

#### **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 (Hötter 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:  $0.95 \pm 0.14 \text{ km}^2$ ). 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

| <b>Habitat</b>          | <b>Definition</b>  |
|-------------------------|--|
| 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,

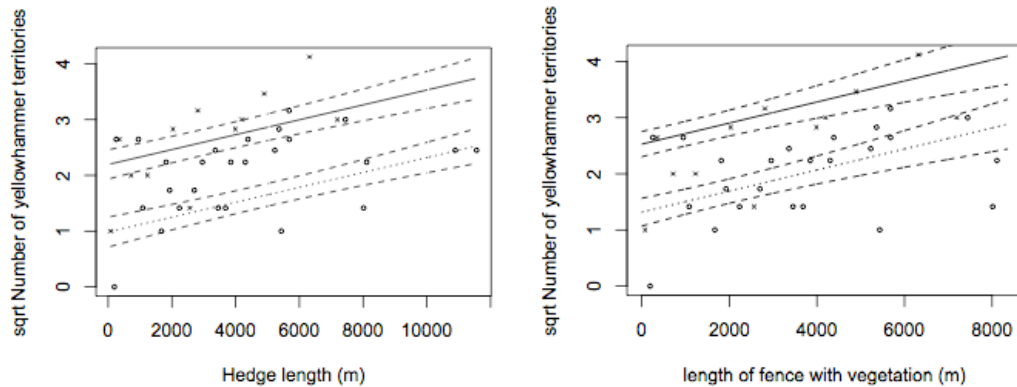
to influence the response variable. A two-way interaction between brood size and invertebrate abundance was also included in the maximal model as this term significantly improved the fit of previous models investigating the effect of corvid activity on provisioning rate (Chapters 3 & 5). Nest ID within 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*

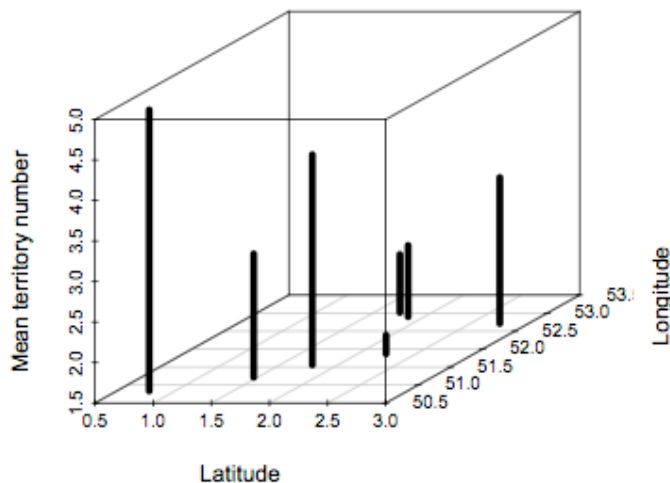
Growth was assessed by tarsus measurements as tarsus growth is likely to be more variable than wing growth (Nilsson and Svensson 1996). Two linear models were constructed, each testing the importance of interactions with either local or farm scale territory density (sample size and subsequent degrees 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:  $7.58 \pm 1.29$ ; 2008:  $4.69 \pm 0.52$  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:  $6.6 \pm 1.16$ ; 2008:  $3.8 \pm 0.84$  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.

