

Chapter 7. Survival analysis and population dynamics of an individually marked yellowhammer population

Abstract

The understanding of factors influencing survival is crucial in the study of population dynamics; demographic and morphological shifts can occur within populations over relatively short time frames as a result of differential survival, influencing population structure. Here I determine the effect of demographic and size variables on survival over four winters in a population of yellowhammers (*Emberiza citrinella*) from North Yorkshire, UK. I also analyse capture data from 21 years since 1986 to determine whether sex ratio, age ratio, or size vary over time. The probability of a bird being recaptured decreased through time, but was unaffected by age, sex or wing length. Survival probability was influenced by sex and wing length, with males having a higher survival probability than females, and survival probability increasing with increasing wing length. Sex ratio did not differ significantly between years, although populations tended to be slightly male biased. Age ratios differed between years but not between months, implying high variation of breeding success resulting in low proportions of first year birds following a poor breeding season; the four most recent winters had a higher proportion of adult birds in the population than previously. Mean wing length, when controlling for the effects of age and sex on wing length, decreased with time. The apparent paradox between wing length decreasing over time, and an increased wing length increasing survival may be explained by smaller wing lengths in first year birds as habitat quality or food availability during the breeding season has declined, leading to a gradual reduction in mean population wing length.

Introduction

The understanding of factors influencing survival is vital in population biology; reproductive success and survival are the two main factors contributing to population trends and are themselves interlinked. Many animals do not survive to reproduce and consequently have an intrinsically reduced fitness. An understanding of the genotypic, phenotypic and environmental issues influencing survival is crucial to the understanding of population dynamics, and is especially important in declining populations where variation in survival may be linked to population decline (Siriwardena et al. 1998).

Survival is often related to age, with animals that have survived one year being more likely to survive to the next (Clobert et al. 1988) due to improved experience and social status increasing the ability of the individual to acquire the necessary resources (Newton et al. 1996). This phenomenon is widespread across many avian species (Clobert et al. 1988); however, in other bird species survival decreases continually from the year of first breeding (Loery et al. 1987).

Survival may also be sex-linked and can frequently be associated with dominance status: in the more common scenario where females are the smaller sex (Domènech and Senar 1999), females are subordinate to males. Subordinate individuals tend to be more vigilant than dominant individuals and consequently spend less time foraging (Domènech and Senar 1999). Thus, competition between the sexes has the potential to lead to a reduction in female survival and consequently a male-biased sex ratio (Clobert et al. 1988; Benkman 1997); this can be reversed in species where female social-dominance is seen (Hogstad 2006). Females can also suffer a peak in mortality following their first breeding season (Smith 1995). A skewed sex ratio in a population with a monogamous mating system reduces the proportion of birds able to breed and is likely to affect the reproductive success of the population as a whole.

A study in 1998 by Siriwardena et al. investigated whether farmland bird population trends could be predicted by age or sex-linked survival across species (Siriwardena et al. 1998). They estimated survival rates of 0.44 – 0.56 for yellowhammers, with no evidence for any significant effect of age or sex on survival probability, although females tended to have higher survival than males (Siriwardena et al. 1998) and no difference in adult or first year survival between 1962 and 1994. Since this study was

carried out, yellowhammer populations have continued to decline in the UK (Eaton et al. 2008) and survival rates may have changed, as may the factors influencing survival.

This chapter aims firstly, to determine whether age, sex or size (wing length) are linked to survival probability in a population of yellowhammers, and secondly, to use ringing data from the same site from the past 21 years to determine whether long term temporal fluctuations or trends in sex ratio, ratio of adults to first year birds, or size are present within this population.

Methods

Study site

Yellowhammers were caught and ringed at Headley Hall Farm near Tadcaster, West Yorkshire, UK (lat. 53° 53'N, long. 1° 15'W). Birds were caught between October and May during the winters of 2005/6 – 2008/09 using mist nets, whoosh nets and cage traps at established supplementary feeding sites. Feeding sites were baited with wheat and weed seed, situated within an experimental agroforestry block surrounded by arable farmland. Birds had been caught and ringed at this site since 1986, with data absent from only two winters: sample sizes per winter ranged from 3 to 205 (Mean 50 ± 13.96). All data were used to analyse temporal changes in yellowhammer populations and the potential for fluctuations in sex ratio, age ratio, and size. Data from 2005 – 2009 were used to analyse factors influencing survival.

