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

Abstract

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

Introduction

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

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

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

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

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

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

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

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

Differences in parental expenditure between the sexes can lead to differential mortality. Females often have higher mortality than males (Liker and Székely 2005) and are

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

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

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

Methods

Sites

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

Provisioning and behavioural data

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

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

Statistical analyses

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

Sex differences in provisioning

To determine whether the sexes differed in their provisioning behaviour in response to environmental variables, a generalised linear mixed-effects model with quasipoisson

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

Male song behaviour

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

Sex differences in time budgets

Generalised linear mixed-effects models were constructed using the lmer function within the lme4 (Pinheiro et al. 2009) library in R (R Core Development Team 2006), to

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

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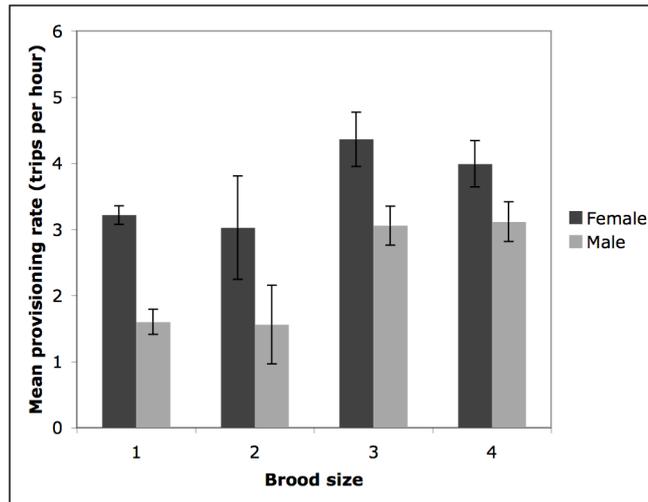
Results

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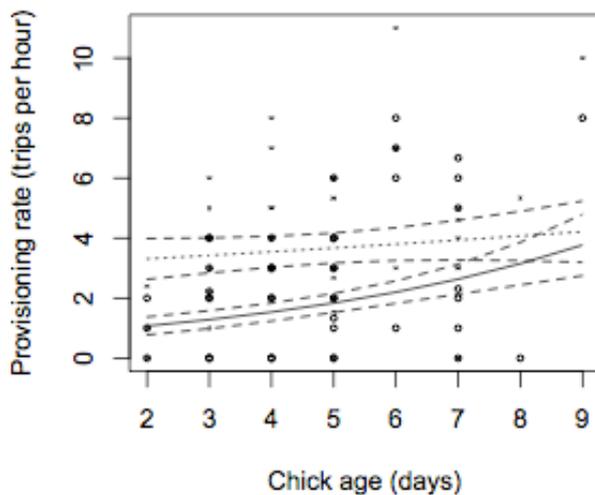

Figure 2. The change in provisioning rate with chick age differed between the sexes (GLMM, $F_{1,42}$=4.55, p=0.04). Points show raw data: crosses represent female provisioning rates; open circles depict male provisioning rates. Lines are predicted from the MAM (Table 1) with a brood size of three nestlings,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

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

Provisioning rate

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

Provisioning rates of both males and females increased with increasing chick age, although

in females this increase was slight (Figure 2). Until chicks were 8 days old, females provisioned more frequently than males (Figure 2) but from 8 days of age males and females provisioned chicks more equally (Figure 2).

