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The impacts of agriculture on an obligate grassland bird of North America

Heidi E.J. van Vliet[a,*], Bridget J.M. Stutchbury[a], Amy E.M. Newman[b], D. Ryan Norris[b,c]

[a] Department of Biology, York University, 4700 Keele Street, Toronto, ON, M3J 1L3, Canada
[b] Department of Integrative Biology, University of Guelph, 50 Stone Rd E, Guelph, ON, N1G 2W1, Canada
[c] Nature Conservancy of Canada, 245 Eglington Avenue East, Toronto, ON, M4P 3J1, Canada

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ABSTRACT

Grassland birds are in decline worldwide and one hypothesis for this decline is habitat loss and degradation through agricultural intensification. The purpose of this study is to investigate the impacts of agriculture 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 radio tracked to quantify survival between agricultural and non-agricultural land-use types. The daily survival rate of nests was negatively influenced by intensive agriculture, but fledgling survival was influenced more by the age of the fledgling and year of the study than habitat. No land-use differences were found in the clutch or brood size, arthropod abundance, nor body condition of adults and nestlings. In the second, but not the first, year of the study, nestling corticosterone levels increased between baseline and 30-minute restraint for offspring from non-agricultural sites whereas nestlings from agricultural sites showed no corticosterone response to acute restraint. Our results provide some evidence that agricultural sites compromise nest survival rates and possibly stress response of nestlings, but further research and long-term monitoring is necessary to fully understand the impacts of agriculture on this species.

1. Introduction

Grassland birds have been experiencing sharp declines throughout North America and Europe (Vickery et al., 1999; Hill et al., 2014; Gil-Tena et al., 2015), which is thought to be primarily related to habitat loss and degradation through agricultural intensification (Newton, 2004; Hill et al., 2014; Quinn et al., 2017; Stanton et al., 2018). Agricultural intensification is the conversion of natural areas and small heterogeneous farms to large crop monocultures that are heavily reliant on chemical use (e.g., pesticides and fertilizers) and mechanization (Matson et al., 1997). Arthropod abundance and diversity are greater on natural land and less-intensively managed farms than on lands subject to intensive agriculture (Attwood et al., 2008; Geiger et al., 2010) and, therefore, agricultural sites are expected to be of poor habitat quality for insectivorous birds. Many studies have demonstrated that increasing agricultural intensification is negatively correlated with bird species abundance and diversity (e.g., Chamberlain et al., 2000; Donald et al., 2001; Bas et al., 2009; Geiger et al., 2010) and that heterogeneous landscapes support higher bird species richness than agriculturally-dominated homogeneous landscapes (Benton et al., 2003; Gil-Tena et al., 2015). Breeding success on intensive agriculture can be negatively impacted by destruction of nests from farm machinery (Galbraith, 1988; Bas et al., 2009; Casas and Viñuela, 2010) and an increased predation risk (Brickle et al., 2000; Evans, 2004; Beja et al., 2014; Kentie et al., 2015; Kuiper et al., 2015). Additionally, adults nesting on farms may have to travel farther for food and be away from the nest for longer periods of time (e.g., Stanton et al., 2016), which could result in nestlings begging for food more often, and thus attract predators to the nest (Whittingham and Evans, 2004).

Surprisingly few studies have examined the direct effects of agricultural intensification on nesting productivity or body condition and the results are somewhat conflicting. A study on Corn Buntings (*Miliaria calandra*) in Britain found that food availability while parents fed nestlings was negatively correlated with increasing agricultural intensification, resulting in lower 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 citrinella*) in agricultural areas was not correlated with habitat variables (Bradbury et al., 2003). In contrast, Linnet (*Carduelis cannabina*) appeared to benefit from agriculture (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

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* Corresponding author. Present address: 309-1620 Townsite Road, Nanaimo, BC, V9S1N2, Canada.
E-mail addresses: Heidi.vanvliet@hotmail.ca (H.E.J. van Vliet), bstutch@yorku.ca (B.J.M. Stutchbury), newman01@uoguelph.ca (A.E.M. Newman), rnorris@uoguelph.ca (D.R. Norris).

