

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

#### **Abstract**

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

## **Introduction**

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

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

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

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

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

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

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

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

associated with high provisioning rates as adult birds maximise the food intake of their chicks.

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

## **Methods**

### **Sites**

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

### **Nest and Chick data**

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

### **Foraging data**

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

### **Chick food availability**

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

### **Predator abundance**

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

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

### **Statistical analysis**

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

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

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

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

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



## Results

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

### *Management effects on nest predator abundance and chick food availability*

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

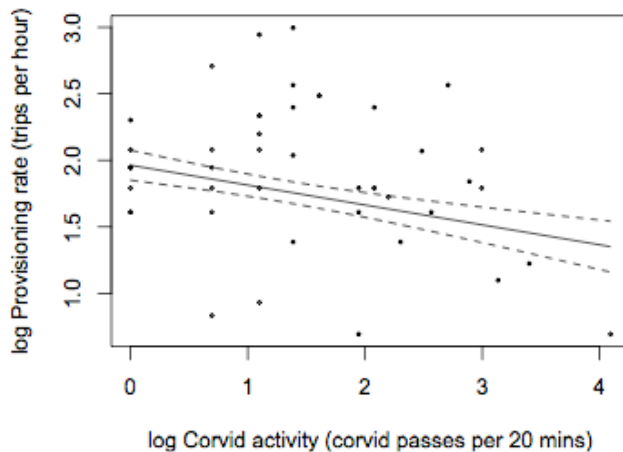
**Table 1.** Results of a generalised linear mixed-effects model determining which variables influence corvid abundance. All models contain random effects of Farm ID to control for effects of repeated measures from the same farm. Statistics presented for non-significant terms are following reinsertion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

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

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

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

### *Parental provisioning behaviour*



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

Corvid point counts prior to provisioning watches were undertaken on 46 occasions for 17 nests. Corvid activity significantly influenced parental provisioning rate (Table 3) with a decrease in provisioning rate with increasing corvid activity (Figure 1). Chick age and year both significantly influenced provisioning rate (Table 3), with higher provisioning rates to older chicks and in 2008 than 2007 (2007:  $5.45 \pm 0.56$ ; 2008:  $8.26 \pm 1.25$  trips per

hour). When substituted into the previous model in place of corvid activity, corvid abundance had no effect upon provisioning rate (GLMM,  $F_{1,24}=0.30$ ,  $p=0.62$ ).

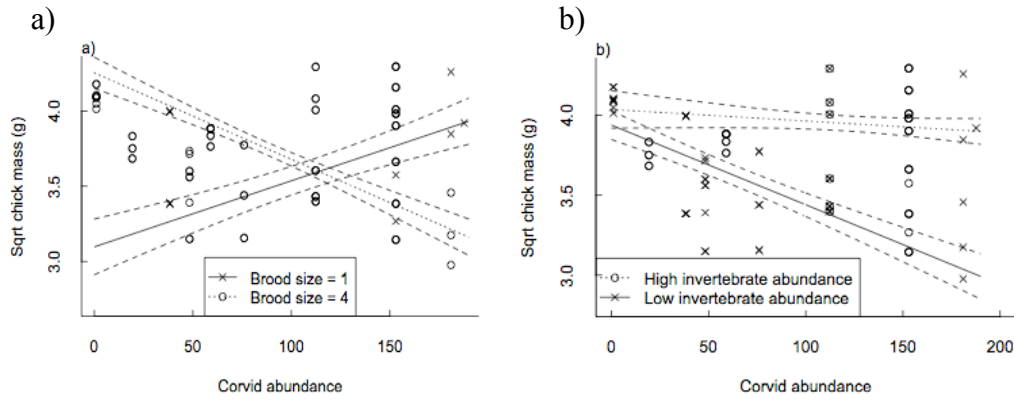
**Table 3.** a) Results of a linear mixed-effects model determining which variables influence the rate at which Yellowhammer parents provision their chicks. All models contain random effects of Nest ID within Farm ID to control for effects of parental quality and localised geographical variation. Back-transformed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

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

<b>b) Variable</b>	<b>df</b>	<b>LRT</b>	<b>p</b>
Temperature <sup>2</sup>	1	1.368	0.242
Time of day <sup>2</sup>	1	0.393	0.531
Management	1	1.970	0.160

