Postfledging first-year survival of skylarks *(Alauda arvensis)* in a semi-natural habitat

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Abstract

Postfledging first-year survival is one of the major parameters determining passerine population dynamics. Despite its importance, it is one of the least studied components in avian population dynamics. Like many farmland birds, skylark (*Alauda arvansis*) populations are declining and the loss of breeding population in the Netherlands is estimated to be about 95% (since 1970s). Empirical estimates of postfledging first-year survival combined with factors that are predictors of this survival are important for effective species conservation and understanding avian population changes.

The study of a skylark population breeding in a semi-natural habitat in the Aekingerzand/Kale Duinen, Appelscha, Drenthe, the Netherlands (52.93178N, 6.30006E) shows a juvenile survival probability (postfledging first-year survival) of 23.5 ± 1.5% and an adult survival probability of 63.2 ± 2.5% (from 2006-2016). Postfledging first-year survival of skylark chicks increased with an increasing body mass. Postfledging first-year survival was higher when the nest was made in a wet area compared to a dry area. Postfledging first-year survival declined during the breeding season, i.e. chicks hatched later in the season have a lower survival probability than chicks hatched early in the season. There is a decline in postfledging first-year survival over the years, while adult survival increased based on the year of birth, i.e. a bird hatched in 2016 has a higher adult survival probability than a bird hatched in 2010.

The British Nest Record Scheme has shown that in skylarks the clutch size, brood size and post-hatching survival rate of nests have increased over time. Together with an increasing adult survival probability in our population this seems to strongly contradict the observed decline in the European skylark population. This decline might likely be due to the decline in postfledging first-year survival rate that we found. Nestling body mass at fledging plays in important role in their postfledging first-year survival. This indicates that degradation of breeding habitat has a stronger effect on postfledging first-year survival than on adult or nest survival, through a carry-over effect from the prefledging stage. It is known that postfledging mortality rates are the highest in the first three weeks in passerine birds, which indicates that local effects near the nest have a major impact on postfledging first-year survival. Because of this, management efforts in the breeding habitat could improve the postfledging first-year survival rates significantly and help stop the major decline in skylark populations.

Introduction

Survival rate is one of the major parameters determining population dynamics (Newton, 1998). Survival rates cannot only be studied in adult breeding birds or during the nesting stage, but also in nestlings after fledging. Postfledging first-year survival plays a major role in songbird population dynamics (Donovan & Thompson, 2001; Bonnot *et al*., 2011). Although postfledging survival has profound effect on population dynamics, it is one of the least studied components of avian population dynamics (Cox *et al*., 2014; Drent, 1984; Hannon & Martin, 2006; Vitz & Rodewald, 2011). Because of the difficulty in tracking and analysing datasets of fledged songbirds that have a low site fidelity (Zimmerman *et al*., 2007; Cooper *et al*., 2008; Faaborg *et al*., 2010; Gilroy *et al*., 2012), postfledging survival rates in songbird populations are estimated and based on 25%-50% of the adult survival rate in that population. This is often done in studies that quantify annual bird population growths (Ricklefs, 1973, Greenberg, 1980). In songbirds, postfledging first-year survival can be particularly low (Perrins, 1979; Perrins, 1980; Magrath, 1991; Naef-Daenzer *et al*., 2001), resulting in a low cohort of recruits to enter the breeding population (Starck & Ricklefs, 1998).

It is generally accepted that postfledging first-year survival rate is influenced by body condition at fledging (Dhondt, 1979; Magrath, 1991; Soler *et al*., 1994; Green & Cockburn, 2001; Greño *et al*., 2008, Vitz & Rodewald, 2011). Larger juveniles are thought to be better in escaping predators (De Laet, 1985) and overcoming periods of food limitations (Perrins, 1965; Blem, 1990; Perrins & McCleery, 2001).
Loss and degradation of breeding habitat could affect nestling condition and therefore result in a decline in postfledging first-year survival over the years. Of course other factors like food availability or weather conditions can also have an important impact on postfledging first-year survival rates (Cox *et al*., 2014). Food availability could be directly influenced by the area of birth, month of birth (Verhulst *et al.,* 1995) or the clutch size of the nest in which the fledgling was born, but again; also by loss and degradation of breeding habitat. Weather conditions during the nesting phase can also directly influence food availability (Avery & Krebs, 2008) or can influence chick development and nestling condition (van der Jeugd & Larsson, 1998; Harrison *et al*., 2011) and therefore affect postfledging first-year survival.

