

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

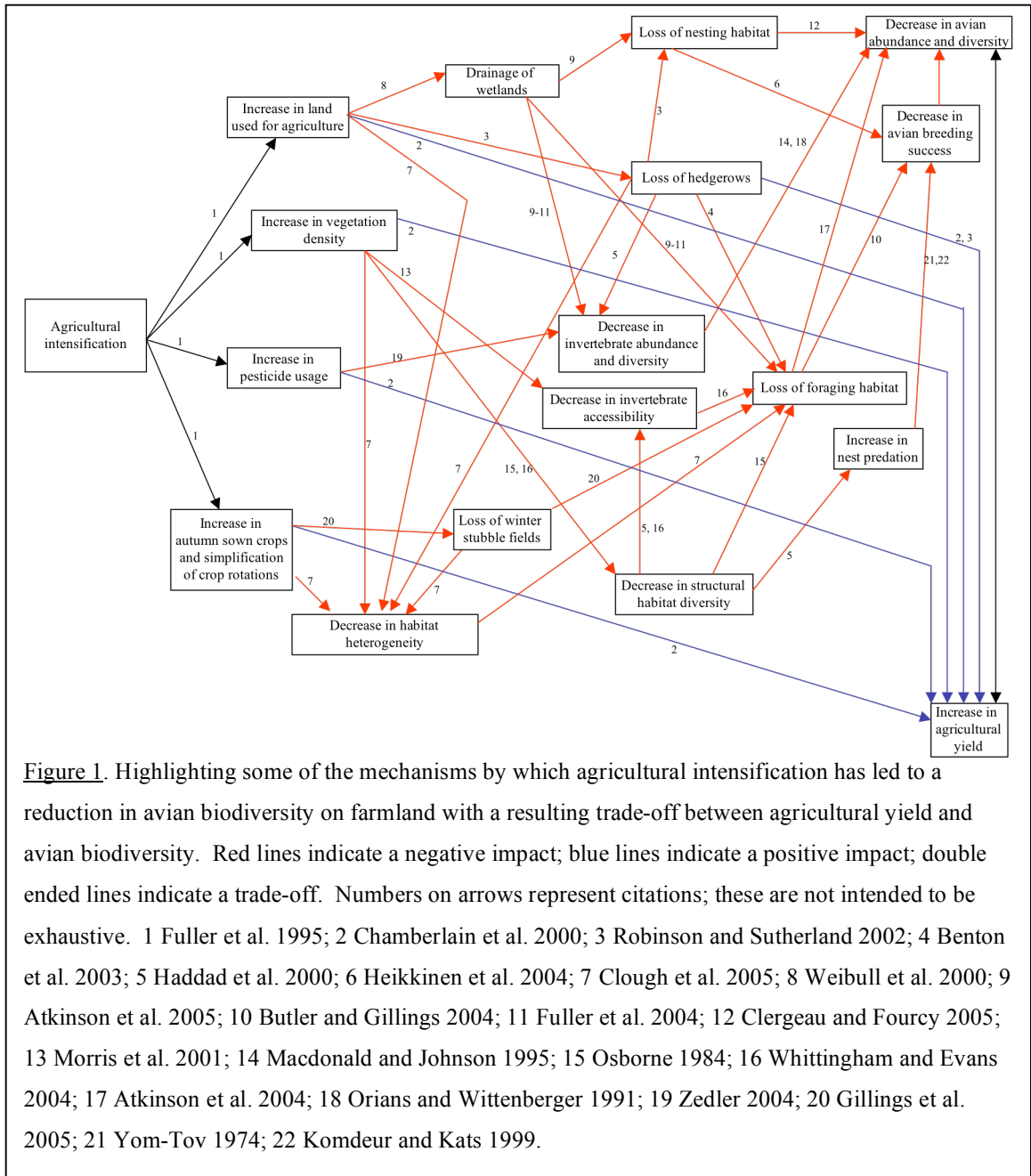
### **Abstract**

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



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 Tallwin 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 circlus*, 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 (Metcalf and Monaghan 2001).

### **Mechanisms of declines: Life history**

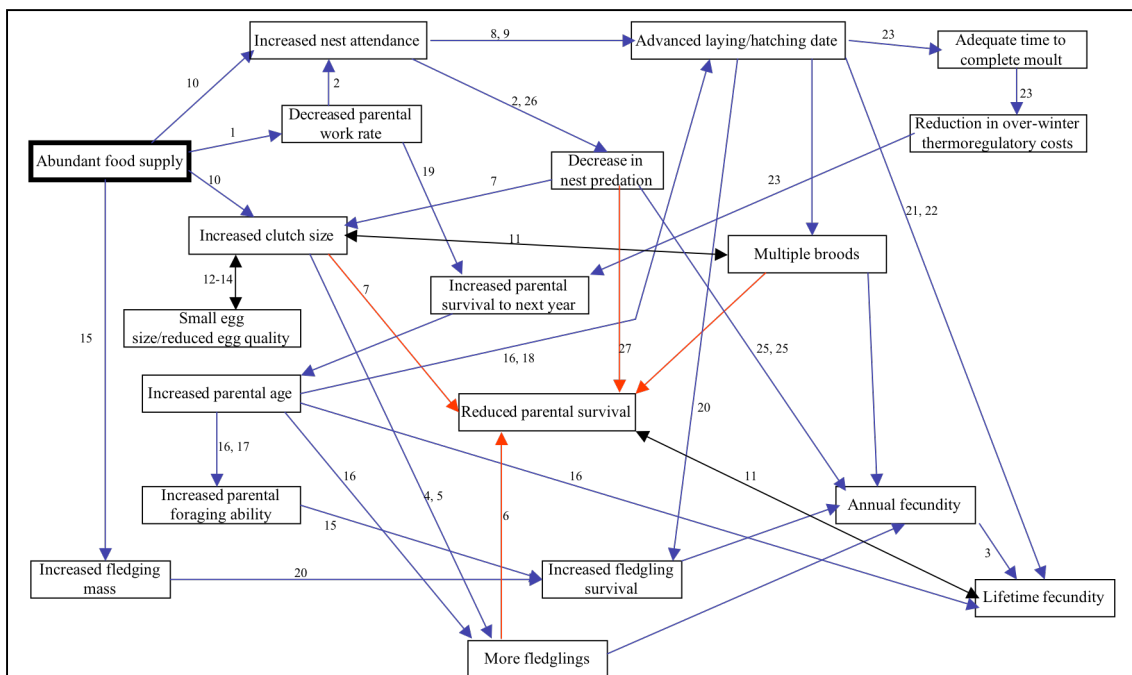
The fitness of an individual is measured by its ability to maintain the presence of its own genes in the population, through reproduction; life-history trade-offs occur as the result of a finite availability of resources. Firstly, some of the direct mechanisms of impact will be discussed: these are separated 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 (Metcalfé 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; Metcalfé 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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