### *Chick mass and growth*

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

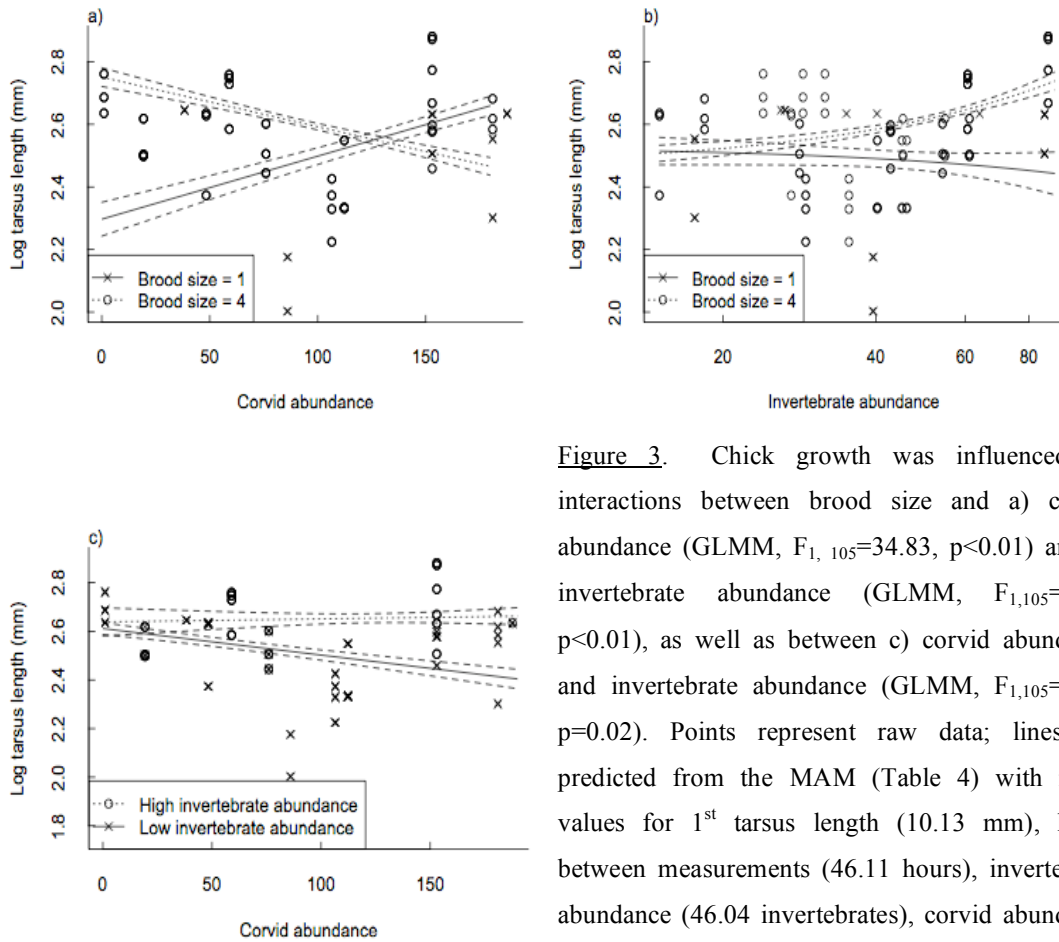


**Figure 2.** Interactions between a) Brood size and Corvid abundance (GLMM,  $F_{1,8}=9.92$ ,  $p=0.02$ ) and b) Corvid abundance and Invertebrate abundance (GLMM,  $F_{1,50}=4.45$ ,  $p=0.04$ ) both influenced chick mass when controlling for size. Points show raw data; Lines are predicted from the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

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

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

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



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

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

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

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

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

## Discussion

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

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

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

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

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

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



both by increasing load size when provisioning rate is reduced (Eggers et al. 2008), and by increasing provisioning rate when corvid activity is low (Eggers et al. 2005). This would allow the maximum possible growth of chicks in order that they fledge quickly and are thus removed from the risk of nest predation.

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

### *Implications*

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

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

## Bibliography

- Andr n, H. (1992). "Corvid density and nest predation in relation to forest fragmentation: a landscape perspective." *Ecology* **73**(3): 794 - 804.
- 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.
- Barnett, P. R., M. J. Whittingham, R. B. Bradbury and J. D. Wilson (2004). "Use of unimproved and improved lowland grassland by wintering birds in the UK." *Agriculture, Ecosystems and Environment* **102**: 49 - 60.
- Beckerman, A., T. G. Benton, E. Ranta, V. Kaitala and P. Lundberg (2002). "Population dynamic consequences of delayed life-history effects." *Trends in Ecology and Evolution* **17**(6): 263 - 269.
- Boonstra, R., D. Hik, G. R. Singleton and A. Tinnikov (1998). "The impact of predator-induced stress on the Snowshoe Hare cycle." *Ecology Monographs* **79**: 371 - 394.
- 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.
- Clinchy, M., L. Zanette, R. Boonstra, J. C. Wingfield and J. N. M. Smith (2004). "Balancing food and predator pressure induces chronic stress in songbirds." *Proceedings of the Royal Society of London Series B* **271**: 2473 - 2479.
- Crawley, M. J. (2007). *The R Book*. Chichester, John Wiley & Sons Ltd.
- Cresswell, W. (2008). "Non-lethal effects of predation in birds." *Ibis* **150**: 3-17.
- Crick, H. Q. P., C. Dudley, A. D. Evans and K. W. Smith (1994). "Causes of nest failure among buntings in the UK." *Bird Study* **41**: 88 - 94.
- 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.
- Douglas, D. J. T., J. A. Vickery and T. G. Benton (2009). "Improving the value of field margins as foraging habitat for farmland birds." *Journal of Applied Ecology* **46**: 353-362.