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agricultural intensity (Ghilain and Bélisle, 2008). Thus, while agricultural intensification has been long thought to be detrimental to avian demographics the empirical evidence on the direct impacts on individual processes is limited and mixed. Early life events have been shown to impact fitness later in life but how agricultural habitat influences this relationship is poorly understood. Nestling body mass has been shown to be correlated with local food abundance (Brickle et al., 2000; Pérez et al., 2016; Teglhøj, 2017) and nestling body mass can carry over to significantly impact fledgling survival (Cox and Kesler, 2012; Cow et al., 2014; Mumme et al., 2015). Few studies have assessed how agricultural intensification impacts nestling condition, and to our knowledge, none have tested its impacts on fledgling survival in grassland birds.

Exposure to stress and subsequently elevated corticosterone (CORT) levels during the early developmental period in vertebrates can impact growth, reproduction and survival (Meylan and Clobert, 2005; Saino et al., 2005; Blas et al., 2007). Early exposure to experimentally elevated CORT in Savannah Sparrow nestlings modifies the hypothalamic-pituitary-adrenal (HPA) axis response to acute stress where, in line with "the ceiling hypothesis", baseline levels of CORT are elevated and thus the magnitude of subsequent increase in plasma corticosterone in response to acute stress is reduced (Pakkala et al., 2016). Food restriction is also known to increase baseline CORT (Pravosudov et al., 2001), and it is possible that nestling songbirds raised in intensive agriculture, where pest management reduces insect availability, also experience food supply limitations (e.g., Geiger et al., 2010). Baseline CORT can be a used as a physiological proxy for exposure to environmental stressors in individuals (Cooke and O'Connor, 2010; Madliger and Love, 2014) and therefore may be useful for investigating the impacts of agricultural intensification on grassland birds.

The Savannah Sparrow (*Passerculus sandwichensis*) is a small (19–20 g; Rising and Somers, 1989) obligate grassland songbird that nests inconspicuously on the ground under the grass (Wheelwright and Rising, 2008) and has experienced significant declines throughout North America (Sauer et al., 2017). Savannah Sparrow is an ideal species for examining potential effects of agriculture because its breeding ecology has been well studied in natural habitats (e.g., Wheelwright and Mauck, 1998; Wheelwright and Rising, 2008; Mitchell et al., 2011) as well as in hayfields and pastures (e.g., Perlut et al., 2006, 2008a, 2008b), but not in intensive agricultural areas (i.e., row crops and monocultures). Adults feed their nestlings arthropods, primarily consisting of Lepidoptera, Hymenoptera, Diptera and Homoptera (Meunier and Bedard, 1984) and thus diet composition and food abundance could be impacted by agricultural practices. There is also no evidence that Savannah Sparrows are negatively affected by wearing radio tags (Rae et al., 2009), which makes them suitable for radio-tracking.

In this study, we investigated the impacts of agricultural intensification on the parents and offspring of the Savannah Sparrow. We test four predictions based on the hypothesis that intensively managed farmland is low quality habitat due to higher predation and lower food supply:

(1) Agricultural sites will have lower daily nest survival probability and lower fledgling survival due to increased predation risk compared to non-agricultural sites.
(2) As a result of poor food supply, successful nests (i.e., those that fledge at least one offspring) on agricultural sites will have lower clutch sizes, brood sizes, and number of fledglings per nest, and lower nestling body condition than at non-agricultural sites.
(3) Baseline plasma corticosterone levels will be elevated in nestlings from agricultural sites due to stress from insect-food supply limitations (Honarmand et al., 2010) but will not have elevated acute stress-induced CORT levels ("ceiling hypothesis;" Pakkala et al., 2016).
(4) Due to lower food supply and/or foraging habitat quality, adults breeding on agricultural sites will have lower body mass and condition compared to adults breeding on non-agricultural sites.

2. Materials and methods

2.1. Study sites

Rather than studying across a gradient of agricultural intensification, we compared the two ends of the land-use gradient to test if there were any differences between the two habitats extremes. Savannah Sparrows were studied on moderately sized intensive agricultural sites (AG) and non-agricultural open/grassland sites (non-AG) in