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

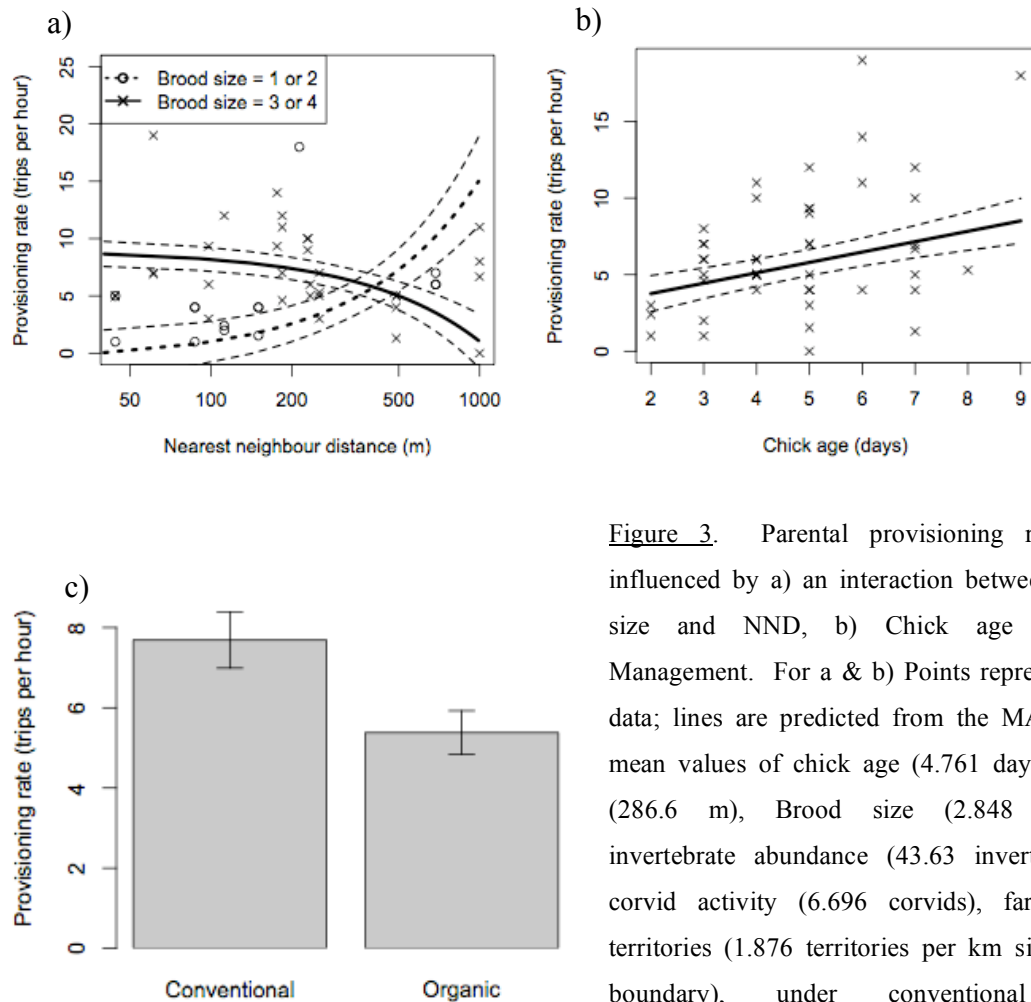
Table 2. Results of a binomial GLM investigating variables that influenced the chances of nests failing, where a failed nest is one that failed to fledge one chick. Farm ID was included in each model to control for localised effects. For non-significant terms, statistics presented are those from model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

| <b>Variable</b> | <b>AIC</b> | <b>df</b> | <b><math>\chi^2</math></b> | <b>p</b> |
|-----------------|------------|-----------|----------------------------|----------|
| 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.

| <b>Variable</b> | <b>AIC</b> | <b>df</b> | <b><math>\chi^2</math></b> | <b>p</b> |
|-----------------|------------|-----------|----------------------------|----------|
| 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  $\pm 1$  SE.