Biometric data

Following capture, birds were aged and sexed by examination of plumage (Svensson 1992; Dunn and Wright *in press*) and categorised as either adult or first-year birds. Birds were weighed using a digital pocket scale ($\pm 0.1\text{g}$; Satrue, Taiwan), and measurements of wing length, measured as the maximum wing chord (Redfern and Clark 2001) were taken using a standard metal wing rule and rounded up to the nearest mm.

Statistical Analyses

Temporal changes in yellowhammer populations

To determine whether populations showed significant fluctuations in sex ratio, the ratio of adults to juveniles, and size, data from 1986 to 2009 were analysed using R version 2.4.1 for Mac (www.R-project.org). Two binomial generalised linear models were constructed, with each of age (first year or adult) and sex (male or female) as the response variable, and winter (as a categorical variable) and month (to control for temporal trapping variability between years) as the predictor variables. As age ratio, and not number of individuals, was being examined, it was not necessary to control for trapping effort. Error structures were adjusted to quasi-binomial where the dispersion parameter indicated that this was necessary. In order to control for the fact that age and sex both influence wing length in yellowhammers (Svensson 1992; Dunn and Wright *in press*), a generalised linear model was constructed with wing length as the response variable, and age, sex, winter (as a continuous variable) and all interactions as predictor

variables to determine whether trends in wing length were evident over time. 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.

Survival analysis

To estimate annual survival, the encounter histories of 321 individual colour-marked yellowhammers captured between December 2005 and May 2009 were analysed using Cormack-Jolly-Seber mark-recapture models. Analysis was carried out in R version 2.8.0 (www.R-project.org) using the package RMark (Laake and Rexstad 2009) to construct models from program MARK (White and Burnham 1999). This allows the calculation of survival probability and recapture probability separately (Gruebler et al. 2008), taking into account the fact that individuals may survive but not be recaptured. Encounter histories of birds were pooled into four time categories, comprising October – May during 2005/06, 2006/07, 2007/08 and 2008/09. Birds were grouped according to sex (male or female) and age (first winter or adult); wing length was also included as a covariate to determine whether survival or recapture probability may be size-dependent.

Firstly, the probability of recapture (p) was examined. The probability of survival (Φ) was set at a constant, and it was hypothesised that the probability of recapture might be dependent upon 1) Age, 2) Sex, 3) Time, and 4) Wing length. As age and sex both influence wing length, the combinations of age and wing length, sex and wing length, and age, sex and wing length were also used to construct models. The \hat{c} variance inflation factor was calculated and adjusted to control for over-dispersion of data, as is common within capture-recapture datasets (Lebreton et al. 1992). This correction did not alter the model selection results.

Models were selected on the basis of ΔQAICc values, with models differing in QAICc from the 'best' model by more than 2 considered to have a real difference from the best

model (Burnham and Anderson 1998); thus, only models differing in QAICc from the best model by less than 2 are considered further.

The best recapture model was used to build survival models. The same factors as were thought to influence the probability of recapture were also considered the most likely to influence survival, with the exception of time. Thus, a further seven models were considered here. Models that did not differ from the best model (i.e. with a ΔQAICc of less than 2) were averaged to provide weighted estimates of the effects of important parameters on survival.

Results

Temporal changes in yellowhammer populations

Data from 994 captures between 1986/87 and 2008/09 were analysed to determine whether variation in sex and age ratios between years was evident, and whether there were any temporal trends in wing length. Sex ratio varied from 31% to 55% female birds, with an overall sex ratio of 47% female birds; however there were no significant differences between years (GLM, $F_{18,956}=1.17$, $p=0.28$), or between months ($F_{7,974}=1.41$, $p=0.20$). Age ratio varied from 0 – 50% of adults in the population, with an average of $25.90 \pm 3.03\%$ adults. Age ratio differed significantly between years (GLM, $F_{18,943}=3.53$, $p<0.01$; Figure 1); upon further investigation using contrasts, 2005 – 2009 differed in age ratio from earlier years (GLM, $F_{1,943}=29.23$, $p<0.01$), with a higher proportion of adult birds in the population (Figure 1). Age ratios did not differ between months (GLM, $F_{7,936}=0.56$, $p=0.79$).