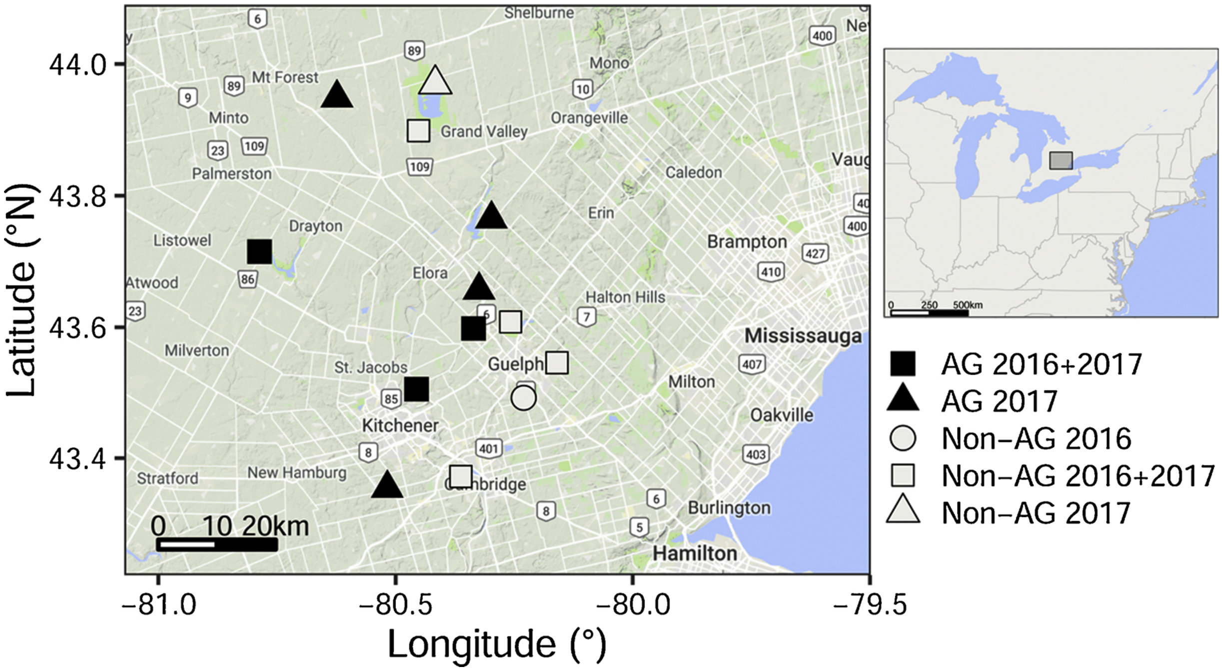

Fig. 1. Map of Study Sites. Location of study sites containing breeding pairs of Savannah Sparrows in Southwestern Ontario for agricultural sites (black symbols, n = 7) and non-agricultural sites (white symbols, n = 6). Shape of symbols represents year of the study when the sites were used. Figure created using R3.4.4 using a Google Maps image.

southwestern Ontario for two consecutive breeding seasons (2016–2017; Fig. 1). The study began in 2016 with 11 AG sites and 10 non-AG sites, and an additional 4 AG sites and 1 non-AG site were added in 2017. The AG sites that had breeding pairs of Savannah Sparrow ($n = 7$) were monocultures of corn, soy or winter wheat, 31–92 ha (50.7 ± 24.4 ha), and were bordered by adjacent farms. The non-AG sites with breeding pairs of Savannah Sparrow ($n = 6$) were open areas covered in grasses and herbaceous plants (e.g. goldenrod), 11–29 ha (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.

Specific vegetation composition within a breeding territory 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., Ghilain and Bélisle, 2008; Gil-Tena et al., 2015; Jeliazkov et al., 2016). To further describe the AG vs. non-AG site types, satellite imagery viewed in ArcMAP (ArcGIS v.10.4.1) was used to characterize nesting habitat within 50-m of each nest location. Land cover was categorized as either arable land (crop), open/grass (any non-agricultural grass or herbaceous plants such as goldenrod), bare ground, urban (e.g., concrete or buildings), shrublands, or, forest.