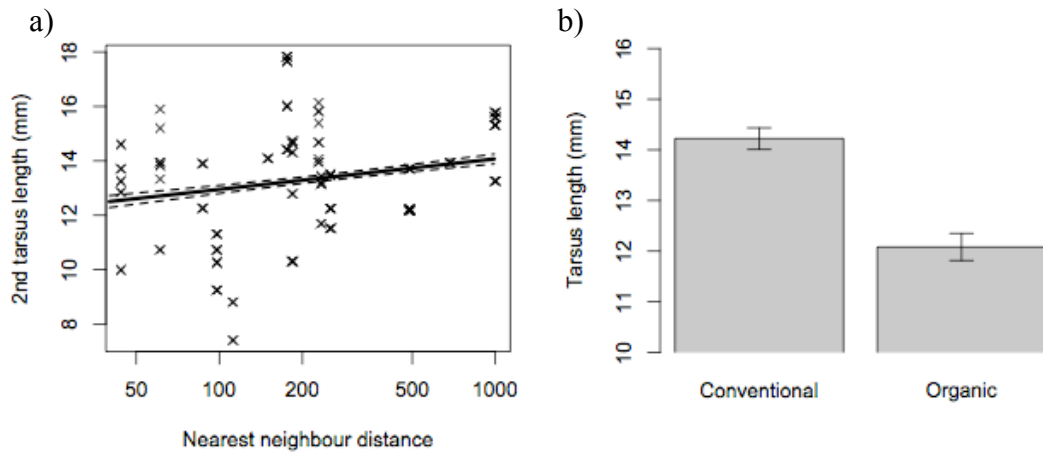
Parental provisioning rate was associated with interactions between local territory density and brood size (Table 4), with provisioning rate increasing with increasing NND in small broods, and decreasing in large broods (Figure 3a). Whilst farm scale territory density remained in the MAM (Table 4), it 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.

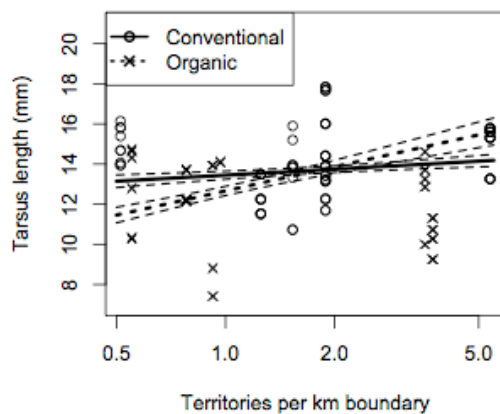
| <b>Variable</b>              | <b>df</b>    | <b>F</b>      | <b>p</b>     | <b>Estimate</b> | <b>SE</b>    |
|------------------------------|--------------|---------------|--------------|-----------------|--------------|
| <b>Management (Organic)</b>  | <b>1, 10</b> | <b>7.002</b>  | <b>0.025</b> | <b>-2.282</b>   | <b>1.030</b> |
| <b>Chick age</b>             | <b>1, 24</b> | <b>12.732</b> | <b>0.002</b> | <b>0.679</b>    | <b>0.287</b> |
| 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        |
| <b>Brood size</b>            | <b>1, 24</b> | <b>6.768</b>  | <b>0.016</b> | <b>3.185</b>    | <b>0.811</b> |
| <b>Corvid activity</b>       | <b>1, 24</b> | <b>5.687</b>  | <b>0.025</b> | <b>-0.090</b>   | <b>0.050</b> |
| Farm scale territory density | 1, 2         | 0.015         | 0.914*       | 1.205           | 0.549        |
| <b>NND x Brood size</b>      | <b>1, 24</b> | <b>12.550</b> | <b>0.002</b> | <b>-0.008</b>   | <b>0.002</b> |
|                              |              |               |              |                 |              |
| <b>Variable</b>              | <b>df</b>    | <b>LRT</b>    | <b>p</b>     |                 |              |
| Time of day <sup>2</sup>     | 1            | 0.285         | 0.594        |                 |              |
| Temperature <sup>2</sup>     | 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 1<sup>st</sup> 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  $\pm 1$  SE.



**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 1<sup>st</sup> 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  $\pm 1$  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).