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

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

Male song behaviour

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

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

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

Nest visitation behaviour
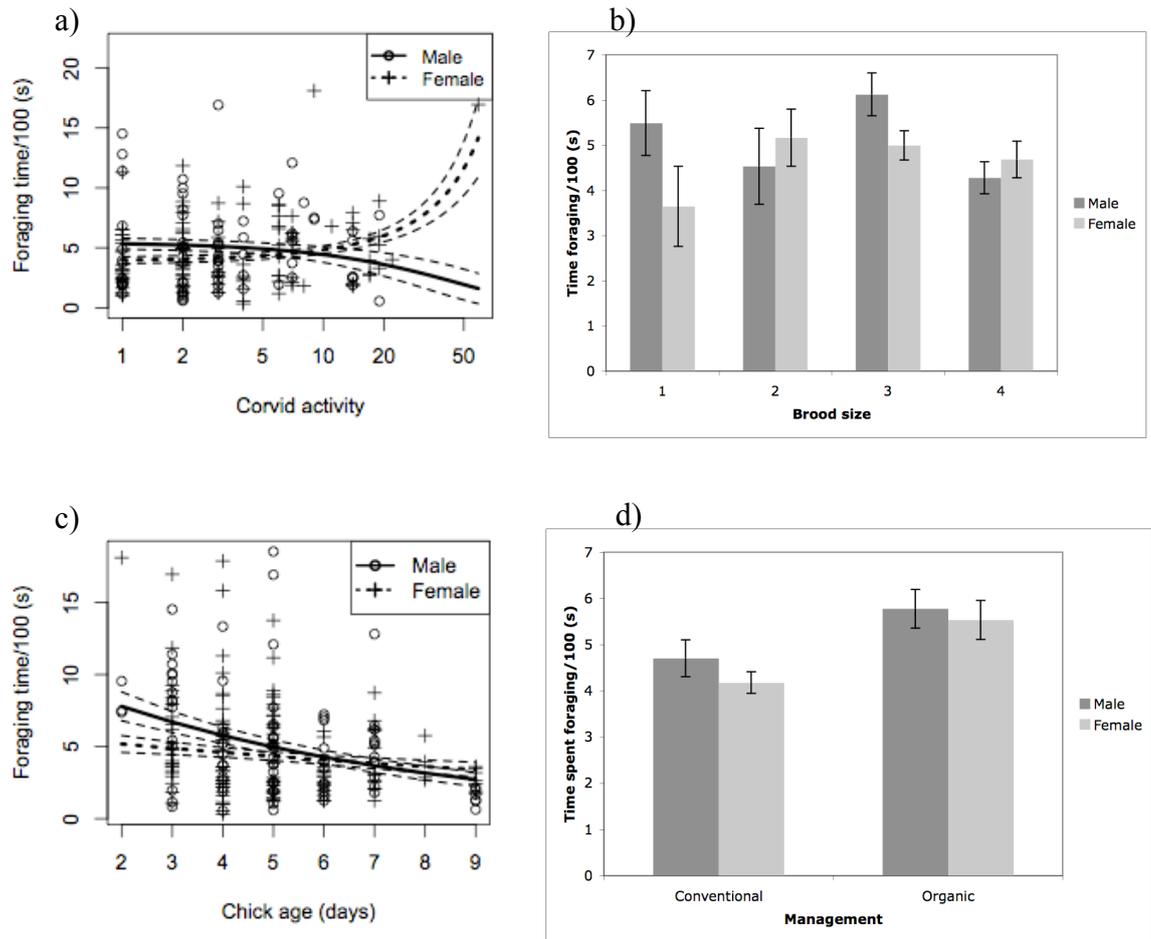
Time spent foraging

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

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

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

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

Time spent in vicinity of nest

Whether or not a parent waited in the vicinity of its nest was influenced only by invertebrate abundance (Table 4). Birds that waited had a higher invertebrate

abundance in the vicinity of their nest than birds that didn't wait (Wait: 95.70 ± 3.64 insects; No wait: 66.41 ± 6.93).

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

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

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

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

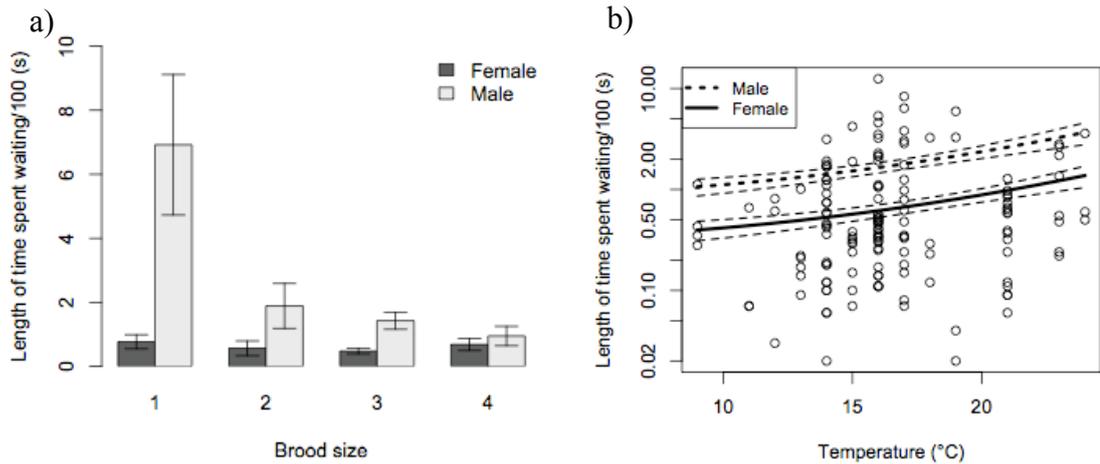| Variable	df	z	p	Estimate	SE
Sex of parent (Male)	1	4.736	<0.001	2.310	0.488
Brood size	1	-1.057	0.291	-0.167	0.157
Temperature^2	1	2.427	0.015	0.002	0.001
Year	1	-1.842	0.066*	-0.561	0.304
Sex of parent x Brood size	1	-2.541	0.011	-0.421	0.166
Variable	df	χ^2	p		
Corvid activity	1	0.016	0.903		
Invertebrate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

