The effects of agricultural intensification on an obligate grassland bird of North America

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A thesis submitted to the Faculty of Graduate Studies in partial fulfillment of the requirements
for the degree of Master of Science

Graduate program in Biology

York University
Toronto, Ontario

NOVEMBER 2017

ABSTRACT

Grassland birds are in decline worldwide and the leading cause of this decline is habitat loss and degradation through agricultural intensification. The purpose of this study is to investigate the impacts of agricultural intensification on a declining grassland bird, the Savannah Sparrow (*Passerculus sandwichensis*). Over two breeding seasons nests were located and monitored, adults and nestlings were measured to assess body condition, and fledglings were manually radio tracked to quantify survival. Nesting success over the two-years was significantly lower on agricultural sites. However, nest predation was higher in agricultural sites in only one of the two years, fledgling survival was not significantly different, and no differences were found in the nest productivity, nor body condition of adults and nestlings. Long-term monitoring is needed to determine if nest predation is consistently higher in intensive agriculture, but at present our results indicate that in some years intensive agriculture may provide adequate habitat.

ACKNOWLEDGEMENTS

Thank you to my MSc supervisory committee, Bridget Stutchbury and Christopher Lortie, for helping me with the planning of and advice during my project, and editing the manuscript at the end. Big thank you to my field assistants, Elsie Hampshire for staying enthusiastic despite the heat in the first field season and Sean Chin in the second field season. My non-agricultural sites were located on Grand River Conservation Authority, rare Charitable Research Reserve, and City of Guelph properties. Thank you to all the landowners and tenants who let me work on their land for my agricultural sites. My project funding was supported through York University Faculty of Graduate Studies, NSERC Discovery, NSERC Engage and Engage Plus, and Syngenta. Help and advice throughout my project from field methods to finding field sites: Ryan Norris (U of Guelph), Paul Hoekstra (Syngenta), Brad Garlough (Syngenta), Stuart Wright (OSCIA). Support from my lab mates: Tehmeena Chaudhry, Sue Hayes and Brendan Boyd. Thank you, Anna Morris for reviewing and proof-reading the manuscript.

TABLE OF CONTENTS

Abstract ii
Acknowledgements iii
Table of Contents iv
List of Tables v
List of Figures vi
List of Supporting Information vii

Introduction 1
Materials and Methods 5
  Study sites 5
  Nesting Success and Nestling Body Condition 6
  Fledgling Survival 7
  Adult Body Condition 9
  Arthropod Abundance 9
  Statistics 10
Results 11
  Nest and Fledgling Survival 11
  Clutch Size, Brood Size and Nestling Body Condition 12
  Arthropod Abundance 13
  Adult Body Condition 14
Discussion 14
  Nest and Fledgling Survival 14
  Clutch Size, Brood Size, Nestling Body Condition, and Arthropod Abundance 17
  Adult Body Condition and Habitat Selection 20
  Conclusions 21
Tables 23
Figures 26
Supporting Information 29
References 30

LIST OF TABLES

Table 1: Breeding productivity for nests compared between agricultural sites and non-agricultural sites. Data were not normally distributed ($p < 0.001$) and site differences were tested using Mann-Whitney U test for each year and 2016-2017 combined. Failed nests were not included for the brood size (number of nestlings hatched) and number of fledglings per nest so as to better understand potential food-related constraints in different habitats. 23

Table 2: Mean (± standard deviation) observed, predicted (tarsus length*0.664 + 1.0485) and residual (observed-predicted) body mass and tarsus length of nestlings for all 7-day old nestlings measured during the study (n = 19 AG, 62 non-AG), females (n = 9 AG, 19 non-AG), and males (n = 7 AG, 32 non-AG), compared between agricultural and non-agricultural sites using independent samples t-tests. 24

Table 3: Arthropod abundances (dry biomass, digital scale 0.0001 g) sorted by order between agricultural and non-agricultural sites for all samples collected. Data were not normally distributed ($p < 0.001$) and tested between site types using Mann-Whitney U tests. 50 sweeps/sample, n = 14 AG, 39 non-AG samples. Bolded p-values are significant ($p < 0.05$). ... 25

LIST OF FIGURES

Figure 1: Study sites containing breeding pairs of Savannah Sparrows in Southwestern Ontario for agricultural sites (circles, n = 7) and non-agricultural sites (squares, n = 6). Shading of symbols indicates year of study. Map created using ArcGIS v.10.4.1. 26

Figure 2: (A) Proportion of fledged nests (nesting success) and (B) fledgling survival during the 3-week fledgling period on agricultural (hatched bars) and non-agricultural (open bars) sites between years and total combined. Fledglings missing before 10 days post fledging presumed dead. Sample size displayed above bars. 27

Figure 3: Mean (+/- SD) body mass of (A) 7-day old nestlings and (B) adults, between sex and site types: agricultural (hatched bars) and non-agricultural (open bars). Samples sizes displayed above bars. Sex of nestlings determined through DNA analysis of blood, and sex of adults determined by presence of physical breeding characteristics. 28

SUPPORTING INFORMATION

Table S1: Landscape proportions around a 50-m radius of the nests per site type. Calculated using ArcGIS v.10.4.1. Urban is any human-made object such as roads or buildings. Data were not normally distributed ($p < 0.01$), and were compared using Mann-Whitney U tests. Bolded p-values are significant ($p < 0.05$). 29

Introduction:

Grassland birds have been experiencing sharp declines throughout North America and Europe (Gil-Tena et al., 2015; Hill et al., 2014; Vickery et al., 1999) which is due primarily to habitat loss and degradation through agricultural intensification (Quinn et al., 2017; Hill et al., 2014; Newton, 2004). Agricultural intensification is the conversion of natural areas and small heterogenous farms to large monoculture crops that are heavily reliant on chemical use (e.g., pesticides and fertilizers) and mechanization; this intensification can lead to detrimental effects on local biota and ecosystems (Tilman et al., 2017; Matson et al., 1997). Arthropod abundance and diversity is greater on natural land and less-intensively managed farms than it is on lands subject to intensive agriculture (Geiger et al., 2010; Attwood et al., 2008) and therefore agricultural sites are expected to be of poor habitat quality for insectivorous birds. Many studies have demonstrated that agricultural intensification is negatively correlated with bird species abundance and diversity (e.g., Donald et al., 2001; Bas et al., 2009; Geiger et al., 2010), and that heterogeneous landscapes support bird species richness better than homogenous landscapes in agriculturally-dominated regions (Gil-Tena et al., 2015; Benton et al., 2003). Throughout Europe, bird populations have been declining while agricultural productivity is increasing (Donald et al., 2001; Chamberlain et al., 2000), and cereal yield explains the greatest amount of the variation in these population trends (Geiger et al., 2010; Donald et al., 2001). Furthermore, ground nesting birds in Europe are more negatively impacted than hedge nesting birds on farmland which is thought to be due to physical disturbances from farm machinery (Bas et al., 2009). Breeding success on intensive agriculture can be negatively impacted by destruction of nests from farm machinery (Casas and Viñueva, 2010; Galbraith, 1988) and an increased predation risk (Kuiper et al., 2015, Evans, 2004). Like European bird population trends, grassland bird diversity and population abundances in North America are also negatively correlated with habitat loss from agricultural intensification (Quinn et al., 2017; Hill et al., 2014).

Although it is well established that agricultural intensification has a negative impact on bird species diversity and population abundances, far less is known about its effects on individual birds. Surprisingly few studies have examined the direct effects of agricultural intensification on nesting productivity or body condition, and the results are somewhat conflicting. For example, a study on Corn Buntings (*Miliaria calandra*) in Britain found that nestling-food abundance decreased with agricultural intensification; this resulted in lowered nestling mass and reduced nesting success (Brickle et al., 2000). Yet, also in the UK, the nestling body condition of Skylarks (*Alauda arvensis*), Chaffinches (*Fringilla coelebs*) and Yellowhammers (*Emberiza citronella*) in agricultural areas had no relation to habitat variables such as crop type, availability of natural margins, and surrounding grasslands and woodlands (Bradbury et al., 2003). However, Linnet (*Carduelis cannabina*) appear to benefit from agriculture because nestling body condition was positively correlated with proximity to rape seed fields which is their primary food source (Bradbury et al., 2003). Tree Swallows (*Tachycineta bicolor*) in southern Quebec experienced lowered nest box occupancy and a decrease in the number of fledglings with increasing agricultural intensity (Ghilain and Bélisle, 2008). However, in the same study region female body mass of Tree Swallows was not correlated with agricultural intensification, even though female body mass was a predictor of brood success (Rioux Paquette et al., 2014). Thus, while agricultural intensification has been long thought to be detrimental to avian demographics the empirical evidence is limited and very mixed.

It is critical to understand how grassland birds are immediately impacted from breeding and being raised on intensive agricultural sites to know if there will be additional carry-over effects into the future. The “silver spoon” hypothesis (Grafen, 1988) states that individuals that are born in better quality habitats will benefit from carry over effects that lead to a greater survival rate and fitness advantage compared with disadvantaged birds born in poor quality habitats (Monaghan, 2008; Mitchell et al., 2011). Not only do these early developmental conditions carry over to affect lifetime survival and fitness (van de Pol et al., 2006b; Lindström, 1999), but they can also impact adult foraging behavior and physiological condition (Krause et al., 2009). Additionally, the quality of habitat occupied in one season can have negative carry-over effects for adults in subsequent seasons (Norris and Marra, 2007). Nestling body mass has been shown to be correlated with local food abundance which is an indicator of the habitat quality they are born on (Teglhøj, 2017; Pérez et al., 2016; Brickle et al., 2000) and nestling body mass can carry over to significantly impact fledgling survival (Mumme et al., 2015; Cow et al., 2014, Cox and Kesler, 2012). Few studies have assessed how agricultural intensification impacts nestling condition, and none have tested its impacts on fledgling grassland birds.