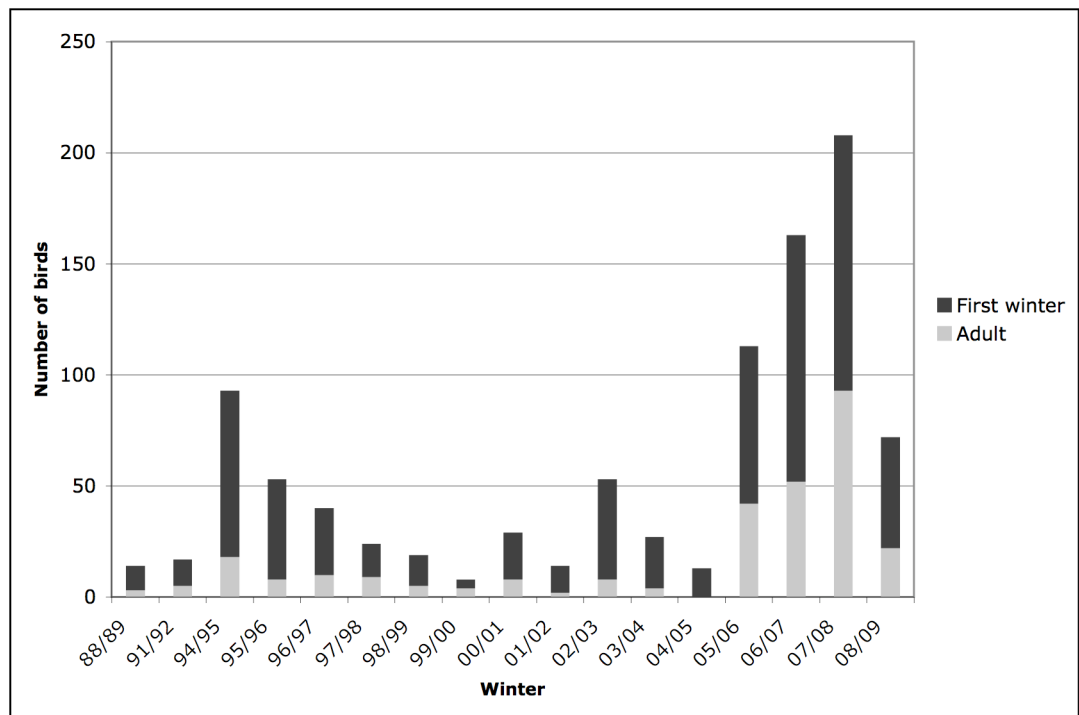


Figure 1. Variation in sample size and age ratio across years. Age ratio differed between years (GLM, $F_{18,946}=3.60$, $p<0.01$) with a higher proportion of adult birds in the population between 2005-2009 than earlier (GLM, $F_{1,963}=29.23$, $p<0.01$)

Table 1. Results of a GLM determining whether temporal trends in wing length were present in a population of yellowhammers. For significant terms, parameter estimates with SE are presented. Two-way interactions of Winter x Age ($F_1=2.14$, $p=0.14$) and Winter x Sex ($F_1=1.80$, $p=0.18$) neither significantly influenced the fit of the model nor significantly influenced the response variable and thus were removed from the MAM.

Variable	df	F	P	Estimate	SE
Age (Juvenile)	1, 828	337.030	<0.001	-2.660	0.215
Sex (Male)	1, 827	1054.898	<0.001	4.935	0.244
Winter	1, 826	39.880	<0.001	-0.090	0.014
Age * Sex	1, 825	4.504	0.034	-0.631	0.297

When controlling for age and sex, wing length changed over time (Table 1). A trend towards shorter wings over time can be seen within both the raw data (Figure 2), and in lines predicted from the MAM (Figure 3).