Like many farmland birds, skylark (*Alauda arvansis*) populations are declining and the loss of breeding population in the Netherlands is estimated to be about 95% from 500.000-750.000 breeding pairs since the 1970s to around 35.000-45.000 in 2015 (Teixeira & Alleijn, 1979; SOVON, 2018; van Dijk *et al*., 2008). Most of this observed loss is caused by loss and degradation of breeding habitat (Chamberlain *et al*., 2000; Newton, 2004; Donald *et al*., 2006). To understand skylark population dynamics, different studies have focussed on survival rates within this species. Adult skylarks breeding North-West England before the steep population decline showed an annual survival rate of 66.5%, 46% of the eggs being laid fledge successfully and postfledging first-year survival is estimated to be 33-38% (Delius, 1965). Another study in England showed an nest success rate of 24.2% (Donald *et al*., 2002). Nest success in Czech Republic is 19% (Praus & Weidinger, 2010). In a skylark population in intensive agriculture in the Netherlands nest success is 15.7% (Kuiper *et al.,* 2015) compared to 27% successful nests on organic farms (Kragten *et al*., 2008).

Previous studies in our study area (Aekingerzand/Kale Duinen, Appelscha, Drenthe, the Netherlands (52.93178N, 6.30006E) have shown an adult return rate of 60-81% (Hegemann *et al.,* 2013; Hegemann, 2012) and a juvenile return rate of 13-32% (Hegemann, 2012). It is however unknown how postfledging first-year survival has changed over time and what factors play an important role in determining postfledging first-year survival.

Empirical estimates of postfledging first-year survival combined with factors that are predictors of this survival are important for effective species conservation and understanding avian population changes. Our aim is to determine if postfledging first-year survival has changed over time and which individual characteristics and environmental factors are important for postfledging first-year survival in a Dutch skylark population. These factors included clutch size, chick biometry, year of birth, month of birth, area of birth, weather conditions during the breeding season and weather conditions during the prefledging stage.

Methods

Study species and method

We studied a population of skylarks *(Alauda arvensis)* breeding in a semi-natural heath- and grassland habitat, in Aekingerzand/Kale Duinen, Appelscha, Drenthe, the Netherlands (52.93178N, 6.30006E). We monitored the population since 2006 and followed nests each year. Every breeding season we obtained the following breeding parameters; date of birth; area of birth (low lying wet areas or high lying dry areas), clutch size and chick biometry (wing length and tarsus in mm, weight in g). Chicks were marked individually and measured on an average age of 7.3 days (range between age 4 and 9 days). Meanwhile, adult breeding birds were observed in the field and/or at the nest site to identify each breeding adult present in this local population. Between 2006-2016, we followed a total of 1435 chicks during the nesting stage.

Weather data and biometry

We calculated a mean day-temperature (in °C) and mean daily precipitation (in mm/day) using data from the nearest meteorological station (weather station KNMI at Hoogeveen, Drenthe, the Netherlands, 52.733333N, 6.516667E) during a chicks nesting stage of 10 days. We also calculated an average season-temperature and season-precipitation for the period 1 April - 31 August of each year as a measure for the mean weather conditions during the breeding season. Body mass, wing length and tarsus length were recalculated as residuals based on the chicks age.

Searching the best model

We used Cormack-Jolly-Seber models (CJS models) (Cormack, 1964; Jolly, 1965; Seber, 1965) within the package RMark (Laake, 2013) in R 3.6.2 (R Core Development) to analyse postfledging survival. CJS models are developed to estimate apparent survival rates (phi) and recapture probabilities (p). Within CJS models, effects of time, age and individual covariates on survival and recapture probability can be studied. Our first step in the modelling process was to find a reference CJS model, to which individual covariates could be added later (Lebreton et al., 1992).

The reference CJS model
Survival probability was modelled to be constant over time and age (phi~constant), or dependent on time (phi~time), age (phi~age), time and age (phi~age+time) or age-class i.e. a split between juveniles and adults (phi~ageclass). The same was done for the recapture probability. Age or time dependency could either be categorical (no trend over time) or continuous (a trend over time). Base models were created based on all possible combination from the list above. Model selection was based on Akaike's information criterion adjusted for sample size (AICc, Burnham & Anderson, 2002) and models with a difference in AICc of less than two units were considered to be similarly supported by the data. We selected the best model (ΔAICc: 5.97) which had an age-class dependent survival probability (phi~ageclass) and a time dependent recapture probability (p~time).

Individual covariates
We created a list of 511 models in which the survival probability was dependent on all different combinations of the individual covariates of interest. Covariates were allowed to interact with ageclass, because of our interest in the effect of the covariate on the postfledging first-year survival. Individual covariates used in the models were: residual body mass (res_BM), year of birth (year), month of birth (month), area of birth (area), clutch size (clutchsize), mean day temperature in prefledging phase (nesttemp), mean precipitation in prefledging phase (nestrain), mean day temperature in breeding season (yeartemp) and mean precipitation in breeding season (yearrain).

