
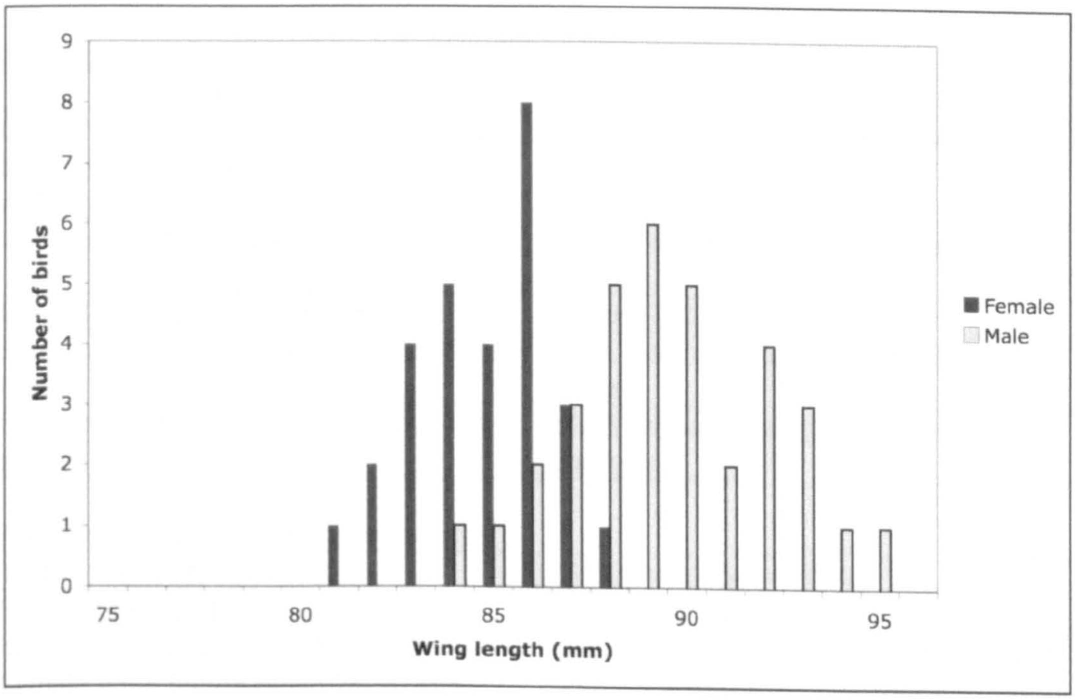

i
ii

Figure 5.

a)


10
9
8
7
6
5
4
3
2
1
0
Number of birds
75
80
85
90
95
Wing length (mm)
■ Female
□ Male

b)


9
8
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6
5
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3
2
1
0
Number of birds
75
80
85
90
95
Wing length (mm)
■ Female
□ Male

Appendix 1. Summary table of characteristics useful for sexing or ageing Yellowhammers, *Emberiza citrinella caliginosa*

Sexing

Male	Female
More than 20% of crown visibly yellow	Less than 10% of crown visibly yellow
May have pure yellow, pure chestnut or chestnut flecks in malar stripe. May also be black or brown.	Malar stripe often, but not always, brown or with brown flecks. Rarely yellow or chestnut
Distinct region of yellow above and behind eye	No distinct region of yellow above and behind eye
White patch on 5th tail feather may be the same size as patch on 6th tail feather; rarely very small in comparison.	White patch on 5th tail feather often very small when compared to white patch on 6th tail feather
No or very little black on shaft of longest upper-tail covert	Completely or mostly black shaft on longest upper-tail covert
Chestnut shaft may be present on short under-tail coverts	Chestnut shaft on short under-tail coverts very rare
Rump feather shaft same colour as rest of feather or paler	Rump feather shaft black or blackish.
Adult wing length range 84-95 mm; 80% of wing lengths above 87mm First year wing length range 80-92 mm	Adult wing length range 81-88 mm; 80% of wing lengths below 87mm First year wing length range 76-90 mm

Ageing

First year	Adult
Central tail feathers worn and bleached but may be fresh where tail has been replaced	Central tail feathers usually fresh
Outer tail feathers sharply angled	Angle of outer tail feathers usually shallow
Central tail feathers usually pointed	Central tail feathers rounded
Some have white on both sides of 6th tail feather shaft	Both sides of 6th tail feather shaft never white
Some have chestnut shaft on under-tail coverts	Shaft on under tail coverts is rarely chestnut
Additional criteria for ambiguous birds:	
Tertial markings distinct	Tertial markings diffuse
Secondaries notched	Secondaries flat
Male wing length range 80-92 mm Female wing length range 76-90 mm	Male wing length range 84-95mm; 80% above 87mm Female wing length range 81-88 mm; 80% below 87mm

Appendix 2. Non-significant results of statistical analyses showing features that do not differ between age classes.

Feature	Resid. Dev	df	p	n
Head				
% crown visibly yellow	0.016	1, 121	0.898	123
Malar stripe colour	200.863	3,142	0.908	146
Distinct bright yellow above and behind eye	200.136	1, 144	0.259	146
Wing				
Shape of 2nd Alula	64.281	1, 51	0.056	53
Shape of 3rd Alula	75.272	1, 58	0.058	60
Yellow/white edged median coverts	0.484	1, 51	0.487	53
Tail				
Fifth tail feather white to shaft	169.561	1, 122	0.216	124
Size of white patch on fifth tail feather	175.80	3, 124	0.914	131
White patch on sixth tail feather	174.09	2, 125	0.277	128
Coverts and body feathers				
Rump feather shaft	183.02	1, 131	0.772	133
Longest under tail covert shaft colour	173.87	1, 124	0.936	126

Statistics presented are the residual deviance (Resid. Dev.), degrees of freedom (df), p value (p) and sample size (n).

Appendix 3. Non significant results of statistical analyses showing features that do not differ between sexes.

Feature	**Resid. Dev**	**df**	**p**	**n**
Wing				
Shape of primary tips	179.60	3, 130	0.606	134
Shape of primary coverts	183.18	1, 133	0.853	135
Width of primary coverts	182.79	1, 133	0.516	135
Shape of secondary tips	150.30	2, 109	0.356	112
Wear and bleaching on tertial feathers	164.27	1, 120	0.741	122
Shape of 2nd alula	0.823	1, 47	0.364	49
Shape of 3rd alula	72.96	1, 54	0.845	56
Yellow/white edged median coverts	61.80	1, 47	0.742	49
Tail				
Shape of central tail feather tips	168.33	3, 123	0.181	130
Width of central tail feathers	174.99	2, 127	0.343	132
Central tail feather wear and bleaching	166.91	2, 122	0.242	125
Angle/shape of outer tail feathers	171.84	1, 125	0.242	127
White patch on fourth tail feather	160.84	2, 118	0.198	121

Statistics presented are the residual deviance (Resid. Dev.), degrees of freedom (df), p value (p) and sample size (n).