2.2. Nesting success and nestling body condition

In both years of the study, nest searching began in mid-May and continued until late July when new nests were no longer found. Nest searching took place every 4–5 days at each site and was focused on the grassy margins between crops on AG sites because it did not appear that the Savannah Sparrows were nesting in the crops. This is likely because early in the season there was no vegetation in the crop fields for them to nest in. To find nests, we used three methods described by Winter et al. (2003). First, pairs that were thought to be in the incubation stage were observed until the female returned to the nest, whereupon, after 3–5 min, we would slowly approach the area using long sticks to sweep the top of the grass to flush her off the nest. Similarly, if we observed parents carrying food items we located nests by carefully hand-searching the area where the parents were taking the food. Second, we systematically walked while sweeping a stick over the grass. The third method was haphazard walking while sweeping a stick over the grass. All nests were marked with twigs or grass above the nest, 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 (e.g., walk to and from the nest within 1 min). A nest was considered successful if at least one young fledged the nest. If the nest was empty on a check after eggs had been laid it was assumed to have been depredated, and, if there were cold eggs after incubation had begun it was assumed to have been abandoned. When nestlings hatched (hatch day = 0), we estimated age based on developmental stage (using picture references of known-age nestlings) and returned when they were 7 days old. Measurements of tarsus (calipers, 0.1 mm) and mass (digital scale, 0.01 g) were taken from 7-day old 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 the residual body mass (observed body mass – predicted body mass). Predicted body mass was calculated from the linear regression of mass and tarsus length of 7-day old nestlings (tarsus length*0.669($\pm$ SE = 0.149) + 0.954($\pm$ SE = 2.955)). Focal nestlings were sexed by blotting a sample of their blood taken via brachial venipuncture (26-gauge needle) 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 (checked on the following site visit 1–4 days later; fledging typically occurs 9 days after hatching) it was assumed to have successfully fledged after confirmation from parent alarm calls and radio tracking (see fledgling survival below).

To examine if agricultural intensification was related to the baseline and acute stress-induced levels of corticosterone, blood samples were collected from the 7-day-old nestlings within 3 min of handling and again after 30 min of restraint in a cloth bag. The blood samples were collected (~75 µL) in a heparinized hematocrit capillary tube and transferred immediately to a microcentrifuge tube before being stored on ice in the field. Within 4 h of collection in the field, the blood was centrifuged (10 minutes10 min at 5000 rpm) to separate the plasma. Plasma was stored at −20 °C until laboratory analysis. Plasma corticosterone concentrations were analyzed using a radioimmunoassay (Corticosterone I^{125} RIA, MP Biomedicals), modified for avian plasma (10 µL plasma in 110 µL of diluent; use 50 µL per duplicate = 4.1 µL plasma per assay tube) (Pakkala et al., 2016; Newman et al., 2017). Each sample was measured in duplicate and averaged.

2.3. Fledgling survival

Radio-transmitters were attached to 1–2 nestlings per nest on day 7 of nestling development. The tagged nestlings weighed ≥ 14 g to ensure that the radio tag and harness was $< 5\%$ 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 weighed 0.67 g and were set to pulse every 12.7 s (battery life: 124 days). Due to lack of Nano Tag 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 and pulsed every 2 s (battery life: 39 days).

Over the two-year study, 48 nestlings were radio-tagged; 34 from non-agricultural sites and 14 from agricultural sites (the latter sample size was constrained due to the high nest failure on agricultural sites, see results). We monitored the fledglings by manually-tracking with a three-element Yagi antenna and SRX-800-M2 (Lotek Wireless Inc., Newmarket, ON) receiver in 2016 and a TRX-1000S (Wildlife Materials, Murphysboro, IL) receiver in 2017. Fledglings were tracked every 3–5 days for 3 weeks after fledging and to quantify survival. 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 of 20 fledglings that survived 10+ days post-fledging were later found dead). Savannah Sparrow fledglings remain with their parents and siblings 10–25 days after leaving the nest (Wheelwright and Mauck, 1998; Wheelwright et al., 2003). Therefore, disappearances after 10 days were not considered a mortality as the fledgling may have already left their natal territory and been out of detectable range. When a fledgling disappeared, we still attempted tracking for 3 consecutive visits (every 3–5 days) throughout the entire natal study sites to attempt to relocate the individual.

2.4. Adult body condition

If AG sites have poor-quality food resources compared to 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. To test this prediction, 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). Tarsus length (calipers, 0.1 mm) and mass (digital scale, 0.01 g) were measured for all adults. Body condition was analyzed in the same method as nestlings using the residual body mass of adult birds (observed body mass – predicted body mass (tarsus length*0.564(± SE = 0.147) + 6.840(± SE = 3.030)). In total, 12 females and 44 males were measured over the 2-year period. Adults were caught after territory establishment between June 4-July 28 (2016) and over one week in the second year of the study, July 2–6 (2017). No adults from the first year were also sampled in the second year of the study.