The purpose of this study is to investigate the impacts of agricultural intensification on the parents and offspring of a declining grassland bird, the Savannah Sparrow (*Passerculus sandwichensis*). I will test four predictions based on the hypothesis that intensive agriculture is low quality habitat due to higher nest predation and lower food supply:

(1) Agricultural sites will have lower nesting success (i.e., nests that fledged at least one young) and lower fledgling survival due to increased predation risk compared to non-agricultural sites.

(2) With failed nests removed, nests on agricultural sites will have a reduced clutch size, brood size, and number of fledglings per nest, and lower nestling body condition as a result of poor food supply.

(3) Arthropod abundance on agricultural sites will be lower than on non-agricultural sites.

(4) Adults breeding on agricultural sites will have lower body mass and condition compared to adults breeding on non-agricultural sites due to lower food supply and/or foraging habitat.

The Savannah Sparrow is an ideal species for this study because it is a grassland songbird that has experienced significant declines throughout North America (Sauer et al., 2014). Their breeding ecology has been well studied in natural habitats (e.g., Mitchell et al., 2011; Wheelwright and Rising, 2008; Wheelwright and Mauck, 1998) as well as in hayfields and pastures (e.g., Perlut et al., 2008a, 2008b; Perlut et al., 2006), but not in intensive agricultural areas (i.e., row crops and monocultures). Savannah sparrows are not negatively affected by wearing radio tags (Rae et al., 2009) which makes them an ideal candidate for radio-tracking. They are a small (19-20g) (Rising and Somers, 1989) obligate grassland bird that nests inconspicuously on the ground under the grass (Wheelwright and Rising, 2008). Savannah Sparrows feed their nestlings arthropods, primarily consisting of Lepidoptera, Hymenoptera, Diptera and Homoptera (Meunier and Bedard, 1984) and thus diet composition and food abundance is likely to be impacted by agricultural practices.

Agricultural intensification is one of the leading causes of decline for grassland birds (Hill et al., 2014) and it is critical to understand the mechanisms, and at which life stages it impacts affected species of declining grassland songbirds. To date, the only studies that examine the effects of agricultural intensification on birds in North America have focused on species diversity and abundance (e.g., Quinn et al., 2017; Hill et al., 2014), and the breeding success of non-grassland, and non-native species that use nest boxes (Tree Swallows and House Sparrows, *Passer domesticus*) (e.g., Ghilain and Belisle, 2008; Robillard et al., 2013). This study is novel because it focusses on breeding success, body condition and fledgling survival on intensive agriculture for a native obligate grassland species, the Savannah Sparrow.

Materials and Methods:

Study Sites:

There is little known about the effects of agricultural intensification on the grassland birds of North America, so rather than studying across a gradient of agricultural intensification, I compared the two ends of the gradient to test if there were any differences between the two habitats. Savannah Sparrows (SAVS) were studied on intensive agricultural sites (AG) and non-agricultural open/grassland sites (non-AG) in southwestern Ontario for two consecutive breeding seasons (2016-2017; Figure 1). The study began (2016) with 11 AG sites and 10 non-AG sites, and an additional 4 AG sites and 1 non-AG site were added in the second year of the study. The AG sites that had breeding pairs of SAVS (n = 7) were monocultures of corn, soy or winter wheat 31-92 hectares in size (50.7 ± 24.4 Ha), and were bordered by adjacent farms. The non-AG sites with breeding pairs of SAVS (n = 6) were open areas covered in grasses and herbaceous plants (e.g. goldenrod) 11-29 hectares in size (18.0 ± 6.8 Ha), and were not being used for agriculture. The non-AG sites were not historically natural grasslands, and 4 of the 6 had been previously used for agriculture but were naturalized to grasslands in conservation areas between 5-15 years ago. The fifth site was a minimally disturbed grassy field on a ground-water collection property, and the sixth site (used only in 2016) was an open grassy undeveloped plot of land on the edge of a city.

Vegetation composition is thought to have little influence on the nesting success of Savannah Sparrows (Winter et al., 2005), however, measuring landscape composition is a commonly used tool in understanding grassland bird population dynamics especially in agricultural landscapes (e.g., Jeliazkov et al., 2016; Gil-Tena et al., 2015; Ghilain and Bélisle, 2008). To further define the site types, satellite imagery viewed in ArcMAP (ArcGIS v.10.4.1) was used to measure landscape composition around a 50-m radius of each nest location. Land was categorized as either arable land (crop), open/grass (any non-agricultural), bare ground, urban (e.g., concrete or buildings), shrublands, or, forest.

Nesting Success and Nestling Body Condition:

Nest searching began in mid-May and continued until late July for both years of the study, 2016-2017, using three methods described by Winter et al., (2003). The first method was behavioural observation; pairs of SAVS that were thought to be in the incubation stage were observed foraging until the female returned to the nest, whereupon after 5 minutes we would slowly approach the area where the female entered the grass, using long sticks to sweep the top of the grass to flush her off the nest. If there were indications of nestlings (i.e., parents carrying food items), we located nests by observing where the parents were taking the food and then carefully searching the area by hand for the nest. Behavioral observation was the most successful on non-AG sites where the SAVS had large territories and density was lower. The second method was systematic walking while sweeping a stick over the grass; this method was relatively successful in grassy laneways of agricultural sites. The third method was haphazard walking while sweeping a stick over the grass. This was useful on non-AG sites with high densities of SAVS and small territories. All nests were marked with twigs or grass above the nest to look natural, and a flag or flagging tape was placed at least 2 m away to avoid revealing the nest location to natural predators.

For each nest found, we recorded the clutch size and monitored nests every 4-5 days with minimal disturbance. A nest was considered successful if at least one young fledged the nest. If the nest was empty on a check it was assumed to have been depredated, and if there were cold eggs it was assumed to have been abandoned. Once the nestlings hatched we estimated age based on developmental stage and returned when they were 7 days old (hatch day = 0). Measurements of tarsus (calipers, 0.1 mm) and mass (digital scale, 0.01 g) were taken from the nestlings to examine differences in body condition in relation to habitat quality. Tarsus length is considered the best estimate of overall body size in Savannah Sparrows (Rising and Somers, 1989). Body condition was analyzed using residual body mass from calculating the predicted body mass from the regression equation of mass and tarsus length, and then subtracting it from the observed (actual) body mass. Focal nestlings were sexed by blotting a sample of their blood taken via brachial venipuncture on a labelled card and sent to HealthGene Laboratories (Concord, ON) for DNA sexing. If a nest was empty after the nestlings were banded at 7 days old it was assumed to have successfully fledged after confirmation of parent alarm calls and radio tracking (see fledgling survival below).

Fledgling Survival:

Radio-transmitters were attached to 1-2 nestlings per nest on day 7 of nestling development (fledging typically occurs 9 days after hatching). The tagged nestlings must have had a mass of at least 14 g to ensure that the radio tag and harness was less than 5 % of the bird's body weight. The radio-transmitters were attached using a figure-eight leg-loop harness (Rappole and Tipton, 1991). In the first year of the study the radio transmitters used were the coded Avian Nano Tag model NTQB-3-2 (Lotek Wireless Inc.) compatible with the Motus Wildlife Tracking System (Taylor et al., 2017). These tags were 0.67 g in weight, and set to pulse every 12.7 s (battery life: 124 days). Due to lack of transmitter availability in the second year of the study, the radio transmitters used were Pip3, battery Ag379 (Biotrack Ltd./Lotek Wireless Inc.) for manual tracking only. These tags were 0.7 g in weight, and pulsed every 2 seconds (battery life: 39 days).

Over the two-year study, a total of 48 nestlings were radio-tagged; 34 from non-agricultural sites and 14 from agricultural sites (for sample size explanation, see results). We monitored the fledglings by manually-tracking with a three-element Yagi antenna and SRX-800-M2 (Lotek Wireless Inc.) receiver in 2016 and a TRX-1000S (Wildlife Materials) receiver in 2017. Fledglings were tracked every 3-5 days for 3 weeks after fledging and to quantify their survival during the 3-week fledgling period. Fledglings were considered dead if their carcasses were found, the transmitter was found with evidence suggestive of predation (e.g., bite marks, feathers), or if the radio-tagged fledglings disappeared within 9 days of leaving the nest. Any fledgling that was confirmed alive ≥10 days post-fledging was considered alive ("apparent survival") unless found dead on a later date (3/20 fledglings found dead 10+ days post-fledging). Savannah Sparrow fledglings remain with their parents and siblings 10-25 days after leaving the nest (Wheelwright et al., 2003; Wheelwright and Mauck, 1998). Therefore, disappearances after 10 days were not considered a mortality as the fledgling may have already left their parents territory and could have been out of detectable range. When a fledgling disappeared, we still attempted tracking for 3 consecutive visits (every 3-5 days) to ensure the fledgling remained undetected.