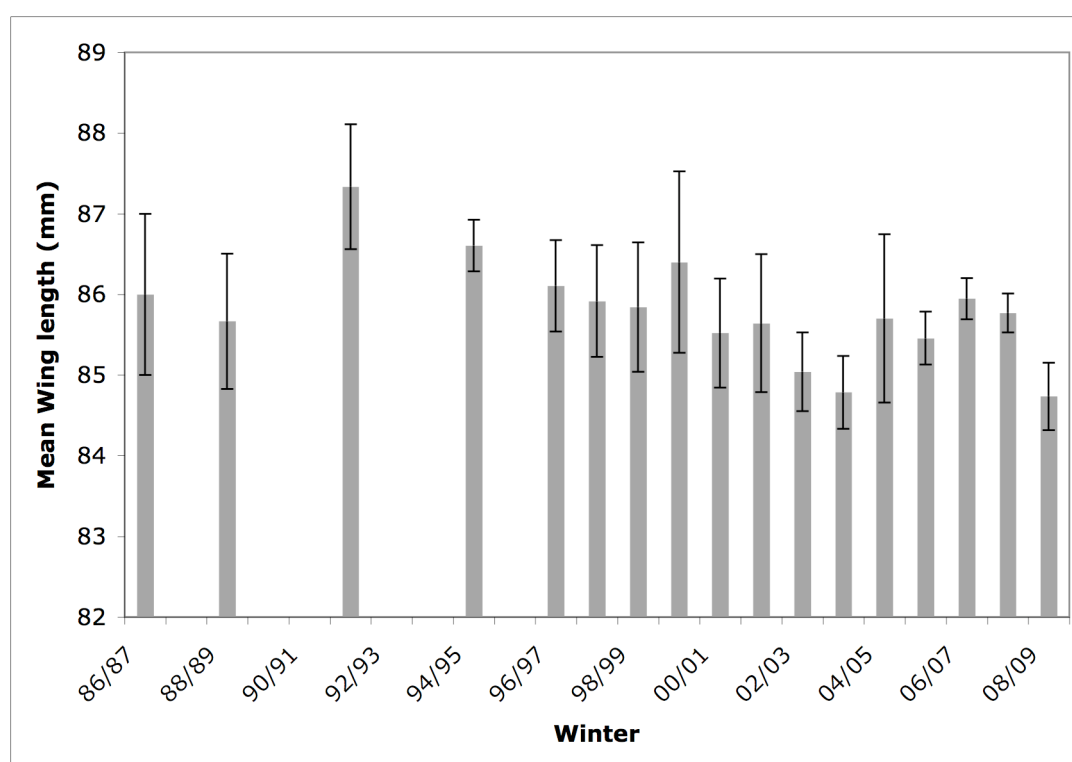


Figure 2. Mean wing length \pm SE over time. Years with no bars are years for which no data are available

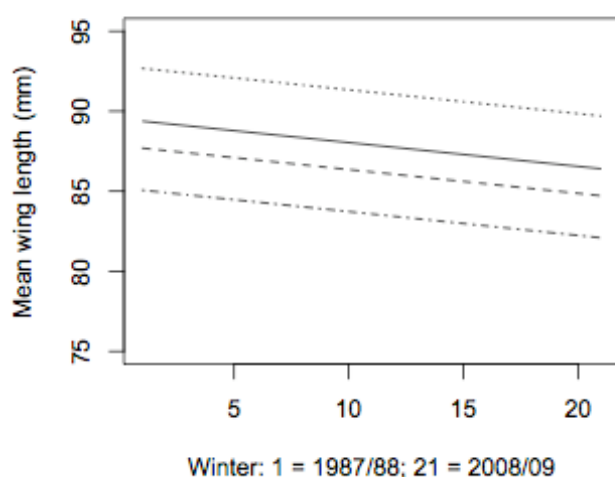
Survival analysis

Figure 3. Predicted trends in mean wing length over time from the minimum adequate model (Table 1) for adult males (dotted line) first-winter males (solid line), adult females (dashed line) and first winter females (dot-dash line)

probability (Table 3).

Data from 321 birds captured across four winters were analysed to determine which factors affected survival. Of the eight candidate models generated to predict the probability of a bird being recaptured, ΔQAICc identified model 1 (Table 2) as the most parsimonious. As ΔQAICc is greater than 2 between models 1 and 2, model 1 can be selected above any other model in the candidate set. This was used to construct models predicting survival

Table 2. Summary of the candidate models predicting the probability of recapture (p)

Model	Φ	P	npar	QAICc	ΔQAICc	Model likelihood
1	1	Time	4	164.52	0.000	1.000
2	1	Constant	2	167.10	2.572	0.276
3	1	Wing length	3	168.34	3.821	0.148
4	1	Sex	3	168.42	3.895	0.143
5	1	Age	3	169.10	4.578	0.101
6	1	Age + Wing length	4	170.26	5.738	0.057
7	1	Sex + Wing length	4	170.29	5.764	0.056
8	1	Age + Sex + Wing length	5	172.25	7.723	0.021

As ΔQAICc between the top three models is less than 2, it can be said that these models are closely linked and that survival estimates can not be taken from any one model.