Because of the strong correlations (66-77%) between the biometry parameters (body mass, tarsus length and wing length), only one of the three biometry parameters could be included in the model as an individual covariate. To find out which biometry parameter fitted our data best we created a list of models in which the survival probability was dependent on one of these biometry parameters. We also added a model with condition (residual body mass divided by residual tarsus length) to this list. The model with residual body mass included as individual covariate (phi~ageclass + res_BM) fitted the data the best (AICc=2427.8 for body mass, vs AICc > 2433.6 for tarsus length, condition and wing length).

Adding month and year of birth to the model as a covariate could be done by adding them as a categorical factor (no trend in survival probability over time) and a continuous factor (trend in survival probability over time). We created a list of models in which the survival probability was dependent on the month and year of birth. All combinations of month and year of birth coded as a categorical or continuous factor were included in the model list. The model with month and year of birth included as a continuous individual covariate was best supported by the data (ΔAICc: 5.12).

There were two models that were equally supported by the data (table 1). The first model included the covariates year, month and area of birth and the residual body mass. The second model included the extra covariate mean precipitation in prefledging phase.

Models	Np	AICc	ΔAIC	AIC weight	DEV
Phi(~ageclass * (res_BM + year + month + area)) p(~time)	21	2379.879	0	2.95E-01	2337.369
Phi(~ageclass * (res_BM + year + month + area + nestrain)) p(~time)	23	2381.197	1.3183	1.53E-01	2334.588
Phi(~ageclass * (res_BM + year + month + area + yeartemp)) p(~time)	23	2382.133	2.2543	9.56E-02	2335.524
Phi(~ageclass * (res_BM + year + month + area + yearrain)) p(~time)	23	2383.118	3.2395	5.84E-02	2336.509
Phi(~ageclass * (res_BM + year + month + area + clutchsize)) p(~time)	23	2383.136	3.2578	5.79E-02	2336.527

Table 1*. Model selection for effects of individual covariates on postfledging first-year survival probabilities. For each model, the values of Akaike's Information Criterion (AICc), difference of AICc values in relation to the best-fitting model (ΔAIC), AIC weights, number of estimable parameters (Np), and deviance (DEV) are shown.*

Finally, we tested for other interaction terms in these two best models. We have only allowed for interaction with month of birth, which seemed the only logical interaction in view of the results and/or their biological meaning. This resulted in a list of 24 models (including the models without interaction term). Model selection showed that including this interaction with month of birth did not improve the models. Hence, we decided to use the first model (Table 1) in further calculations. The second model will only be used for calculating the effect of the mean precipitation in the prefledging phase on the postfledging first-year survival. To test the strength of the effect of the covariates in the model we assumed that when the 95% confidence interval of its β-estimates (provided by RMark in the model output file) did not include zero, the effect was significant.

Results

Survival and recapture probabilities

Of the 1435 chicks that were marked, 1161 were never reencountered, 168 were reencountered as adult in one breeding season, 62 in two breeding seasons, 25 in three breeding seasons, 16 in four breeding seasons and 3 in five breeding seasons (multiple encounters are not necessarily consecutive breeding season).

Of all chicks 47% (675) were born in the dry areas and 53% (758) in the wet areas, 0.7% (10) were individually marked at an age of 4 days, 1.5% (21) at 5 days, 10.5% (151) at 6 days, 41.1% (591) at 7 days, 43.0% (617) at 8 days and 3.1% (45) at an age of 9 days.

Survival and recapture probability were best explained by an age-class dependent constant survival probability and a time dependent recapture probability. Based on the first model the survival probability for the juveniles (postfledging first-year survival) was 23.5 ± 1.5%. Adult survival probability was 63.2 ± 2.5%. Yearly recapture probability ranged between 15.7 ± 4.8% (in 2013) and 84.3 ± 5.5% (in 2011). Over the 11 years of fieldwork the mean recapture probability was 55.6 ± 6.2%.

Individual covariates affecting postfledging first-year survival

The two models showed effects of year of birth, month of birth, area of birth, residual body mass at fledging and the mean precipitation in the nestling phase (Table 2 and 3). Covariates that significantly affect survival are shown in bold.