Adult Body Condition:

Adults in both the AG and non-AG sites were caught using monofilament mist nets and were sexed by their physical breeding characteristics (brood patch and cloacal protuberance). Females were selectively caught by setting up the mist net within 1-2 m of the opening to the nest and flushing her into the net during the incubation stage, and from flying into the mist nets that were targeting males. Males were caught using song playback beneath the mist net. Tarsus length (calipers, 0.1 mm) and mass (digital scale, 0.01 g) were measured for all adults. A total of 12 females and 44 males were measured over the two-year period. Adults were caught after territory establishment between June 4-July 28 (2016) and July 2-6 (2017), and no adults from the first year were measured in the second year of the study.

Arthropod Diversity and Abundance:

Arthropod abundance was measured as an indicator of food availability and habitat quality in the AG and non-AG sites (Johnson, 2007). Based on the methods by Chadbourne and Anderson (2015), arthropod abundance was measured by sweep-netting the upper vegetation at each nest site for 2 transects of 25 sweeps (180 degrees per sweep), covering a distance of about 25 m per transect. All samples were collected by the same person over the two breeding seasons to reduce collection biases between samples. In the first year of the study arthropods were sampled during the egg, nestling and fledgling stages and during the second year of the study only the nestling stage was sampled as it is the most relevant for assessing nestling body condition. All samples collected were used to test arthropod abundance between habitat types. Samples were collected between 1000-1500 when the temperature was between 15-25 °C, cloud cover was less than 50%, and wind was less than 22 km/hour. The 50 sweeps from each nest site was pooled and placed in a large plastic Ziploc bag and frozen to kill the arthropods. Not all nests could be sampled for arthropods due to adverse weather conditions (5/29 successful nests with 7-day old nestlings measured not sampled during the nestling stage). After the field season, arthropods were painstakingly separated from plant material and sorted into orders before being dried at 70 °C for 48 hours. Dry biomass was recorded to 0.0001 g for each insect order, class Arachnida, and unknown (loose body parts and damaged arthropods that could not be identified).

Statistics:

For statistical analysis, first egg date was estimated by subtracting 12 days for incubation plus the number of eggs per nest (assuming one egg is laid per day) from the hatch date. If the nest was depredated before hatch date, laying date was estimated to early, middle or late in the month which for statistical purposes, was marked as the 5th, 15th or 25th of the month based on when the nest was found. All statistical tests were run on SPSS (IBM SPSS Statistics v.24). Data were pooled for all AG sites and non-AG sites. Nestling body mass and condition had normal distributions are were analyzed using independent samples t-tests. Residual nestling body mass was also examined with a general linear model (univariate analysis of variance) to investigate if the different variables (e.g., site type, sex, brood size, arthropod biomass) had any predictive power when analyzed together. Arthropod abundance, clutch size, number of nestlings per nest and number of fledglings per nest were not normally distributed ($p < 0.001$) and were tested instead using Mann-Whitney U tests. Both nesting success and fledgling survival were analyzed using Pearson’s Chi Square tests. If the assumptions of Pearson’s Chi Square were not met (>0 cells have expected cell count less than 5), Fisher’s exact test was used instead.

Results:

Nest and Fledgling Survival

Over the two-year study period 34 nests were found on 7 agricultural sites (AG) and 60 nests were found on 6 non-agricultural (non-AG) sites. In the first year of the study, 3 of 11 AG sites and 6 of 10 non-AG sites had breeding pairs of SAVS present ($\chi^2(1) = 2.29$, $p = 0.130$). In the second year of the study we added another 4 AG sites and 1 non-AG site but selectively chose them based on experience from the first year so there was 100 % occupancy of breeding pairs. On the agricultural sites, all nests were found in the grassy laneways and margins in between the crops and were composed of 84.7 ± 5.4 % (mean ± SD) arable land/crop cover within a 50-m radius of the nest. The non-agricultural sites were composed of 95.3 ± 8.4 % (mean ± SD) open/grass cover within a 50-m radius of the nest (supporting Table S1).

Nesting success (proportion of nests that successfully fledged at least one young) was determined primarily by nest predation (52 of 56 failed nests) rather than nest abandonment (4 of 56). Over the entire study period, nesting success was significantly lower on AG sites (26.5 %) compared to non-AG sites (50.0 %) (Figure 2a; n = 94, $\chi^2(1) = 4.307$, p = **0.038**). The nesting success was not significantly different between AG and non-AG sites in 2016 (Fisher's exact test: p = 1.000) but was significantly lower on AG sites in 2017 (Figure 2a, $\chi^2(1) = 6.061$, p = **0.014**). Although there appeared to be strong year to year differences (Figure 2a), nesting success was not significantly different between years (n = 94, $\chi^2(1) = 0.037$, $p = 0.847$).

Fledgling survival for the 3-week fledgling period over both years was marginally lower on AG sites (21.4 %) than non-AG sites (35.3 %) but was not significantly different (Fisher's exact test: p = 0.498, n = 14 AG, 34 non-AG; Figure 2b). Post-fledging survival in the first 9 days after leaving the nest was also not significantly different between AG (28.6 %) and non-AG sites (52.9 %) across both years ($\chi^2(1) = 1.394$, p = 0.238, n = 14 AG, n = 34 non-AG). Fledgling survival (3 weeks post-fledging) was not significantly different between AG and non-AG sites in 2016 (Fisher's exact test, p = 1.000, n = 6 AG, 14 non-AG), or in 2017 (Fisher's exact test, p = 0.371, n = 8 AG, 20 non-AG; Figure 2b). Fledgling survival (3 weeks post-fledging) was not significantly different between years ($\chi^2(1) = 0.224$, p = 0.636, n = 20 in 2016, 28 in 2017) nor between sexes ($\chi^2(1) = 0.041$, p = 0.839, n = 17 females, 31 males).

Clutch Size, Brood Size and Nestling Body Condition

Surprisingly, with failed nests removed to isolate habitat quality effects (i.e., those that escaped predation), no significant difference was found between AG and non-AG sites in clutch size, brood size (number hatched), or number of fledglings per nest when combining years nor for each separate year of the study (Table 1).

Nestling body mass at 7 days old was not significantly different on AG sites compared to non-AG sites (Table 2, Figure 3a). Tarsus length was significantly correlated with body mass ($R^2 = 0.20$, t = 4.405, p = 0.000) and this regression equation (tarsus length*0.664 + 1.0485) was used to calculate the predicted body mass. As a measure of relative body condition, the residual body mass was calculated from the observed body mass minus the predicted body mass. The residual body mass of 7-day old nestlings was also not significantly different between nestlings hatched on AG sites compared to non-AG sites (Table 2). Although the observed (t = 5.081, p = **0.000**), predicted (t = 4.75, p = **0.000**) and residual (t = 2.829, p = **0.006**) body mass of 7-day old nestlings were significantly different between male and female nestlings (n = 28 females, 39 males), there was no difference between site types when accounting for sex (Table 2, Figure 3a).

Brood size is expected to influence nestling body condition, because the more nestlings per nest the more parental investment is needed to feed all of the nestlings. Brood size and nestling body mass were significantly correlated with a weak negative trend ($R^2 = 0.05$, t = -2.084, p = **0.040**). When combining all the variables in a general linear model to examine residual body mass ($R^2 = 0.22$, F = 3.551, p = **0.007**), sex of nestlings was a significant predictor (F = 5.141, p = **0.009**), but site type (Ag vs. non-AG: F = 1.036, p = 0.313), brood size (F = 2.401, p = 0.126), and total arthropod biomass (F = 3.046, p = 0.086) were not significant predictors.

To examine carry-over effects from poor quality nestling condition irrespective of habitat type, I tested if low nestling condition predicted fledgling survival. However, residual nestling body mass was not correlated with fledgling survival during the first 9 days after leaving the nest ($R^2 = 0.03$, Wald = 1.183, p = 0.277) or for the 3-week fledgling period ($R^2 = 0.03$, Wald = 1.001, p = 0.317).

Arthropod Abundance

The total dry biomass of arthropods was not significantly different between AG and non-AG sites over the study period (df = 53, U = 318, p = 0.364, Table 3) but was almost significantly correlated with residual body mass with was a slight negative trend ($R^2 = 0.056$, t = -1.972, p = 0.053). Homoptera, Coleoptera larva and Arachnids were more abundant on non-AG sites, but Diptera, Orthoptera, and Coleoptera adults were more abundant on the agricultural sites (Table 3). Homopterans are an important nestling food for savannah sparrows (Meunier and Bédard, 1984) and the biomass was significantly higher on non-AG sites (Table 3) but even so did not predict nestling body condition ($R^2 = 0.02$, t = -1.145, p = 0.256).

Adult Body Condition

If the AG sites have poor-quality food resources compared to the non-AG sites, this could be reflected in differences in adult body condition due to low food abundance and/or greater commuting distances to foraging habitat. The mean (± SD) body mass of adult males was 18.8 ± 0.8 g on AG sites (n = 21) and 18.5 ± 0.9 g on non-AG sites (n = 23), which was not significantly different (df = 44, t = 1.028, p = 0.310, Figure 3b). The mean (± SD) body mass of adult females was 18.2 ± 1.4 g on AG sites (n = 5) and 17.3 ± 1.1 g on non-AG sites (n = 7) which was also not significantly different (df = 10, t = 1.301, p = 0.222, Figure 3b). When accounting for skeletal size (tarsus length), residual body mass (observed – predicted (0.3848*tarsus length + 13.477)) was not significantly different between AG and non-AG sites for adult males (df = 39, t = 0.813, t = 0.421) nor for adult females (df = 10, t = -0.071, p = 0.945). Day of the year (date of capture) and adult male residual body mass were also not correlated (n = 44, R^2 = 0.01, t = 0.699, p = 0.489).