**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.

| <b>Variable</b>                                | <b>df</b>     | <b>F</b>       | <b>p</b>         | <b>Estimate</b> | <b>SE</b>    |
|--|---------------|----------------|------------------|-----------------|--------------|
| <b>1<sup>st</sup> tarsus measurement</b>       | <b>1, 110</b> | <b>235.452</b> | <b>&lt;0.001</b> | <b>0.598</b>    | <b>0.076</b> |
| <b>Hours between measurements</b>              | <b>1, 110</b> | <b>14.471</b>  | <b>&lt;0.001</b> | <b>0.040</b>    | <b>0.012</b> |
| <b>Log NND</b>                                 | <b>1, 11</b>  | <b>8.811</b>   | <b>0.013</b>     | <b>0.487</b>    | <b>0.164</b> |
| <b>Management</b>                              | <b>1, 11</b>  | <b>9.299</b>   | <b>0.011</b>     | <b>-0.688</b>   | <b>0.305</b> |
| <b>Chick age at 2<sup>nd</sup> measurement</b> | <b>1, 110</b> | <b>5.165</b>   | <b>0.025</b>     | <b>0.550</b>    | <b>0.190</b> |
| <b>Log territories per km</b>                  | <b>1, 11</b>  | <b>4.712</b>   | <b>0.053*</b>    | <b>0.457</b>    | <b>0.210</b> |
|  |               |                |                  |                 |              |
| <b>Variable</b>                                | <b>df</b>     | <b>F</b>       | <b>p</b>         |                 |              |
| Temperature <sup>2</sup>                       | 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.

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

## Bibliography

- Alatalo, R. V. and A. Lundberg (1984). "Density-dependence in breeding success of the Pied Flycatcher (*Ficedula hypoleuca*)." Journal of Animal Ecology **53**: 969-977.
- Arcese, P., J. N. M. Smith, W. M. Hochachka, C. M. Rogers and D. Ludwig (1992). "Stability, Regulation, and the Determination of Abundance in an Insular Song Sparrow Population." Ecology **73**(3): 805-822.
- Arvidsson, B., C. Askenmo and R. Neergaard (1997). "Food supply for settling male rock pipits affects territory size." Animal Behaviour **54**: 67-72.
- Baillie, S. R., J. H. Marchant, H. Q. P. Crick, D. G. Noble, D. E. Balmer, L. P. Beaven, R. H. Coombes, I. S. Downie, S. N. Freeman, A. C. Joys, D. I. Leech, M. J. Raven, R. A. Robinson and R. M. Thewlis (2005). Breeding Birds in the Wider Countryside: their conservation status 2004. BTO Research Report No. Thetford, BTO. 385.
- Baillie, S. R., J. H. Marchant, D. I. Leech, A. C. Joys, D. G. Noble, C. Barimore, M. J. Grantham, K. Risely and R. A. Robinson (2009). Breeding Birds in the Wider Countryside: their conservation status 2008. BTO Research Report No. 516. Thetford, British Trust for Ornithology.
- Berg, M. L., N. H. Beintema, J. A. Welbergen and J. Komdeur (2005). "Singing as a handicap: the effects of food availability and weather on song output in the Australian reed warbler *Acrocephalus australis*." Journal of Avian Biology **36**: 102-109.
- Both, C. (2000). "Density dependence of avian clutch size in resident and migrant species: is there a constraint on the predictability of competitor density?" Journal of Avian Biology **31**: 412-417.
- Both, C. and M. E. Visser (2000). "Breeding Territory Size Affects Fitness: An Experimental Study on Competition at the Individual Level." Journal of Animal Ecology **69**(6): 1021-1030.
- Bradbury, R. B., A. Kyrkos, A. J. Morris, S. C. Clark, A. J. Perkins and J. D. Wilson (2000). "Habitat associations and breeding success of yellowhammers on lowland farmland." Journal of Applied Ecology **37**: 789 - 805.
- Bradbury, R. B., J. D. Wilson, D. Moorcroft, A. J. Morris and A. J. Perkins (2003). "Habitat and weather are weak correlates of nestling condition and growth rates of four UK farmland passerines." Ibis **145**: 295 - 306.