- 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.
- Evans, K. L. (2004). "The potential for interactions between predation and habitat change to cause population declines of farmland birds." Ibis **146**(1 - 13).
- Fuller, R. J., L. R. Norton, R. E. Feber, P. J. Johnson, D. E. Chamberlain, A. C. Joys, F. Mathews, R. C. Stuart, M. C. Townsend, W. J. Manley, M. S. Wolfe, D. W. Macdonald and L. G. Firbank (2005). "Benefits of organic farming to biodiversity vary among taxa." Biology Letters **1**: 431 - 434.
- Gooch, S., S. R. Baillie and T. R. Birkhead (1991). "Magpie *Pica pica* and Songbird Populations. Retrospective Investigation on Trends in Population Density and Breeding success." Journal of Applied Ecology **28**(3): 1068 - 1086.
- Gosler, A. G. (1995). "Predation risk and the cost of being fat." Nature **377**: 621.
- Gregory, R. D. and J. H. Marchant (1995). "Population trends of Jays, Magpies, Jackdaws and Carrion Crows in the United Kingdom." Bird Study **43**: 28 - 37.
- 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.
- Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale and K. M. R. Turkington (1995). "Impact of Food and Predation on the Snowshoe Hare Cycle." Science **269**: 1112 - 1115.
- Luginbuhl, J. M., J. M. Marzluff, J. E. Bradley, M. G. Raphael and D. E. Varland (2001). "Corvid survey techniques and the relationship between corvid relative abundance and nest predation." Journal of Field Ornithology **72**(4): 556 - 572.
- Marchant, J. H., R. Hudson, S. P. Carter and P. A. Whittingham (1990). Population Trends in British Breeding Birds. Tring, BTO.
- Martin, T. E., J. Scott and C. Menge (2000). "Nest predation increases with parental activity: separating nest site and parental activity effects." Proceedings of the Royal Society of London Series B **267**: 2287 - 2293.
- Metcalf, N. B. and P. Monaghan (2001). "Compensation for a bad start: grow now, pay later?" Trends in Ecology and Evolution **16**(5): 254 - 260.

- Møller, A. P. (2001). "The effect of dairy farming on barn swallow *Hirundo rustica* abundance, distribution and reproduction." Journal of Applied Ecology **38**: 378-389.
- Morris, A. J. and R. B. Bradbury (2002). "Determinants of patch selection by yellowhammers *Emberiza citrinella* foraging in cereal crops." Aspects of Applied Biology **67**: 43 - 50.
- Murtaugh, P. A. (2009). "Performance of several variable-selection methods applied to real ecological data." Ecology Letters **12**: 1061-1068.
- Nilsson, J. A. and M. Svensson (1996). "Sibling Competition Affects Nestling Growth Strategies in Marsh Tits." J. Anim. Ecol. **65**(6): 825 - 836.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar and R Core Team (2009). nlme: Linear and Nonlinear Mixed Effects Models.
- R Core Development Team (2006). *R: A language and environment for statistical computing* (<http://www.R-project.org>).
- Rands, S. A. and I. C. Cuthill (2001). "Separating the effects of predation risk and interrupted foraging upon mass changes in the blue tit *Parus caeruleus*." Proc. R. Soc. Lond. B **268**: 1783 - 1790.
- Remes, V. (2005). "Nest concealment and parental behaviour interact in affecting nest survival in the blackcap (*Sylvia atricapilla*): an experimental evaluation of the parental compensation hypothesis." Behavioral Ecology and Sociobiology **58**: 326 - 333.
- Ricklefs, R. E. (1969). "An analysis of nestling mortality in birds." Smithsonian Contributions to Zoology **9**: 1 - 48.
- Rogers, C. M., M. J. Taitt, J. N. M. Smith and G. Jongejan (1997). "Nest predation and cowbird parasitism create a demographic sink in wetland-breeding Song Sparrows." The Condor **99**: 622 - 633.
- Schwagmeyer, P. L. and D. W. Mock (2008). "Parental provisioning and offspring fitness: size matters." Animal Behaviour **75**: 291 - 298.
- Skutch, A. F. (1949). "Do tropical birds rear as many young as they can nourish?" Ibis **91**: 430 - 455.
- Stoate, C., S. J. Moreby and J. Szczur (1998). "Breeding ecology of farmland Yellowhammers *Emberiza citrinella*." Bird Study **45**: 109 - 121.
- Taborsky, B. (2006). "The influence of juvenile and adult environments on life-history trajectories." Proceedings of the Royal Society of London Series B **273**: 741 - 750.

- Takahashi, A., Y. Watanuki, K. Sato, A. Kato, N. Arai, J. Nishikawa and Y. Naito (2003). "Parental foraging effort and offspring growth in Adelie Penguins: does working hard improve reproductive success?" Functional Ecology **17**(5): 590 - 597.
- Whittingham, M. J., P. A. Stephens, R. B. Bradbury and R. P. Freckleton (2006). "Why do we still use stepwise modelling in ecology and behaviour?" Journal of Animal Ecology **75**: 1182-1189.
- Wright, J., C. Both, P. A. Cotton and D. Bryant (1998). "Quality vs. quantity: energetic and nutritional trade-offs in parental provisioning strategies." Journal of Animal Ecology **67**: 620 - 634.

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

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