Therefore the relative weights of each of these three models were used in constructing model estimates (Table 4).

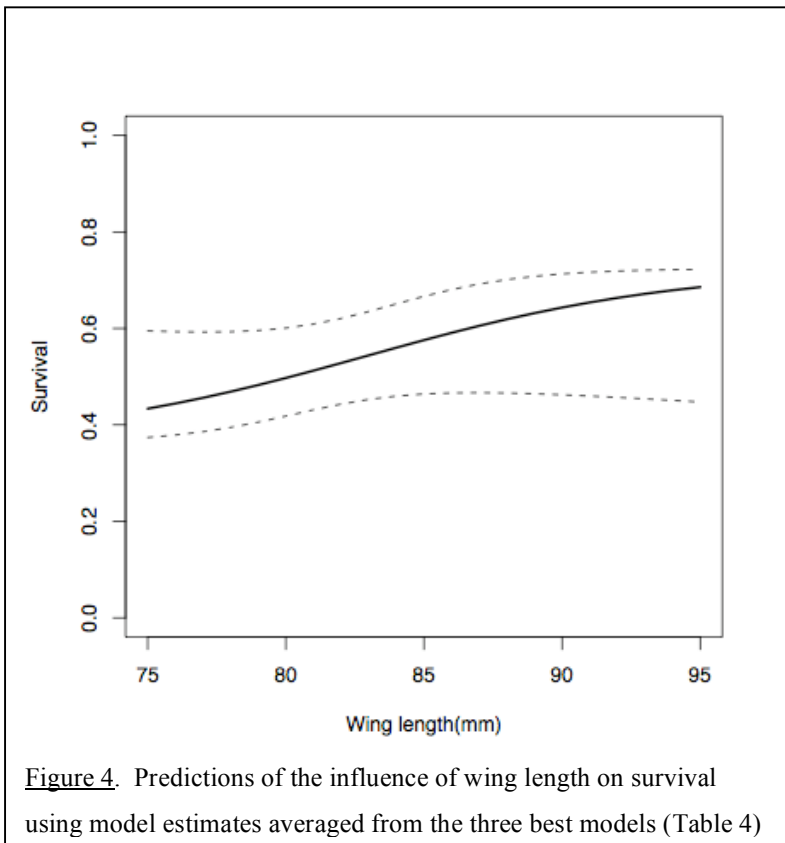
Table 3. Summary of the candidate models predicting the probability of survival (Φ)

Model	Φ	p	npar	QAICc	Δ QAICc	Model likelihood
1	Constant	Time	4	163.68	0.000	1.000
2	Wing length	Time	5	163.86	0.185	0.911
3	Sex	Time	5	164.67	0.995	0.608
4	Age	Time	5	165.71	2.034	0.361
5	Age + Wing length	Time	6	165.85	2.176	0.337
6	Sex + Wing length	Time	6	165.92	2.243	0.326
7	Age + Sex + Wing length	Time	7	167.93	4.257	0.119

The averaged model estimates indicate a positive effect of increased wing length on survival (Table 4; Figure 4), and a reduced female survival compared to males (Table 4). Probability of recapture decreased with increasing time, although not linearly (Table 4).

Table 4. Averaged model estimates predicting survival (Φ) and recapture (p) probabilities for yellowhammers.

	Estimate	SE	LCL	UCL
Φ				
Wing length (75 mm)	0.434	0.058	0.374	0.595
Wing length (95 mm)	0.686	0.058	0.447	0.722
Sex Male	0.632	0.170	0.322	0.920
Sex Female	0.588	0.141	0.263	0.767
p				
Time 2 (2006/07)	0.206	0.069	0.102	0.372
Time 3 (2007/08)	0.160	0.108	0.038	0.478
Time 4 (2008/09)	0.150	0.204	0.008	0.801