Discussion:

Nesting Success and Fledgling Survival

As predicted, nesting success was significantly lower on agricultural sites compared to the non-agricultural sites, when both years were combined, and was almost entirely caused by nest predation. Nesting success (20-55%) was similar to other studies of the same species in Vermont (7-48 % in grazed pastures and hayfields: Perlut and Strong, 2011; Perlut et al., 2006) and New Bunswick (10-80 % in non-agricultural sites: Wheelwright et al., 2012; Wheelwright and Schultz, 1994; Dixon, 1978). Unlike in hayfields, nests were not directly destroyed from agricultural practices because planting of soy, corn and wheat occurred before nesting began (early-May) and harvesting occurred after nesting was complete (mid-August).

Nesting success for many bird species can be negatively impacted by agricultural intensification for many reasons but is primarily due to predation and physical destruction of nests from farm machinery. An explanation for the increase of predation rates on farmland is that parents must travel farther for food and be away from the nest for longer periods of time (e.g., Stanton et al., 2016) which would result in nestlings begging for food more often, and thus attract predators to the nest (Whittingham and Evans, 2004). Predator densities can also increase in human-disturbed areas such as agriculturally intensive landscapes (Evans, 2004). An experimental study in the Mediterranean with artificial nests found that predation was the leading cause of nest failure on farmland in the study region (Beja et al., 2014). Nesting success decreased with increasing agricultural intensity due to predation for Corn Buntings in the UK (Brickle et al., 2000). Skylarks (*Alauda arvensis*) in the Netherlands experienced reduced nesting success on intensive agriculture due to both higher predation and mowing practices (Kuiper et al., 2015). Despite an overall increase in predator densities in the Netherlands over the past few decades, Black-tailed Godwits (*Limosa limosa*) only experienced increased nest predation on managed monoculture grasslands and not on natural meadows indicating that high quality habitat provides some protection against predators (Kentie et al., 2015). Grassland bird populations are not viable in the agriculturally extensive (i.e., hayfields and pastures) areas of the Champlain Valley of Vermont and New York (Perlut et al., 2008b) and in this study, we show that another anthropogenic habitat, intensive agriculture (i.e., row crops), may be detrimental to Savannah Sparrow populations in Ontario.

To our knowledge, this is the first study to examine the effects of agricultural intensification on the fledgling survival of grassland songbirds in North America. Attaching radio transmitters to nestlings has made it possible to quantify fledgling survival for cryptic grassland bird fledglings (e.g., Berkeley et al., 2007). In this study, fledgling survival was 21.4 % on agricultural sites and 35.3 % on non-agricultural sites over the two breeding seasons but it was not statistically significantly different owing to low statistical power. Due to the high nest failure on agricultural sites, fewer nestlings (n = 14) could be radio tagged compared with non-agricultural sites (n = 34). We could not quantify cause of death for fledglings because it is difficult to attribute mortality to predation versus scavenging/decomposition after starvation or exposure when tracking every 3-5 days. Very few studies have investigated fledgling survival in agricultural areas. Survival of fledgling White-throated Robins (*Turdis assimilis*) in Costa Rica was lower on agricultural coffee plantations compared to pastures (Cohen and Lindell, 2004). Often the highest mortality experienced by an individual after fledging is during the first three weeks after leaving the nest when mobility and experience is limited (Cox et al., 2014) and thus should be a point of focus for research on the effects of habitat quality because it is a life stage where populations may be highly impacted (Faaborg et al., 2010). Studying fledgling survival is important because it puts an upper-limit on first year survival estimates and gives us a better understanding of bird population trends in relation to natal habitats (Cox et al., 2014).

On agricultural sites, we observed that fledglings dispersed into the crop fields and did not stay in the grassy laneways or margins where the nest was located. We expect that there is less insect food for the fledglings if they disperse into the crop fields compared to staying in the margins (Denys and Tscharntke, 2002), but this may not be an issue as the parents will continue feeding them and supplement their diet (Wheelwright et al., 2003). Some studies have shown that plant height, species composition and presence of exotic species in grasslands can strongly influence the breeding success (e.g., Lloyd and Martin, 2005) and fledgling survival (e.g., Fisher and Davis, 2011) of grassland birds. In an agricultural landscape of Nebraska and Iowa, Dickcissel (*Spiza Americana*) fledgling survival was 33 % but there was no relationship to field habitat (plant composition, density and height), however, fledglings dispersed into crop fields more than would be expected based on the surrounding landscape composition (Berkeley et al., 2007). Further radio-tracking of Savannah Sparrow fledglings while they are still dependent on their parents is needed to better understand if dispersing into crop fields is beneficial or detrimental to their immediate or long-term survival.

Clutch size, Brood size, Nestling Body Condition, and Arthropod Abundance

Lower productivity of nests that escape predation can be driven by low food availability and result in poor nestling condition. Tree Swallows in Southern Quebec experienced reduced clutch size and nesting success with increasing agricultural intensity presumably due to insect availability rather than nest predation (Ghilain and Bélisle, 2008). European Starlings (*Sturnus vulgaris*) in Finland experienced lower nesting success on monocultures than mixed farming/pastures due to nestling starvation (Tiainen et al., 1989). However, in this study, with failed nests removed, the clutch size, brood size and number of fledglings per nest was not different between the two site types. This indicates that Savannah Sparrow parents apparently do not face food limitations in agriculturally intensive areas. This result is consistent with many species in Europe, for which clutch size was not impacted by agricultural intensification for European Starlings (Tiainen et al., 1989), Corn Buntings (Brickle et al., 2000), Lapwings (Galbraith, 1988), or Skylarks (Kuiper et al., 2015). Future studies could focus on parental feeding behaviour (e.g. Stanton et al. 2016) to directly measure foraging effort and distance as well as delivery rates and quantities to nestlings.

Also, contrary to the prediction, nestling body condition was not significantly different between nestlings from agricultural sites compared to the non-agricultural sites. Many studies have demonstrated that insect abundance decreases with increasing agricultural intensity (e.g., Rioux Paquette et al., 2013; Geiger et al., 2010) so it was predicted that nestling body mass would decrease in intensive agriculture. However, in this study total arthropod biomass was not significantly different between agricultural and non-agricultural sites and did not predict nestling body condition. Certain orders of insects and arachnids were different between the two types of sites (Table 3) and thus future research could investigate nutritional quality and specific diet of Savannah Sparrow nestlings between the two habitat types (e.g., Brickle et al., 2000).

There have been only a few studies to date examining nestling body mass in relation to agricultural intensification and these have had conflicting results. In the UK, agricultural habitat variables (e.g., crop type and availability of natural margins) had no effect on the nestling body mass of Skylarks, Yellowhammers and Chaffinches (Bradbury et al., 2003). However, the amount of pesticides used in the breeding habitat did influence nestling body condition of Skylarks, Yellowhammers and Corn Buntings through a reduction in chick-food abundance (Morris et al., 2005; Boatman et al., 2004). Nestling body mass significantly decreased with increasing agricultural intensity for Corn Buntings in Britain (Brickle et al., 2000), Skylarks in the Netherlands (Kuiper et al., 2015), and Barn owl nestlings in Switzerland (Almasi et al., 2015). Granivorous birds such as Linnets showed increased nestling body mass with closer proximity to rape-seed fields which is their primary food source (Bradbury et al., 2003). It is possible for nestling body mass to not be impacted from low food supply in the local habitat when the parental effort is increased to sustain nestling growth (Lee et al., 2016; Tremblay et al., 2005).

Early nutritional conditions can have a great impact on birds later in their life (Searcy et al., 2004; Metcalfe and Monaghan, 2001) and if nestling body mass was impacted by agricultural intensification then offspring could also be negatively impacted later in their life (Lindström, 1999). However, in this study, Savannah Sparrow nestling body condition was not negatively impacted by being reared in intensive agriculture and irrespective of habitat, did not predict fledgling survival. There have been very few studies investigating the survival and dispersal of juvenile songbirds prior to fall migration because once they leave their parents territory they are very difficult to track. A new monitoring system, the Motus wildlife tracking system is the perfect solution to fill the knowledge gap (Taylor et al., 2017). Recent research using the Motus Wildlife Tracking System in Eastern Canada, has found that juvenile Ipswich Sparrows (*Passerculus sandwichensis princeps*), a sub-species of Savannah Sparrows, leave for fall migration earlier than adults, and take different migratory routes (Crysler et al., 2016). Juvenile Savannah Sparrows from Kent Island in New Brunswick, were found to be less efficient in their migratory flights (Mitchell et al., 2015), and leave earlier for fall migration than compared to adult birds (Mitchell et al., 2012). By utilizing the dense array of Motus radio towers in SW Ontario, juvenile pre-migration movements and the timing of fall migration can be studied to understand how these important life stages are affected by agricultural intensification. This was the original goal of this study (in 2016 nestlings were tagged with Nanotags for detection by Motus) but in 2017 theses custom tags could not be produced by the manufacturer.

Adult Body Condition and Habitat Selection

Very few studies have examined adult body mass in intensive agriculture, and in this study neither adult males nor females had lower body condition on agricultural sites. The body mass of female Tree Swallows in Quebec was not correlated with agricultural intensification (Rioux Paquette et al., 2014) and female body mass was found to influence the trade-off between clutch size and egg mass, where lighter females lay smaller eggs when they have larger clutches across an agricultural gradient (Pellerin et al., 2016). Adult body mass and condition can also have a strong effect on nesting success in songbirds (e.g., Rioux Paquette et al., 2014) and parental quality can greatly affect the developmental conditions of their offspring (van de Pol et al., 2006a). Studying the relationship between habitat quality and individual bird condition is important in understanding the drivers of population declines, as habitat quality is not only important for early developmental conditions but also towards the overall breeding success of songbirds (Przybylo et al., 2001).