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

Time at nest

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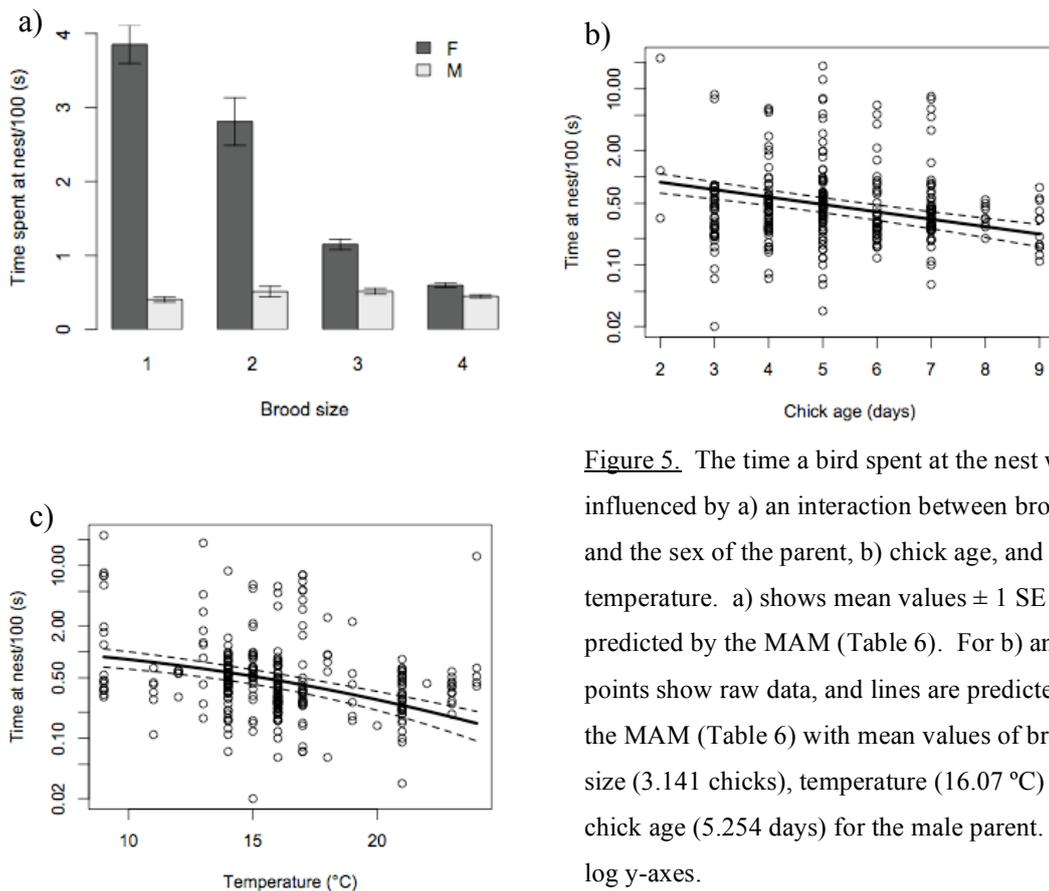

Figure 5. The time a bird spent at the nest was influenced by a) an interaction between brood size and the sex of the parent, b) chick age, and c) temperature. a) shows mean values ± 1 SE as predicted by the MAM (Table 6). For b) and c) points show raw data, and lines are predicted from the MAM (Table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

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

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

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

Discussion

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

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

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

As chick age increased, the foraging trip duration of both parents decreased. This correlates with an increased provisioning rate and suggests that as the food demands of

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

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

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

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

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

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

It appears likely that female Yellowhammers are working at the ceiling of possible energy expenditure during chick provisioning: as females are thought more susceptible to the costs of reproduction (Dawson and Bortolotti 2008), this may lead to a high female-biased over-winter mortality. Conversely, the requirement from large broods and older chicks for a higher work rate from males may lead to a high male-biased mortality, as males can show a cost of increased parental care on survival (Liker and Székely 2005). It remains unclear whether this would lead to a skewed sex ratio, or just

to a high overall adult mortality. A brood manipulation experiment would be able to confirm these results experimentally, and an intensive population study linking breeding work-rate and over-winter survival would be necessary in order to establish both whether a link exists and the implications that increased breeding work rates may have for Yellowhammer population dynamics.

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