Table 2. *The estimates of β-values, standard errors and 95% confidence intervals of the parameters in the best model. Significant effects are in bold.*

Parameter	**Beta**	**SE**	**Lower 95% confidence level**	**Upper 95% confidence level**
Juveniles	212.68	4.85	203.17	222.19
Adults	**-468.10**	**2.97**	**-473.93**	**-462.28**
Juveniles month	**-0.54**	**0.10**	**-0.76**	**-0.33**
Juveniles bodymass residuals	**0.12**	**0.03**	**0.06**	**0.18**
Juveniles year	**-0.10**	**0.00**	**-0.11**	**-0.10**
Juveniles area	**0.48**	**0.16**	**0.18**	**0.79**
Adults month	0.32	0.19	-0.04	0.69
Adults bodymass residuals	-0.06	0.06	-0.17	0.04
Adults year	0.23	0.00	0.23	0.24
Adults area	-0.65	0.27	-1.19	-0.12

Table 3*. The estimates of β-values, standard errors and 95% confidence intervals of the parameters in the second best model. Significant effects are in bold.*

Parameter	**Beta**	**SE**	**Lower 95% confidence level**	**Upper 95% confidence level**
Juveniles	211.13	4.88	201.56	220.69
Adults	**-451.03**	**3.06**	**-457.03**	**-445.02**
Juveniles month	**-0.51**	**0.11**	**-0.73**	**-0.29**
Juveniles bodymass residuals	**0.12**	**0.03**	**0.06**	**0.18**
Juveniles year	**-0.10**	**0.00**	**-0.11**	**-0.10**
Juveniles area	**0.48**	**0.16**	**0.17**	**0.78**
Juveniles nestrain	-0.05	0.04	-0.13	0.03
Adults month	0.31	0.19	-0.07	0.68
Adults bodymass residuals	-0.07	0.06	-0.17	0.04
Adults year	0.22	0.00	0.22	0.23
Adults area	-0.65	0.27	-1.18	-0.11
Adults nestrain	0.02	0.07	-0.12	0.16

β-values in both models show that there is a significant effect of ageclass on survival probability, meaning the survival probability between first-year birds and adults differs significantly. Survival probability for juveniles (postfledging first-year survival) was 23.5 ± 1.5% and adult survival probability was 63.2 ± 2.5%.

Postfledging first-year survival of skylark chicks increased with an increasing residual body mass. Postfledging first-year survival was higher when the nest was made in a wet area than when it was made in a dry area. Postfledging first-year survival declined during the breeding season (later hatched chicks have a lower postfledging first-year survival probability). There is a decline in postfledging first-year survival over the years while adult survival increased based on the year of birth (0.128 ± 0.002, bèta-estimate with standard deviation).