Occupancy of habitats can be an indicator of habitat quality (Sergio and Newton, 2003), although in human-altered landscapes birds often select poor quality habitat for their breeding grounds and fall into ecological traps (Hollander et al., 2011; Batten, 2004). In the first year of the study there were both agricultural and non-agricultural sites without breeding pairs of Savannah Sparrows. Farms without Savannah Sparrows were to be expected because bird population abundances decrease with increasing agricultural intensity (e.g., Koleček et al., 2015; Hill et al., 2014) but it was surprising to find many non-agricultural sites vacant of breeding pairs that appeared to be good habitat (4 of 10 sites) given that agricultural sites within 5 km had breeding pairs present. For agricultural sites, it appeared that Savannah Sparrows chose farmland that had open grassy laneways and field margins (Marshall and Moonen, 2002) without large trees in between crops, away from the main roads and buildings, and they were not present on farms without grassy laneways. This pattern fit with other studies that found that Savannah Sparrows avoided nesting near edges and preferred open habitat (Keyel et al., 2013). Savannah Sparrows are declining more rapidly in Ontario compared to the rest of North America (Sauer et al., 2017) which may explain why suitable habitat is unoccupied by breeding pairs. It is possible with the significant decrease in breeding success and reduced fledgling survival observed in this study that grassy laneways and margins in intensive agricultural could be an ecological trap for grassland birds (Batten, 2004). To investigate the possibility of an ecological trap, future research should investigate if Savannah Sparrows are preferentially or equally choosing these sites over non-agricultural sites by measuring site preference (e.g., arrival dates and age class distribution) and fitness of adult individuals (survival and reproductive success) (Robertson and Hutto, 2006).

Conclusion

Although agricultural habitats are often vastly different from natural grasslands, previous studies on grassland birds have provided very mixed results on whether individual breeding birds and their offspring are negatively impacted by breeding in agricultural habitats. The answer is critical for understanding the mechanisms through which agricultural intensification contributes to population declines on large geographic scales. For Savannah Sparrows in this study, where we compared two extremes in habitat, we nevertheless found mixed results and overall little evidence of a strong negative impact of agricultural intensification on breeding birds. Nest predation was higher in agricultural sites in only one of the two years, fledgling survival was not significantly different, and no differences were found in body condition of parents or young, arthropod abundance, or productivity from successful nests. The logistical challenges of assessing impacts on breeding pairs across many study sites, scattered over a large study area, partly explains the insufficiency of such studies in the literature. In addition, our nesting success results indicate that a long-term study is needed to determine whether nest predation is consistently higher in agricultural sites and what the long-term impact of this would be on regional population declines. It is critical to study grassland birds throughout their different life stages (i.e., nesting success, fledgling survival, migration survival) to understand where they are the most heavily impacted by agricultural intensification. This knowledge in turn can be used to focus conservation efforts (Faaborg et al., 2010) and inform how to balance grassland bird conservation with efficient agricultural practices (Kleijn et al., 2011; Firbank, 2005). At present, it would be premature to consider agriculturally intensive sites as ecological traps or population sinks and the possibility remains that these sites may provide adequate habitat to Savannah Sparrows at least in some years.

TABLES

Table 1: Breeding productivity for nests compared between agricultural sites and non-agricultural sites. Data were not normally distributed ($p < 0.001$) and site differences were tested using Mann-Whitney U test for each year and 2016-2017 combined. Failed nests were not included for the brood size (number of nestlings hatched) and number of fledglings per nest so as to better understand potential food-related constraints in different habitats.

	Year	Site Type	Mean ± SD	Median	n	U	p
Clutch size	2016	AG	4.00 ± 0.94	4.0	10	122.5	0.766
		Non-AG	4.00 ± 0.80	4.0	26		
	2017	AG	4.21 ± 1.06	4.0	24	358.0	0.385
		Non-AG	4.12 ± 0.73	4.0	34		
	All	AG	4.15 ± 1.02	4.0	34	902.5	0.307
		Non-AG	4.07 ± 0.76	4.0	60		
Brood size	2016	AG	3.57 ± 0.79	4.0	7	56.5	0.678
		Non-AG	3.33 ± 1.24	3.5	18		
	2017	AG	3.90 ± 0.99	4.0	10	110.5	0.380
		Non-AG	3.56 ± 1.05	4.0	27		
	All	AG	3.76 ± 0.90	4.0	17	328.5	0.371
		Non-AG	3.47 ± 1.12	4.0	45		
Fledglings/nest	2016	AG	3.25 ± 0.96	3.5	4	18.0	0.582
		Non-AG	2.91 ± 1.04	3.0	11		
	2017	AG	3.80 ± 0.45	4.0	5	47.5	0.836
		Non-AG	3.72 ± 1.07	4.0	18		
	All	AG	3.56 ± 0.73	4.0	9	125.5	0.866
		Non-AG	3.41 ± 1.12	4.0	30		

Table 2: Mean (± standard deviation) observed, predicted (tarsus length*0.664 + 1.0485) and residual (observed-predicted) body mass and tarsus length of nestlings for all 7-day old nestlings measured during the study (n = 19 AG, 62 non-AG), females (n = 9 AG, 19 non-AG), and males (n = 7 AG, 32 non-AG), compared between agricultural and non-agricultural sites using independent samples t-tests.

	Sex	**Agriculture**	**Non-AG**	**df**	**t**	**p**
Observed (g)	All	13.93 ± 0.96	14.23 ± 1.11	79	-1.075	0.286
	Male	14.83 ± 0.46	14.72 ± 1.03	22	0.436	0.667
	Female	13.43 ± 0.87	13.72 ± 0.73	26	-0.909	0.372
Predicted (g)	All	14.07 ± 0.43	14.19 ± 0.49	79	-0.972	0.334
	Male	14.37 ± 0.36	14.38 ± 0.46	37	-0.052	0.958
	Female	13.93 ± 0.42	13.87 ± 0.34	26	0.376	0.710
Residual	All	-0.14 ± 0.76	0.04 ± 1.02	79	-0.714	0.477
	Male	0.46 ± 0.52	0.34 ± 1.09	37	0.281	0.780
	Female	-0.50 ± 0.72	-0.16 ± 0.72	26	0.983	0.250
Tarsus Length (mm)	All	19.6 ± 0.6	19.8 ± 0.7	79	-0.972	0.334
	Male	20.1 ± 0.5	20.1 ± 0.7	37	-0.052	0.958
	female	19.4 ± 0.6	19.3 ± 0.5	26	0.376	0.710

Table 3: Arthropod abundances (dry biomass, digital scale 0.0001 g) sorted by order between agricultural and non-agricultural sites for all samples collected. Data were not normally distributed ($p < 0.001$) and tested between site types using Mann-Whitney U tests. 50 sweeps/sample, n = 14 AG, 39 non-AG samples. Bolded p-values are significant ($p < 0.05$).

Order	Site Type	Mean ± SD (g)	Median (g)	U	p
Diptera	AG	0.201 ± 0.132	0.197	116.0	**0.002**
	Non-AG	0.089 ± 0.098	0.056		
Lepidoptera: Adult	AG	0.010 ± 0.012	0.005	272.5	0.992
	Non-AG	0.013 ± 0.018	0.009		
Lepidoptera: Larva	AG	0.020 ± 0.031	0.005	336.5	0.196
	Non-AG	0.038 ± 0.072	0.016		
Homoptera	AG	0.137 ± 0.143	0.106	400.0	**0.010**
	Non-AG	0.424 ± 0.409	0.293		
Hymenoptera	AG	0.033 ± 0.055	0.015	280.0	0.888
	Non-AG	0.026 ± 0.038	0.017		
Hemiptera	AG	0.330 ± 0.275	0.224	202.0	0.152
	Non-AG	0.217 ± 0.214	0.153		
Coleoptera: Adult	AG	0.086 ± 0.077	0.071	163.0	**0.026**
	Non-AG	0.054 ± 0.081	0.024		
Coleoptera: Larva	AG	0.007 ± 0.012	0.000	476.0	**0.000**
	Non-AG	0.344 ± 0.789	0.088		
Orthoptera	AG	0.102 ± 0.128	0.059	171.0	**0.037**
	Non-AG	0.036 ± 0.064	0.007		
Odonata	AG	0.006 ± 0.013	0.000	239.0	0.333
	Non-AG	0.003 ± 0.012	0.000		
Arachnida	AG	0.022 ± 0.016	0.020	394.0	**0.015**
	Non-AG	0.041 ± 0.031	0.036		
Total	AG	0.996 ± 0.450	1.052	318.0	0.364
	Non-AG	1.311 ± 1.037	1.224		

