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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