2.5. Arthropod diversity and abundance

Arthropod abundance was measured as an indicator of food availability and habitat quality in 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 through 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 (H.V.) walking at approximately the same speed over the two breeding seasons to reduce collection biases between samples. Although sweep netting can be biased against ground-dwelling arthropods, it still provides a good relative measure of local arthropod abundance (Chadbourne and Anderson, 2015). 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, arthropods were sampled during the nestling stage because this is the most relevant period for assessing nestling body condition. All samples collected were used to compare arthropod abundance between land-use types. Samples were collected between 1000–1500 when the temperature was between 15 and 25 °C, cloud cover was less than 50%, and wind was less than 22 km/hour. The 50 sweeps from each nest site were 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 h. Dry biomass was recorded for each insect Order (digital scale, 0.0001 g), Class Arachnida, and unknown (loose body parts and damaged arthropods that could not be identified).

2.6. Statistics

Daily survival rates for nest success and fledgling survival were calculated on Program MARK (v. 8.2; White and Burnham, 1999) using the nest survival model (Dinsmore and Dinsmore, 2007). The nest survival model on Program MARK is the best model to analyze fledgling survival for our data because we did not track all fledglings in discrete intervals (i.e., on the same day). For modelling nest survival, data were analyzed using the covariates land-use type (AG vs non-AG), nest age, and year of the study. Nest age began at the start of incubation and was estimated by subtracting 12 days of incubation from hatch day. For nests that were found during the egg stage and depredated before hatching (32 of 94 nests), nest age was estimated to the 5th, 15th or 25th of the month closest to when the nest was found or depending on how long it had been monitored for (i.e., if the nest had been monitored for 10+ days then we assumed the nest had been found 1–2 days into incubation). For modelling fledgling survival, data were analyzed with combinations of the covariates land-use type (AG vs non-AG), age, year, and sex. Models were ranked using the Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Anderson, 2008) and the Akaike weight (w_i). We considered strongly supported models to have a ΔAIC_c of less than 2.00 and moderately supported models to have a ΔAIC_c between 2.00 and 4.00 (Anderson, 2008).

A linear mixed model (JMP PRO v14.0) was used to analyze LOG-transformed plasma CORT levels in 7-day old nestlings. Stress response (baseline vs. 30 min acute restraint stress-induced) and land-use type (AG vs non-AG) were included as fixed effects, and nestling ID and nest ID set as random effects.

All of the following statistical tests were run on SPSS (IBM SPSS Statistics v.24): Body mass and condition had normal distributions and were analyzed using independent samples t-tests. A general linear model (univariate analysis of variance) was used to determine how nestling body condition was related to land use type, sex, brood size and arthropod biomass. 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. Number of fledglings per nest was also examined with a general linear model to account for clutch initiation date. Binary logistic regression was used to determine if nestling body condition had an effect on fledgling survival.

3. Results

3.1. Nest and fledgling survival

Over the two-year study period, 34 nests were found on 7 AG sites and 60 nests were found on 6 non-AG sites (mid-May to early July for both land-use types). On the agricultural sites, all nests were found in the grassy laneways and margins in between the crops and sites were composed of 85 ± 5% (mean ± SD) arable land/crop cover within a 50-m radius of the nest. No nests were found in the grass between crops and roadways. The non-agricultural sites were composed of 95 ± 8% (mean ± SD) open/grass cover within a 50-m radius of the nest (Supporting Table S1).

Nest failure was primarily a result of nest predation (52 of 56 failed nests; 23 AG, 31 non-AG) rather than nest abandonment (4 of 56; 2 on each land-use type). The highest ranked model for the daily survival of nests included nest age and land-use type (Table 1, Fig. 2A) with daily survival rate decreasing with nest age. Four additional models were strongly supported ($\Delta\text{AIC}_c \leq 2.00$) and the 3 other models were moderately supported ($2.00 < \Delta\text{AIC}_c < 4.00$; Table 1). The cumulative weight for models that included 'land-use type' was 0.63 and all top three models included land-use type. Using the daily survival rate calculated from the highest ranked model (Fig. 2A), the estimated probability of a nest surviving the duration of the 22 day nesting period (12 days incubation and 10 days with nestlings) was 0.11 ± 0.05 (95% CI: 0.04, 0.25) on AG sites and 0.27 ± 0.07 (95% CI: 0.16, 0.42) on non-AG sites, where the estimates for land-use types had overlapping 95% CIs.

The highest ranked model for the daily survival rate of fledglings included only age of the fledgling (Table 2) in which daily survival rate increased with fledgling age. Three additional models were strongly

Table 1

Models for daily survival rate of nests calculated on Program MARK (v. 8.2). Land-use type is agricultural versus non-agricultural and year is 2016 vs 2017. Nest age refers to the days since the estimated start of incubation (i.e., "day 0" is the start of incubation; see methods). Model rankings are based on the Akaike's Information Criterion for small sample sizes (AIC_c) and Akaike weight (w_i). K is the number of parameters.