FIGURES

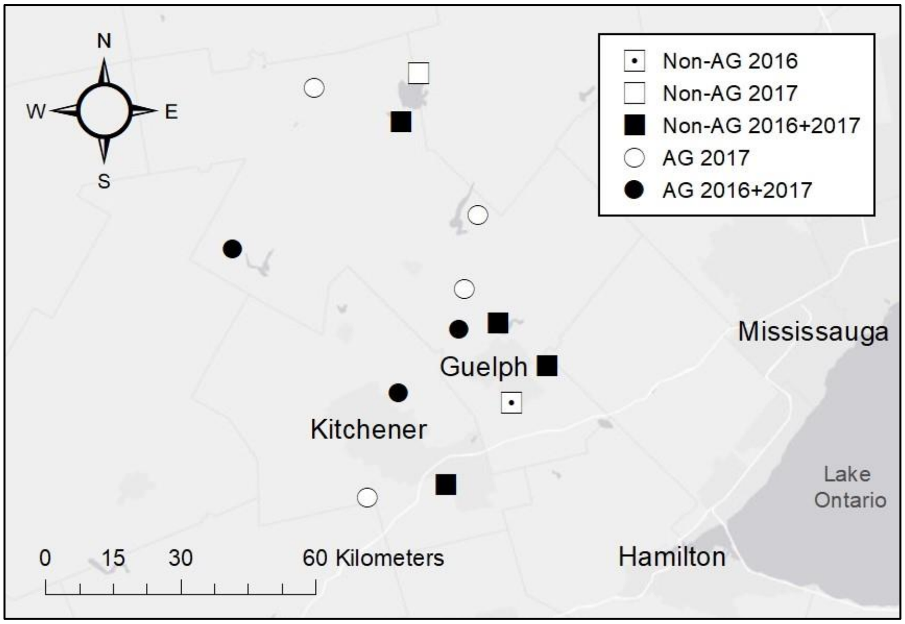

Figure 1: Study sites containing breeding pairs of Savannah Sparrows in Southwestern Ontario for agricultural sites (circles, n = 7) and non-agricultural sites (squares, n = 6). Shading of symbols indicates year of study. Map created using ArcGIS v.10.4.1.

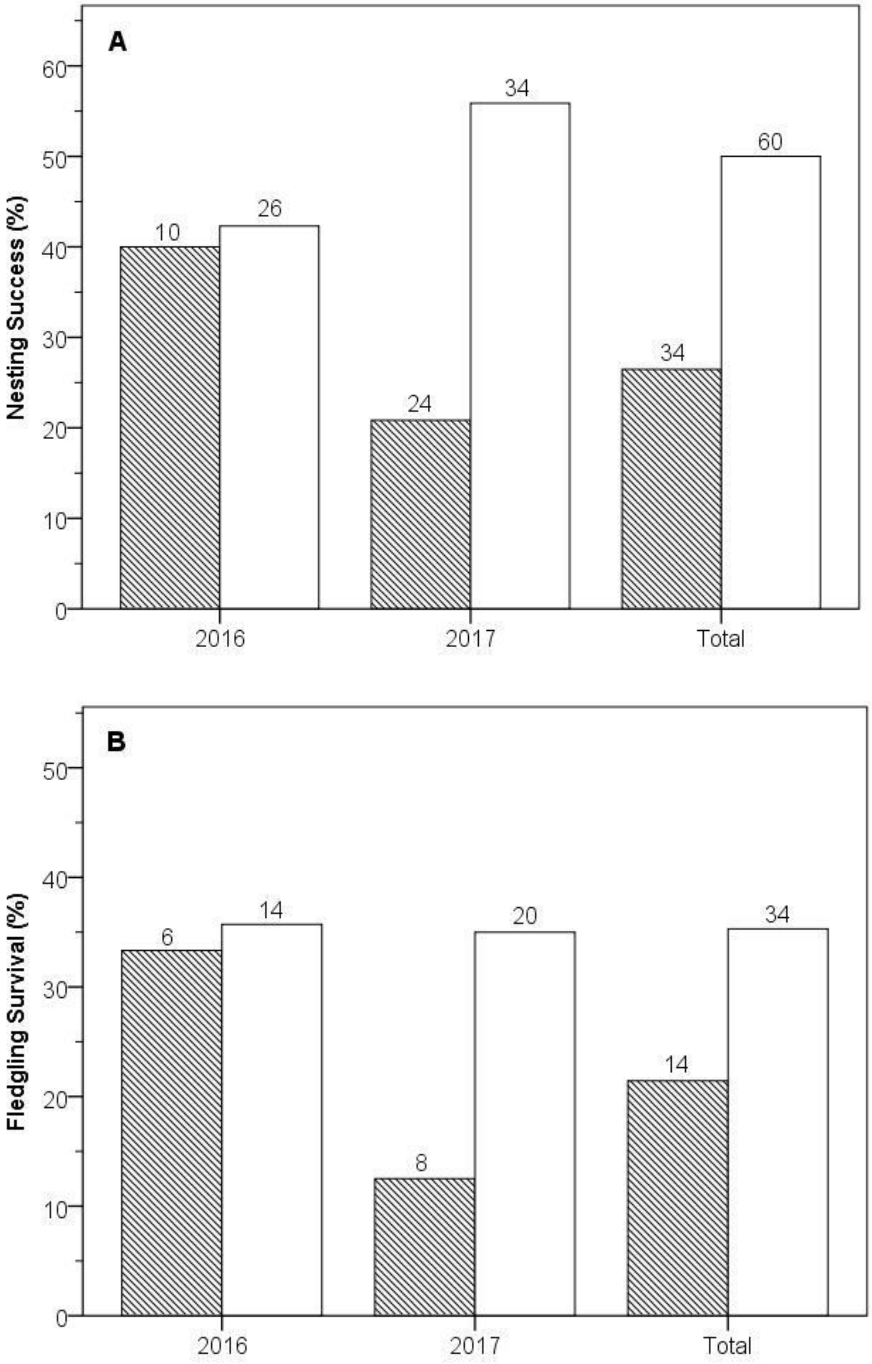

Figure 2: (A) Proportion of fledged nests (nesting success) and (B) fledgling survival during the 3-week fledgling period on agricultural (hatched bars) and non-agricultural (open bars) sites between years and total combined. Fledglings missing before 10 days post fledging presumed dead. Sample size displayed above bars.

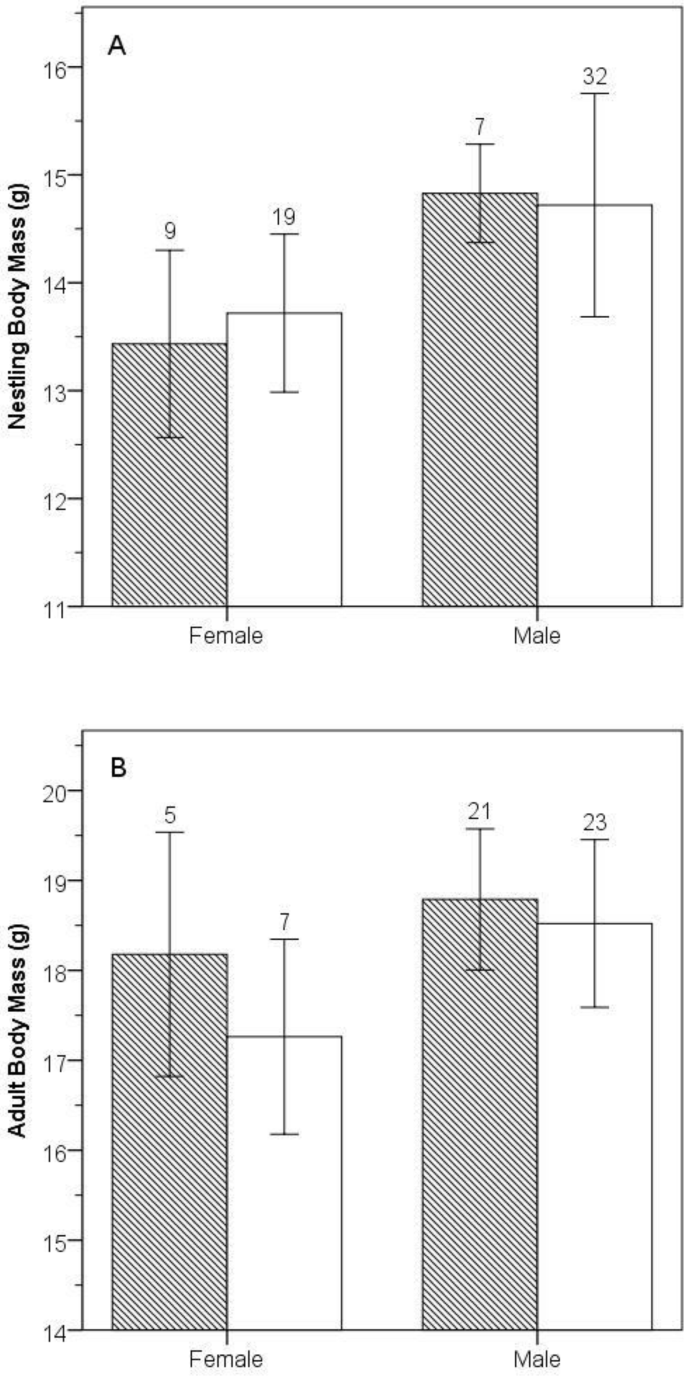

Figure 3: Mean (+/- SD) body mass of (A) 7-day old nestlings and (B) adults, between sex and site types: agriculture (hatched bars) and non-agricultural (open bars). Samples sizes displayed above bars. Sex of nestlings determined through DNA analysis of blood, and sex of adults determined by presence of physical breeding characteristics.

SUPPORTING INFORMATION

Table S1: Landscape proportions around a 50-m radius of the nests per site type, calculated using ArcGIS v.10.4.1. Urban is any human-made object such as roads or buildings. Data were not normally distributed ($p < 0.01$), and were compared using Mann-Whitney U tests. Bolded p-values are significant ($p < 0.05$).