- Brouwer, L., J. M. Tinbergen, C. Both, R. Bristol, D. S. Richardson and J. Komdeur (2009). "Experimental evidence for density-dependent reproduction in a cooperatively breeding passerine." Ecology **90**(3): 729-741.
- Chalfoun, A. D. and T. E. Martin (2009). "Habitat structure mediates predation risk for sedentary prey: experimental tests of alternative hypotheses." Journal of Animal Ecology **78**: 497-503.
- Cornulier, T., R. A. Robinson, T. G. Benton, X. Lambin, W. J. Sutherland and D. Elston (in prep). "Bayesian reconstitution of environmental change from disparate historical records: hedgerow loss and farmland bird declines."
- Davies, N. B. and I. R. Hartley (1996). "Food patchiness, territory overlap and social systems: an experiment with dunnocks *Prunella modularis*." Journal of Animal Ecology **65**: 837-846.
- Davies, N. B. and A. Lundberg (1984). "Food Distribution and a Variable Mating System in the Dunnock, *Prunella modularis*." Journal of Animal Ecology **53**(3): 895-912.
- Donald, P. F. and J. A. Vickery (1999). The importance of cereal fields to breeding and wintering Skylarks *Alauda arvensis* in the UK. Ecology and Conservation of Lowland Farmland Birds. N. J. Aebischer, A. D. Evans, P. V. Grice and J. A. Vickery. Tring, British Ornithologists' Union: 140 - 150.
- Douglas, D. J. T., J. A. Vickery and T. G. Benton (2009). "Improving the value of field margins as a foraging habitat for farmland birds." Journal of Applied Ecology **46**(2): 353-362.
- Dunn, E. (1977). "Predation by Weasels (*Mustela nivalis*) on Breeding Tits (*Parus Spp.*) in Relation to the Density of Tits and Rodents." Journal of Animal Ecology **46**(2): 633-652.
- Eberhard, J. R. and P. W. Ewald (1994). "Food Availability, Intrusion Pressure and Territory Size: An Experimental Study of Anna's Hummingbirds (*Calypte anna*)." Behavioral Ecology and Sociobiology **34**(1): 11-18.
- Ebersole, J. P. (1980). "Food Density and Territory Size: An Alternative Model and a Test on the Reef Fish *Eupomacentrus leucostictus*." American Naturalist **115**(4): 492-509.
- Eggers, S., M. Griesser, T. Andersson and J. Ekman (2005). "Nest predation and habitat change interact to influence Siberian jay numbers." Oikos **111**: 150 - 158.