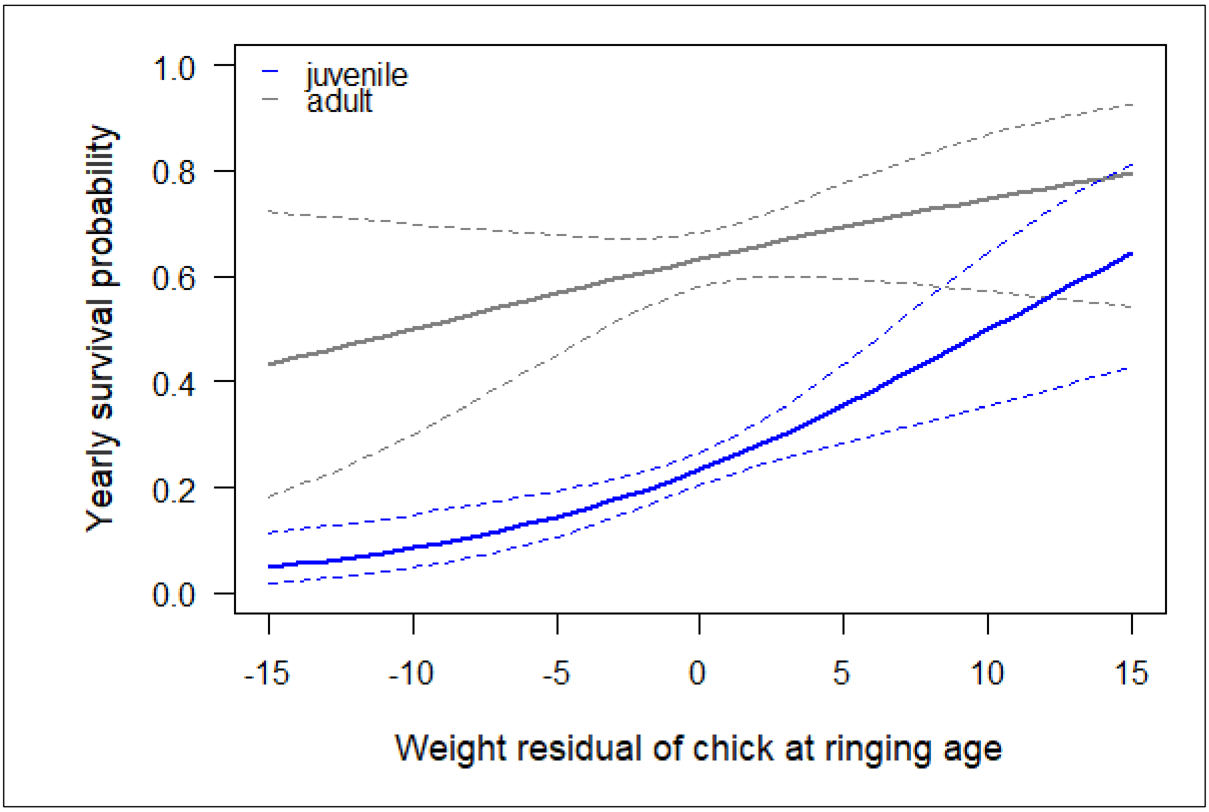

Figure 1. *Effect of residual body mass at fledging on survival in juvenile and adult life stage of skylarks breeding in the Netherlands, Aekingerzand. Dotted lines represent 95% confidence interval.*

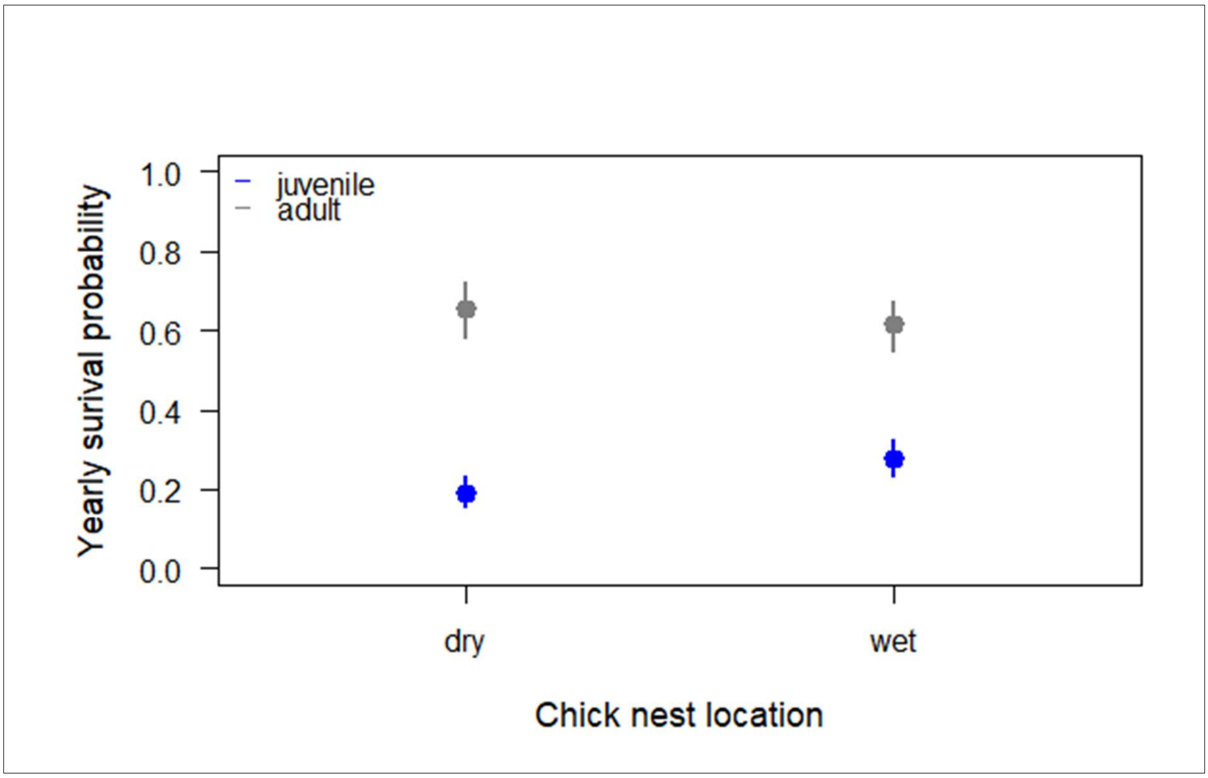

Figure 2. *Effect of birth location (wet/heath or dry/grass) on survival in juvenile and adult life stage of skylarks breeding in the Netherlands, Aekingerzand. Dotted lines represent 95% confidence interval.*