Landscape	Site type	n	Mean ± SD	Minimum	Maximum	U	p
Arable/Crop	AG	34	0.847 ± 0.054	0.759	0.934	0.000	**0.000**
	Non-AG	60	0.003 ± 0.014	0.000	0.088		
Grass	AG	34	0.137 ± 0.052	0.048	0.242	2040	**0.000**
	Non-AG	60	0.953 ± 0.084	0.698	1.000		
Shrub	AG	34	0.006 ± 0.022	0.000	0.093	1226	**0.037**
	Non-AG	60	0.030 ± 0.063	0.000	0.292		
Urban	AG	34	0.001 ± 0.006	0.000	0.030	1078	0.371
	Non-AG	60	0.005 ± 0.022	0.000	0.110		

References:

Almasi, B., Béziers, P., Roulin, A., Jenni, L., 2015. Agricultural land use and human presence around breeding sites increase stress-hormone levels and decrease body mass in barn owl nestlings. Oecologia. 179, 89-101.

Attwood, S.J., Maron, M., House, A.P.N., Zammit, C., 2008. Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management? Glob. Ecol. Biogeogr. 17(5), 585-599.

Bas, Y., Renard, M., Jiguet, F., 2009. Nesting strategy predicts farmland bird response to agricultural intensity. Agric. Ecosys. Environ. 134, 143-147.

Batten, J., 2004. When good animals love bad habitats: Ecological traps and the conservation of animal populations. Conserv. Biol. 18(6), 1482-1491.

Beja, P., Schindler, S., Santana, J., Porto, M., Morgado, R., Moreira, F., Pita, R., Mira, A., Reino, L., 2014. Predators and livestock reduce bird nest survival in intensive Mediterranean farmland. Eur. J. Wildl. Res. 60(2), 249-258.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol. and Evol. 18(4), 182-188.

Berkeley, L.I., McCarty, J.P., Wolfenbarger, L.L., 2007. Postfledging survival and movement in Dickcissels (Spiza Americana): implications for habitat management and conservation. The Auk. 124(2), 396-409.

Boatman, N.D., Brickle, N.W., Hart, J.D., Milsom, T.P., Morris, A.J., Murray, A.W.A., Murray, K.A., Robertson, P.A., 2004. Evidence for the indirect effects of pesticides on farmland birds. Ibis. 146, 131-143.

Bradbury, R.B., Wilson, J.D., Moorcroft, D., Morris, A.J., Perkins, A.J., 2003. Habitat and weather are weak correlates of nestling condition and growth rates of four UK farmland passerines. Ibis. 145, 295-306.

Brickle, N.W., Harper, D.C.G., Aebischer, N.J., Cockayne, S.H., 2000. Effects of agricultural intensification on the breeding success of corn buntings *Miliaria calandra*. J. Appl. Ecol. 37, 742-755.

Casas, F., Viñuela, J., 2010. Agricultural practices or game management: which is the key to improve red-legged partridge nesting success in agricultural landscapes? Environ. Conserv. 37(2), 177-186.

Chadbourne, K.A., Anderson, J.T., 2015. Invertebrate biomass in mowed and unmowed fields of Canaan Valley. Canaan Valley Environs Southeastern Naturalist. 14(Special Issue 7), 252-260.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C., Shrubb, M., 2000. Changes in the abundance of farmland birds in relation to the timing on agricultural intensification in England and Wales. J. Appl. Ecol. 37, 771-788.

Cohen, E.B., Lindell, C.A., 2004. Survival, habitat use, and movements of fledgling White-throated Robins (*Turdus assimilis*) in a Costa Rican agricultural landscape. The Auk. 121(2), 404-414.

Cox, A.S., Kesler, D.C., 2012. Reevaluating the cost of natal dispersal: Post-fledgling surivival of Red-bellied Woodpeckers. The Condor. 114(2), 341-347.

Cox, W.A., Thompson III, F.R., Cox, A.S., Faaborg, J., 2014. Post-fledging survival in passerine birds and the value of post-fledging studies to conservation. J. Wildl. Manage. 78(2), 183-193.

Crysler, Z.J., Ronconi, R.A., Taylor, P.D., 2016. Differential fall migratory routes of adult and juvenile Ipswich Sparrows (Passerculus sandwichensis princeps). Mov. Ecol. 4(1), 3-10.

Denys, C., Tscharntke, T., 2002. Plant-insect communities and predator-prey ratios in field margin strips, adjacent crop fields, and fallows. Oecologia. 130, 315-324.

Dixon, C.L., 1978. Breeding biology of the Savannah Sparrow on Kent Island. The Auk. 95(2), 235-246.

Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proc. R. Soc. B. 268, 25-29.

Evans, K.L., 2004. The potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis. 146, 1-13.

Faaborg, J., Holmes, R.T., Anders, A.D., Bildstein, K.L., Dugger, K.M., Gauthreaux, S.A., Heglund, P., Hobson, K.A., Jahn, A.E., Johnson, D.H., Latta, S.C., 2010. Conserving migratory land birds in the New World: do we know enough? Ecol. Appl. 20(2), 398-418.

Firbank, L.G., 2005. Striking a balance between agricultural production and biodiversity. Annals Appl. Biol. 146, 163-175.

Fisher, R.J., Davis, S.K., 2011. Post-fledging dispersal, habitat use, and survival of Sprague's pipits: Are planted grasslands a good substitute for native? Biol. Conserv. 144(1), 263-271.

Galbraith, H., 1988. Effects of agriculture on the breeding ecology of lapwings *Vanellus vanellus*. J. Appl. Ecol. 25(2), 487-503.

Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tscharntke, T., Winqvist, C., Eggers, S., Bommarco, R., Part, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Onate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hanke, S., Fischer, C., Goedhart, P.W., Inchausti, P., 2010. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic. Appl. Ecol. 11, 97-105.

Ghilain, A., Bélisle, M., 2008. Breeding success of Tree Swallows along a gradient of agricultural intensification. Ecol. Appl. 18(5), 1140-1154.

Gil-Tena, A., De Cáceres, M., Ernoult, A., Butet, A., Brotons, L., Burel, F., 2015. Agricultural landscape composition as a driver of farmland bird diversity in Brittany (NW France). Agric. Ecosys. Environ. 205, 79-89.

Grafen, A., 1988. On the uses of data on lifetime reproductive success, in: Clutton-Brock, T., Reproductive success. University of Chicago Press, Chicago, IL: pp. 454-471

Hill, J.M., Egan, J.F., Stauffer, G.E., Diefenbach, D.R., 2014. Habitat availability is a more plausible explanation than insecticide acute toxicity for US grassland bird species declines. PLoS ONE. 9(5), e98064.

Hollander, F.A., Van Dyck, H., San Martin, G., Titeux, N., 2011. Maladaptive habitat selection of a migratory passerine bird in a human-modified landscape. PLoS ONE. 6(9), e25703.

Jeliazkov, A., Mimet, A., Chargé, R., Jiguet, F., Devictor, V., Chiron, F., 2016. Impacts of agricultural intensification on bird communities: New insights from a multi-facet approach of biodiversity. Agric. Ecosys. Environ. 216, 9-22.

Johnson, M.D., 2007., Measuring habitat quality: A review. The Condor. 109(3), 489-504.

Kentie, R., Both, C., Hooijmeijer, J.C., Piersma, T., 2015. Management of modern agricultural landscapes increases nest predation rates in Black-tailed Godwits Limosa limosa. Ibis. 157(3), 614-625.

Keyel, A.C., Strong, A.M., Perlut, N.G., Reed, J. M., 2013. Evaluating the roles of visual openness and edge effects on nest-site selection and reproductive success in grassland birds. The Auk. 130(1), 161-170.

Kleijn, D., Rundlöf, M., Scheper, J., Smith, H.G., Tscharntke, T., 2011. Does conservation on farmland contribute to halting the biodiversity decline? Trends Ecol. Evol. 26(9), 474-481.

Koleček, J., Reif, J., Weidinger, K., 2015. The abundance of a farmland specialist bird, the skylark, in three European regions with contrasting agricultural management. Agric. Ecosys. Environ. 212, 30-37.

Krause, E.T., Honarmand, M., Wetzel, J. Naguib, M., 2009. Early fasting is long lasting: Differences in early nutritional conditions reappear under stressful conditions in adult female zebra finches. PloS ONE. 4(3), e5015.

Kuiper, M.W., Ottens, H.J., van Ruijven, J., Koks, B.J., de Snoo, G.R., Berendse, F., 2015. Effects of breeding habitat and field margins on the reproductive performance of Skylarks (*Alauda arvensis*) on intensive farmland. J. Ornithol. 156, 557-568.

Lee, J.K., Jang, W., Chung, O.S., Lee, W.S., 2016. The relationships between prey size, nestling age, provisioning rate, and elevation in the Varied Tit Parus varius. Ornithol. Sci. 15(1), 29-36.

Lindström, J., 1999. Early development and fitness in birds and mammals. Trends Ecol. Evol. 14(9), 343-348.

Lloyd, J.D., Martin, T.E., 2005. Reproductive success of Chestnut-collared Longspurs in native and exotic grassland. The Condor. 107(2), 363-374.

Marshall, E.J.P., Moonen, A.C., 2002. Field margins in northern Europe: their functions and interactions with agriculture. Agric. Ecosys. Envion. 89, 5-21.

Matson, P.A., Parton, W.J., Power, A.G., Swift, M.J., 1997. Agriculture intensification and ecosystem properties. Science. 277, 504-509.

Metcalfe, N.B., Monaghan, P., 2001. Compensation for a bad start: grow now, pay later? Trends Ecol. Evol. 16(4), 254-260.