- Eggers, S., M. Griesser and J. Ekman (2005). "Predator-induced plasticity in nest visitation rates in the Siberian jay (*Perisoreus infaustus*)." Behavioral Ecology **16**(1): 309 - 315.
- Eggers, S., M. Griesser and J. Ekman (2008). "Predator-induced reductions in nest visitation rates are modified by forest cover and food availability." Behavioral Ecology **19**(5): 1056 - 1062.
- Elmberg, J., K. Folkesson, M. Guillemain and G. Gunnarsson (2009). "Putting density dependence in perspective: nest density, nesting phenology, and biome, all matter to survival of simulated mallard *Anas platyrhynchos* nests." Journal of Avian Biology **40**: 317-326.
- Fuller, R. J., R. D. Gregory, D. W. Gibbons, J. H. Marchant, J. D. Wilson, S. R. Baillie and N. Carter (1995). "Population Declines and Range Contractions among Lowland Farmland Birds in Britain." Conservation Biology **9**: 1423 - 1441.
- Gilroy, J. J. and W. J. Sutherland (2007). "Beyond ecological traps: perceptual errors and undervalued resources." Trends in Ecology and Evolution **22**(7): 351-356.
- Green, R. E., P. E. Osborne and E. J. Sears (1994). "The distribution of passerine birds in hedgerows during the breeding season in relation to characteristics of the hedgerow and adjacent farmland." Journal of Applied Ecology **31**: 677 - 692.
- Hart, J. D., T. P. Milsom, G. Fisher, V. Wilkins, S. J. Moreby, A. W. A. Murray and P. A. Robertson (2006). "The relationship between yellowhammer breeding performance, arthropod abundance and insecticide applications on arable farmland." Journal of Applied Ecology **43**: 81 - 91.
- Hazler, K. R. (2004). "Mayfield logistic regression: a practical approach for analysis of nest survival." The Auk **12**(3): 707-716.
- Hixon, M. A. (1980). "Food Production and Competitor Density as the Determinants of Feeding Territory Size." American Naturalist **115**(4): 510-530.
- Hoi-Leitner, M., H. Nechtelberger and J. Dittami (1993). "The relationship between individual differences in male song frequency and parental care in blackcaps." Behaviour **126**(1-2): 1-12.
- Hötker, H. (2000). "Intraspecific variation in size and density of Avocet colonies: effects of nest-distances on hatching and breeding success." Journal of Avian Biology **31**: 387-398.
- Johnson, C. A., L.-A. Giraldeau and J. W. A. Grant (2006). "Intensity of interference affects the distribution of house sparrows, *Passer domesticus*, at food patches." Animal Behaviour **71**: 965-970.



- Kyrkos, A., A. Wilson and J. D. Fuller (1998). "Farmland habitat change and abundance of Yellowhammers *Emberiza citrinella*: an analysis of Common Birds Census data." Bird Study **45**: 232 - 246.
- Mayes, J. (2008). "Editorial: special issue - the wet summer of 2007 in the UK." Weather **63**(9): 251-252.
- Mayfield, H. F. (1975). "Suggestions for calculating nest success." The Wilson Bulletin **87**(4): 456-466.
- Møller, A. P., M. Martin-Vivaldi, S. Merino and J. J. Soler (2006). "Density-dependent and geographical variation in bird immune response." Oikos **115**(3): 463-474.
- Morris, A. J., J. D. Wilson, M. J. Whittingham and R. B. Bradbury (2005). "Indirect effects of pesticides on breeding yellowhammer (*Emberiza citrinella*)." Agriculture, Ecosystems and Environment **106**: 1 - 16.
- Mougeot, F. (2000). "Territorial intrusions and copulation patterns in red kites, *Milvus milvus*, in relation to breeding density." Animal Behaviour **59**: 633-642.
- Newton, I. (1992). "Experiments on the limitation of bird numbers by territorial behaviour." Biological Reviews **67**: 129-173.
- Nilsson, J. A. and M. Svensson (1996). "Sibling Competition Affects Nestling Growth Strategies in Marsh Tits." J. Anim. Ecol. **65**(6): 825 - 836.
- Nordby, J. C., A. N. Cohen and S. R. Beissinger (2009). "Effects of a habitat-altering invader on nesting sparrows: An ecological trap?" Biological Invasions **11**(3): 565-575.
- Penteriani, V. (2003). "Breeding density affects the honesty of bird vocal displays as possible indicators of male/territory quality." Ibis **145**: E127-E135.
- Perrins, C. M. (1965). "Population Fluctuations and Clutch-Size in the Great Tit, *Parus major* L." Journal of Animal Ecology **34**(3): 601-647.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar and R Core Team (2009). nlme: Linear and Nonlinear Mixed Effects Models.
- Remes, V. (2003). "Effects of Exotic Habitat on Nesting Success, Territory Density, and Settlement Patterns in the Blackcap (*Sylvia atricapilla*)." Conservation Biology **17**(4): 1127-1133.
- Risely, K., D. G. Noble and S. R. Baillie (2009). The Breeding Bird Survey 2008. BTO Research Report. Thetford, British Trust for Ornithology.
- Robinson, R. A. (2005). BirdFacts: profiles of birds occurring in Britain & Ireland (v1.24, June 2009). BTO Research Report 407. Thetford, BTO.