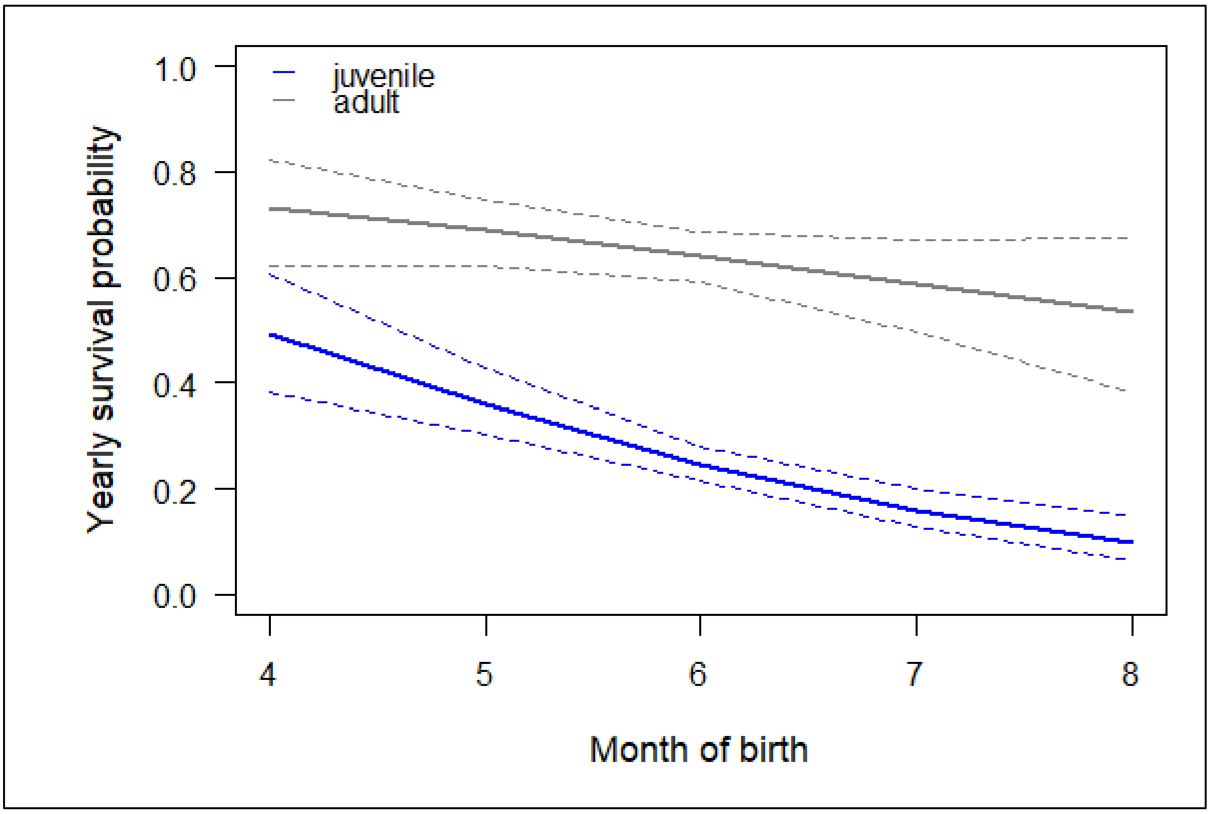

Figure 3. *Effect of month of birth on survival in juvenile and adult life stage of skylarks breeding in the Netherlands, Aekingerzand. Dotted lines represent 95% confidence interval.*