Meunier, M., Bédard, J., 1984. Nestling foods of the savannah sparrow. Can. J. Zool. 62, 23-27.

Mitchell, G.W., Guglielmo, C.G., Wheelwright, N.T., Freeman-Gallant, C.R., Norris, D.R., 2011. Early life events carry over to influence pre-migratory condition in a free-living songbird. PLoS ONE. 6(12), e228838.

Mitchell, G.W., Newman, A.E.M., Wikelski, M, Norris, D.R., 2012. Timing of breeding carries over to influence migratory departure in a songbird: an automated radiotracking study. J. Anim. Ecol. 81, 1024-1033.

Mitchell, G.W., Woodworth, B.K., Taylor, P.D., Norris, D.R., 2015. Automated telemetry reveals age specific differences in flight duration and speed are driven by wind conditions in a migratory songbird. Mov. Ecol. 3(1), 19-31.

Monaghan, P., 2008. Early growth conditions, phenotypic development an environmental change. Philos. Trans. R. Soc. B. 363, 1635-1645.

Morris, A.J., Wilson, J.D., Whittingham, M.J., Bradbury, R.B., 2005. Indirect effects of pesticides on breeding Yellowhammer (*Emberiza citrinella*). Agric. Ecosys. Environ. 106, 1-16.

Mumme, R.L., Bowman, R., Pruett, M.S., Fitzpatrick, J.W., 2015. Natal territory size, group size, and body mass affect lifetime fitness in the cooperatively breeding Florida Scrub Jay. The Auk. 132, 634-646.

Newton, I., 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation efforts. Ibis. 146, 579-600.

Norris, D.R, Marra, P.P., 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. The Condor. 109: 535-547.

Pérez, J.H., Krause, J.S., Chmura, H.E., Bowman, S., McGuigan, M., Asmus, A.L., Meddle, S.L., Hunt, K.E., Gough, L., Boelman, N.T., Wingfield, J.C., 2016. Nestling growth rates in relation to food abundance and weather in the Arctic. The Auk. 133(2), 261-272.

Pellerin, S., Rioux Paquette, S., Pelletier, F. Garant, D., Bélisle, M., 2016. The trade-off between clutch size and egg mass in tree swallows Tachycineta bicolor is modulated by female body mass. J. Avian. Biol. 47, 500-507.

Perlut, N.G., Strong, A.M., 2011. Grassland birds and rotational-grazing in the Northeast: Breeding ecology, survival and management opportunities. J. Wildl. Manage. 75(3): 715-720.

Perlut, N.G., Strong, A.M., Donovan, T.M., Buckley, N.J., 2008a. Regional population viability of grassland songbirds: Effects of agricultural management. Biol. Conserv. 141, 3139-3151.

Perlut, N.G., Strong, A.M., Donovan, T.M., Buckley, N.J., 2008b. Grassland songbird survival and recruitment in agricultural landscapes: implications for source-sink demography. Ecology. 89(7), 1941-1952.

Perlut, N.G., Strong, A.M., Donovan, T.M., Buckley, N.J., 2006. Grassland songbirds in a dynamic management landscape: behavioral responses and management strategies. Ecol. Appl. 16(6), 2235-2247.

Przybylo, R., Wiggins, D.A., Merilä, J., 2001. Breeding success in Blue Tits: Good territories or good parents? J. Avian Biol. 32, 214-218.

Quinn, J.E., Awada, T., Trindade, F., Fulginiti, L., Perrin, R., 2017. Combining habitat loss and agricultural intensification improves our understanding of drivers of change in avian abundance in a North American cropland anthrome. Ecol. Evol. 7, 803-814.

Rae L.F., Mitchell, G.W., Mauck, R.A., Guglielmo, C.G., Norris, D.R., 2009. Radio transmitters do not affect the body condition of Savannah Sparrows during the fall premigratory period. J. Field Ornithol. 80(4), 419-426.

Rappole, J.H., Tipton, A.R., 1991. New harness design for attachment of radio transmitter to small passerines. J. Field Ornithol. 62(3), 335-337.

Rioux Paquette, S., Garant, D., Pelletier, F., Bélisle, M., 2013. Seasonal patterns in tree swallow prey (Diptera) abundance are affected by agricultural intensification. Ecol. Appl. 23(1), 122-133.

Rioux Paquette, S., Pelletier, F., Garant, D., Bélisle, M., 2014. Severe recent decrease of adult body mass in a declining insectivorous bird population. Proceeding of the Royal Society B. 281, 20140649.

Rising, J.D., Somers, K.M., 1989. The measurement of overall body size in birds. The Auk. 106, 666-674.

Robertson, B.A., Hutto, R.L., 2006. A framework for understanding ecological traps and an evaluation of existing evidence. Ecology. 87(5), 1075-1085.

Robillard, A., Garant, D., Bélisle, M., 2013. The swallow and the sparrow: How agricultural intensification affects abundance, nest site selection and competitive interactions. Landsc. Ecol. 28, 201-215.

Sauer, J.R., Niven, J.K., Hines, J.E., Ziolkowski Jr., D.J., Pardieck, K.L., Fallon, J.E., Link, W.A., 2017. The North American Breeding Bird Survey, Results and Analysis 1966 - 2015. Version 2.07.2017 USGS Patuxent Wildlife Research Center, Laurel, MD

Searcy, W.A., Peters, S., Nowicki, S., 2004. Effects of early nutrition on growth rate and adult size in Song Sparrows *Melospiza melodia*. J. Avian. Biol. 35, 269-279.

Sergio, F., Newton, I.A.N., 2003. Occupancy as a measure of territory quality. J. Anim. Ecol. 72(5), 857-865.

Stanton, R.L., Morrissey, C.A., Clark, R.G., 2016. Tree Swallow (*Tachycineta bicolor*) foraging responses to agricultural land use and abundance of insect prey. Can. J. Zool. 94, 637-642.

Taylor, P., Crewe, T., Mackenzie, S., Lepage, D., Aubry, Y., Crysler, Z., Finney, G., Francis, C., Guglielmo, C., Hamilton, D., Holberton, R., 2017. The Motus Wildlife Tracking System: a collaborative research network to enhance the understanding of wildlife movement. Avian Conserv. Ecol. 12(1), 8.

Teglhøj, P.G., 2017. A comparative study of insect abundance and reproductive success of barn swallows *Hirundo rustica* in two urban habitats. J. Avian Biol. 48, 846-853.

Tiainen, J., Hanski, I.K., Pakkala, T., Piiroinen, J., Yrjölä, R., 1989. Clutch size, nestling growth and nestling mortality of the starling *Sturnus vulgaris* in south Finnish agroenvironments. Ornis Fennica. 66(1), 41-48.

Tilman, D., Clark, M., Williams, D.R., Kimmel, K., Polasky, S., Packer, C., 2017. Future threats to biodiversity and pathways to their prevention. Nature. 546(7656), 73-81.

Tremblay, I., Thomas, D., Blondel, J., Perret, P., Lambrechts, M.M., 2005. The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican Blue Tits *Parus caeruleus*. Ibis. 147(1), 17-24.

van de Pol, M., Bakker, T., Saaltink, D. Verhulst, S., 2006a. Rearing conditions determine offspring survival independent of egg quality: a cross-foster experiment with Oystercatchers *Haematopus ostralegus*. Ibis. 148, 203-210.

van de Pol, M., Bruinzeel, L.W., Heg, D., van der Jeugd, H.P., Verhulst, S., 2006b. A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of Oystercatchers (*Haematopus ostralegus*). J. Anim. Ecol. 75, 616-626.

Vickery, P.D., Tubaro, P.L., Cardoasa da Silva, J.M., Peterjohn, B.G., Herkert, J.R., Cavalcanti, R.B., 1999. Conservation of Grassland Birds in the Western Hemisphere. Stud. Avian Biol. 19, 2-26.

Wheelwright, N.T., Graff, E.S., Norris, D.R., 2012. Relative consistency in size, shape and colouration of Savannah Sparrow eggs within and between breeding seasons. The Condor. 114(2), 412-420.

Wheelwright, N.T., Mauck, R.A., 1998. Philopatry, natal dispersal and inbreeding avoidance in an island population of Savannah Sparrows. Ecology. 79(3), 755-767.

Wheelwright, N.T., Rising, J.D., 2008. Savannah Sparrow, *Passerculus sandwichensis*, in: Rodewald, P.G. (eds), The Birds of North America. Version 2.0. Cornell Lab of Ornithology, Ithaca, New York, USA. 45, pp. 1-28.

Wheelwright, N.T., Schultz, C.B., 1994. Age and reproduction in Savannah Sparrows and Tree Swallows. J. Appl. Ecol. 63, 686-702.

Wheelwright, N.T., Tice, K.A., Freeman-Gallant, C.R., 2003. Postfledging parental care in Savannah Sparrows: Sex, size, and survival. Anim. Behav. 65, 435-443.

Whittingham, M.J., Evans, K.L., 2004. The effects of habitat structure on predation risk of birds in agricultural landscapes. Ibis. 146, 210-220.

Winter, M., Hawks, S.E., Shaffer, J.A., Johnson, D.H., 2003. Guidelines for finding nests of passerine birds in tallgrass prairie. The Prairie Naturalist. 35(3), 197-211.

Winter, M., Johnson, D.H., Shaffer, J.A., 2005. Variability in vegetation effects on density and nesting success of grassland birds. J. Wildl. Manage. 69(1), 185-197.