Discussion

No evidence was found for skewed sex ratios in any year, although the sex ratio was consistently biased towards males. Sex was also found to influence survival, with females showing lower survival rates. This could be due to male social dominance: male yellowhammers are the larger sex and are therefore likely to be dominant over females in the feeding hierarchy (Domènech and Senar 1999) possibly resulting in female biased mortality as found in great tits and crossbills (Clobert et al. 1988; Benkman 1997). Alternatively, sex-linked mortality may be occurring post-breeding, corresponding to differential effort during reproduction (e.g. Smith 1995). Chapter 5 suggests that females may be working at the upper ceiling of effort during chick provisioning, whilst males vary their reproductive effort according to the requirements of chicks (Chapter 5). This is supported by a similar pattern in great tits, where handicapped females maintained a similar work rate during chick provisioning to non-handicapped females, whereas handicapped males reduced their work rate (Sanz et al. 2000). An increased work rate during the breeding season can result in increased mortality and thus in this species may result in female biased mortality post-breeding. A male-biased population also allows sexual selection to maintain sexually selected traits within the population, as a proportion of males will remain non-breeding ‘floaters’ each breeding season.

Age ratio varied between years, with large fluctuations in the proportions of juveniles in the population: this ratio can be used to assess the health of the population, in terms of recruitment success (Newton 1999) and has been validated as an effective way of monitoring changes in reproductive success (Peery et al. 2007). Whilst Newton (1999) used the adult: juvenile ratio in October as a measure of annual productivity, survival rates of first year and adult yellowhammers do not differ (Siriwardena et al. 1998; Robinson 2005; this study) and the adult:juvenile ratio did not differ between months in this study; thus the use of data from entire winters is unlikely to cause any bias in this measure. Whilst different trapping methods may also influence the proportion of adults captured (Domènech and Senar 1997), mist netting was used for the majority of captures during this study: cage traps were used on only three successful capture occasions, and whoosh nets on one successful capture occasion during years of high capture effort. Therefore, fluctuations in adult: juvenile ratio are likely to be an accurate representation of either breeding success or post-fledging survival, resulting in differential recruitment to the breeding population between years (Newton 1999), and

the higher ratio of adults in the population during the latter four winters indicates either that breeding or fledging success has been reduced, or that post-fledging survival has decreased since 2005. It would be useful to see whether this variation is due to environmental effects such as mean summer temperature or number of rain days during the breeding season, as rain and temperature influence nestling growth and condition (Bradbury et al. 2003), which in turn have the potential to influence future survival and reproductive success (Lindström 1999; Metcalfe and Monaghan 2001; Lummaa and Clutton-Brock 2002; Taborsky 2006). Demonstrating a direct link between poor growth and condition in the nest and lower survival in wild birds would provide an important demographic mechanism behind population changes through reduced juvenile recruitment.

Wing length was also found to differ between years, with a trend for decreasing wing length since 1986 within this population. Wing feathers finish growing post-fledging (after leaving the nest) in first years and are moulted and re-grown post-breeding in adults. A decreasing wing length could be due to three mechanisms: 1) Decreased survival of birds with longer wing lengths; 2) Decreasing wing lengths in individual adult birds between years, or 3) Reduced wing length in first year birds leading to a reduced population average. The survival analysis showed that birds with longer wings had a higher survival and directly contradicts hypothesis 1. Unpublished data from this study indicates that wing length can increase slightly within individuals between years, but only rarely decreases (J. Dunn, unpubl. data), supported by another study which found tail length to be stable within individuals following re-growth (De La Hera et al. 2009). Food availability and other environmental stressors can influence feather growth rate, with slower growth rates where food is limiting or conditions are harsher (Swaddle and Witter 1997; Carlson 1998; Talloen et al. 2008). Dominance hierarchies may also influence feather growth (Hogstad 2003) with subordinates growing feathers more slowly than dominant individuals, probably as a result of differential food availabilities through competition for favourable foraging habitats (Grubb 1989). Extending the feather growth period can compensate for slower growth rates (White et al. 1991); however, in temperate species with extended breeding seasons, adverse weather may limit the time available for moult and a slower feather growth rate may potentially result in shorter feathers, or feathers of lower quality which may impact on thermal maintenance. Evidence that feather length can be influenced by habitat quality in young birds (Grubb et al. 1998) lends support to hypothesis 3, whereby habitat quality and

food availability have declined leading to reductions in juvenile feather length and an overall reduction in mean wing length within the population.

This work provides support for changing demography and morphology in a population of a declining farmland bird, impacting on survival, and temporally correlated with changing habitat quality through decreasing invertebrate abundance. This work has implications for other species influenced by environmental change and suggests that long-term physiological changes within populations can result. A physiological mechanism behind the trend is suggested for this species, although further work is necessary to confirm this.

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