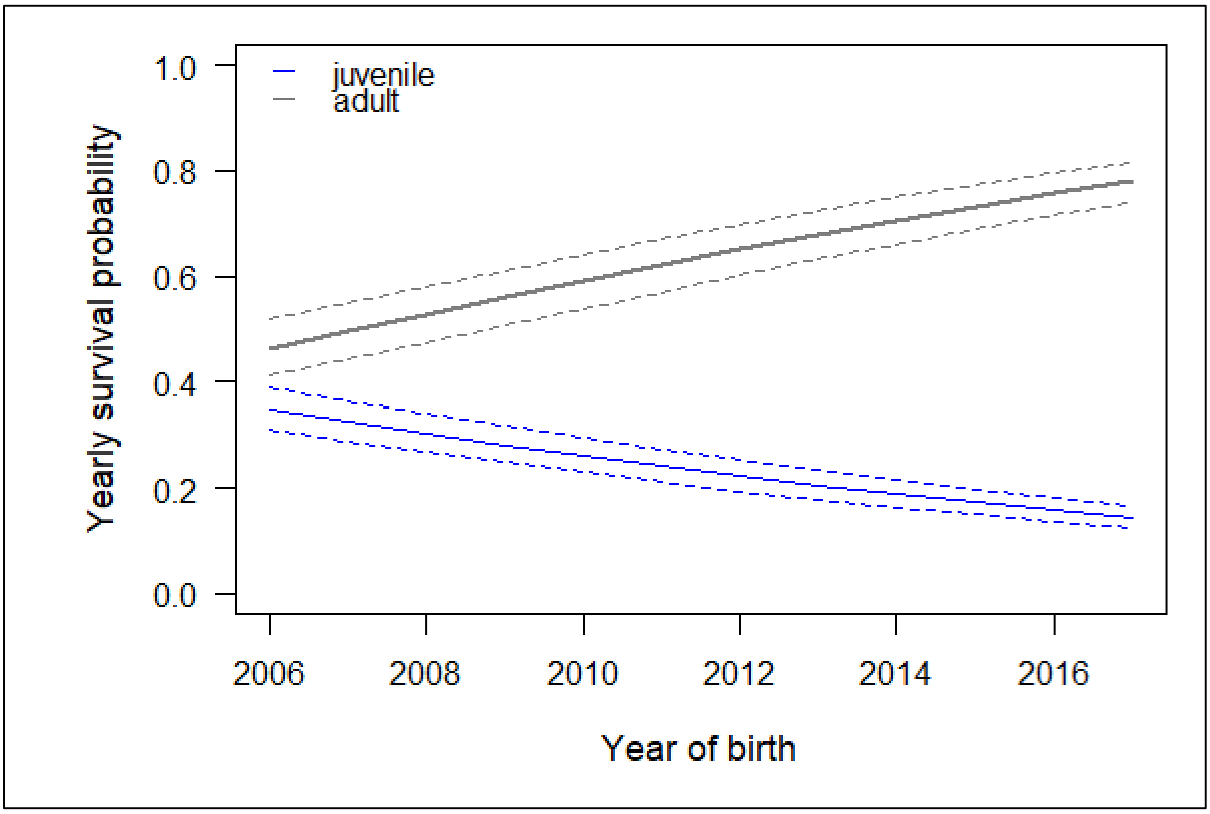

Figure 4. *Effect of year of birth on survival in juvenile and adult life stage of skylarks breeding in the Netherlands, Aekingerzand. Dotted lines represent 95% confidence interval.*

Discussion

Survival and recapture probabilities

Our results show that postfledging first-year survival in skylarks is 23.5% and adult survival is 63.2%. One must keep in mind that CJS-models estimate apparent survival probability, i.e. mortality and emigration, which can lead to an underestimation of the true survival. Apparent survival probability is the product of true survival probability and side fidelity. However, skylarks are known for their high annual return rates (Delius, 1965; Jenny, 1990b) and site fidelity (Duncan, 1987; Wolfenden, 1990 cited in Dougall, 1996; Paradis *et al.,* 1998; Dougall, 1999; Wernham, 2002).

Individual covariates affecting postfledging first-year survival

Our study shows that having a higher body mass at fledging results in a higher postfledging first-year survival chance. Positive links between a chick's body mass and its survival probability are widely known in passerine birds (Cox *et al.,* 2014). Chick body mass can be influenced by breeding habitat quality, i.e. food availability (Wilkin *et al*., 2009), resulting in a carry-over effect from the prefledging stage on the postfledging first-year survival probability (Mitchell *et al*., 2011).

We also found a higher postfledging first-year survival probability in the low lying wet areas than in the high lying dry areas. One could argue that this is due to local food availability, but based on personal field experience it is known that skylarks not only use food sources in close proximity of the nest. The difference in survival probability between both areas might be due to the difference in distance to available good quality food sources. A higher distance results in a lower food intake rate for the nestlings, which in turn can lead to a lower body mass at fledging (Nour *et al*., 1998; Stauss *et al*., 2005). It is also possible that nest disturbance happens more frequently in the drier areas, because these areas are more accessible for recreation, which could result in a lower body mass at fledging, due to a lower food intake rate. Also climatic effects could play a role in explaining the difference between the two types of areas, where high summer temperatures might have a stronger effect on the condition of chicks in the dry areas. Temperatures could fluctuate more in the dry areas due to the shorter vegetation around the nests. Finally, local differences that act on survival probability directly after fledging can also explain the difference in survival probability, for example predation rates differences between both areas.

We found a decline in postfledging first-year survival probability during the breeding season. This decline is a common trend in bird populations (Perrins, 1965; Nilsson & Smith, 1988; Daan *et al.,* 1989; Verhulst & Tinbergen, 1991; Naef-Daenzer *et al.,* 2001) and is often linked to an optimum in food availability (Gosler, 1993; Burger *et al.,* 2012), higher predations rates later in the breeding season (Newton, 1978; Naef-Daenzer *et al*., 1999; Sim *et al.,* 2012) and detrimental environmental conditions (Naef-Daenzer *et al.,* 2001; Oberg *et al.,* 2014).