- Rohner, C. (1997). "Non-territorial 'floaters' in great horned owls: space use during a cyclic peak of snowshoe hares." *Animal Behaviour* **53**: 901-912.
- Roos, S. and T. Pärt (2004). "Nest predators affect spatial dynamics of breeding red-backed shrikes (*Lanius collurio*)." *Journal of Animal Ecology* **73**: 117-127.
- Rubenstein, D. R. (2007). "Territory quality drives intraspecific patterns of extrapair paternity." *Behavioral Ecology* **18**: 1058-1064.
- Sæther, B.-E. and S. Engen (2002). "Pattern of Variation in Avian Population Growth Rates." *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **357**(1425): 1185-1195.
- Sæther, B.-E., J. Tufto, S. Engen, K. Jerstad, O. W. Røstad and J. E. Skåtan (2000). "Population Dynamical Consequences of Climate Change for a Small Temperate Songbird." *Science* **287**: 854-856.
- Sibly, R. M. and J. Hone (2002). "Population growth rate and its determinants: an overview." *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **357**: 1153-1170.
- Sillett, T. S., R. T. Holmes and T. W. Sherry (2000). "Impacts of a Global Climate Cycle on Population Dynamics of a Migratory Songbird." *Science* **288**: 2040-2042.
- Sillett, T. S., N. L. Rodenhouse and R. T. Homes (2004). "Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird." *Ecology* **85**(9): 2467-2477.
- Silverin, B. (1998). "Territorial behaviour and hormones of pied flycatchers in optimal and suboptimal habitats." *Animal Behaviour* **56**: 811-818.
- Sundberg, J. and A. Dixon (1996). "Old, colourful male yellowhammers, *Emberiza citrinella*, benefit from extra-pair copulations." *Animal Behaviour* **52**: 113 - 122.
- Sutherland, W. J. and K. Norris (2002). "Behavioural Models of Population Growth Rates: Implications for Conservation and Prediction." *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **357**(1425): 1273-1284.
- Tarof, S. A., B. J. M. Stutchbury, W. H. Piper and R. C. Fleischer (1998). "Does breeding density covary with extra-pair fertilizations in Hooded Warblers?" *Journal of Avian Biology* **29**: 145-154.
- Václav, R., H. Hoi and D. Blomqvist (2003). "Food supplementation affects extrapair paternity in house sparrows (*Passer domesticus*)." *Behavioral Ecology* **14**(5): 730-735.

- Vander Werf, E. A. (2004). "Demography of Hawai'i 'Elepaio: Variation within habitat disturbance and population density." Ecology **85**(3): 770 - 783.
- Webster, M. S., H. C. Chuang-Dobbs and R. T. Holmes (2001). "Microsatellite identification of extrapair sires in a socially monogamous warbler." Behavioral Ecology **12**(4): 439-446.
- Whittingham, M. J., R. D. Swetnam, J. D. Wilson, D. E. Chamberlain and R. P. Freckleton (2005). "Habitat selection by yellowhammers *Emberiza citrinella* on lowland farmland at two spatial scales: implications for conservation management." Journal of Applied Ecology **42**: 270 - 280.
- Woolfenden, B. E., B. J. M. Stutchbury and E. S. Morton (2005). "Male Acadian flycatchers, *Empidonax virescens*, obtain extrapair fertilizations with distant females." Animal Behaviour **69**: 921-929.

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.

| <b>Variable</b>          | <b>df</b> | <b>LRT</b> | <b>p</b> |
|--------------------------|-----------|------------|----------|
| 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    |