Juvenile and adult survival over time

Postfledging first-year survival shows a decline over the years. CJS models measure apparent survival, which could mean that the decline in survival is actually a decline in site fidelity. The last years, the area around the study area has become a more suitable breeding habitat for skylarks because of the deforestation of the area and the transition to an open grass-heather landscape. Several breeding skylarks have also been observed. Despite repeated efforts to collect resightings of birds that were born and ringed in the study area, none were found (own data). However, ringed individuals from our study area could have been missed due to the tall grass vegetation in these areas.

In contrast with the decrease in postfledging first-year survival, our analysis shows an increasing adult survival when looking at the year of birth, i.e. a bird hatched in 2016 has a higher adult survival probability than a bird hatched in 2010. This finding indicates a carry-over effect from the year of birth. The selection pressure on juveniles has increased, because of the declining postfledging first-year survival. This could mean that birds that actually survive this first year are overall better fit to cope with selection pressure in the adult life stage, which results in an increasing adult survival rate over the years.

Another probability is because of the declining cohort of recruits that enter the breeding population, the interspecific competition has decreased. This could overall have an effect on the adult survival probability. This decline in cohort of recruits could also mean that fewer adults are settling elsewhere because there is now sufficient space in the breeding habitat for all interested individuals, which in turn results in an increase in site fidelity instead of survival (Pyle, Sydeman, & Hester, 2001).

We also tested if adult survival probability changes with the age of the birds by adding time as a factor in the models. This did not improve the fit of the models (ΔAICc>5.76) which means there is no time (i.e. age) effect on the survival probability of adult skylarks.

Declining populations

The British Nest Record Scheme has shown that in skylarks the clutch size, brood size and post-hatching survival rate of nests have increased over time and that differences between natural and agricultural habitats have decreased (Chamberlain, 1991). Together with an increasing adult survival probability in our population this seems to strongly contradict the observed decline in the European skylark population. In 2000, Wolfenden and Peach (2001) also found an increase in adult return rate averaging 39% (1980-1985) increasing to an average of 66% (1995-1998).

However, contrasting this increase in adult survival rates both we and Wolfenden and Peach (2001) have found a decreasing first-year survival rate over time. As previously mentioned, postfledging survival rates have a profound effect on avian population changes. The decline in European skylark populations is likely due to the decline in postfledging survival rates. Therefore each year, fewer new recruits enter the breeding population. With an adult survival rate of 60% and two nesting attempts per breading season, calculations show that to maintain a sustainable skylark breeding population postfledging survival should be at least be 29% in a set-aside breeding habitat (Wolfenden & Peach, 2001). We consider these set-aside habitats to be the best comparison to our semi-natural habitat, in other habitats these threshold levels of postfledging first-year survival range from 30% up to 100%.

Our analysis shows that although adult survival seems to be a little over 60%, the postfledging first-year survival rate in our study population has dropped under this important threshold level of 29%. By analyzing our own database, proper estimates for nesting success (number of fledglings per nesting attempt) and number of yearly breeding attempts can be retrieved which gives the opportunity to model population dynamics within our study area and test for its sustainability over time.

For effective species conservation it is always very important to not only look at adult or nest survival, but also at the survival between the time of fledging and entering the breeding population as a new recruit. We have shown that postfledging first-year survival within our skylark population has declined over the years. Together with the significant influence of body mass on this survival one could easily assume that food availability tends to become a problem within the study area. Our data however seems to show that body mass of chicks has increased over the same timeframe (x^2= 0.44), which would indicate that the observed decline of survival cannot be explained by food availability. It could be that other factors, like more severe weather conditions, play a major role in explaining the decline in postfledging first-year survival.

Postfledging first-year survival is not only determined in the period just after fledging but also in a juveniles first winter. The skylark population we have studied is known for its partial migratory strategy. Studies have shown that the choice (adaptive choice) for an individual skylark to migrate south or to winter locally is related to structural size and immune function. Individuals that winter locally show a lower return rate in a future years (Hegemann, Marra & Tieleman 2015). This could indicate that juveniles that winter locally also show lower return rates compared to juveniles that migrate south. An recent increase in flower bulb cultivation in close proximity of the study area in the past years could have led to degradation of the local wintering area, which in turn could lead to decline in postfledging first-year survival. A recent study of ours that equipped skylarks with geolocaters did not find any skylark that wintered locally (unpublished own data). This seems to confirm the theory that locally wintering birds show very low survival rates. Of course factors that influence survival of migratory individuals could also explain the decline we have found in postfledging first-year survival.

To get a better understanding of how management efforts could help stop the steep decline in the skylarks breeding population, future research should focus on explaining the decline in postfledging first-year survival using the factors that we, in this study, have shown to be of significant importance.

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