Model	ΔAIC_c	w_i	K	Deviance
Nest Age + Land-use	0.000	0.243	3	222.9
Land-use	0.612	0.179	2	225.5
Nest Age + Land-use + Year	1.279	0.128	4	222.2
Constant	1.392	0.121	1	228.3
Nest Age	1.515	0.114	2	226.4
Land-use + Year	2.197	0.081	3	225.1
Nest Age + Year	2.517	0.069	3	225.4
Year	2.669	0.064	2	227.6

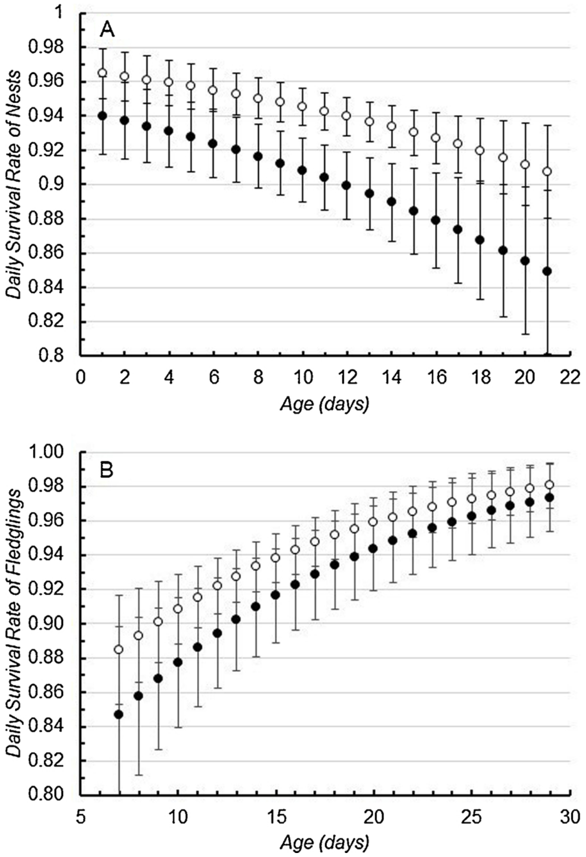

Fig. 2. Nest and Fledgling Daily Survival Rate. The daily survival rate for each day during the (A) nesting and (B) fledgling periods between land-use types using the Age + Land-use models calculated on Program MARK (v.8.2). Black circles represent AG sites and open circles represent non-AG sites in both graphs. Error bars represent standard error. Day 0 represents (A) the start of incubation, and (B) hatch day. Nestlings were tagged for radio tracking at 7–9 days old and fledged between 8–10 days old.

supported ($\Delta AIC_c \leq 2.00$; Table 2). The second and third highest ranked models included Age + Year, and Age + Land-use type, respectively (Table 2). The cumulative weighting of all models that included land-use type was 0.34. The estimated probability of a fledgling surviving 3 weeks post-fledging (using the model Age + Land-use type) was 0.17 ± 0.10 (95% CI: 0.05, 0.45) on AG sites and 0.27 ± 0.08 (95% CI: 0.14, 0.45) on non-AG sites (Fig. 2B) with widely overlapping CIs.

Table 2
Models for the daily survival rate of fledglings calculated on Program MARK (v. 8.2). Land-use type is agricultural vs. non-agricultural and year is 2016 vs. 2017. Age refers to the number of days since hatching (tagged at 7–9 days old). Model rankings are based on the Akaike's Information Criterion for small sample sizes (AIC_c) and Akaike weight (w_i). K is the number of parameters. Models with weighting < 0.025 are not shown in the table.

Model	ΔAIC_c	w_i	K	Deviance
Age	0.000	0.258	2	130.6
Age + Year	1.099	0.149	3	129.7
Age + Land-use	1.409	0.128	3	130.0
Age + Sex	1.972	0.096	3	130.0
Age + Land-use + Year	2.304	0.082	4	130.5
Age + Sex + Year	2.974	0.058	4	128.8
Constant	3.404	0.047	1	129.5
Age + Land-use + Sex	3.449	0.046	4	136.0
Age + Sex + Land-use + Year	4.288	0.030	5	130.0
Land-use	4.658	0.025	2	128.7

3.2. Clutch size, brood size and nestling body condition

With failed nests removed to isolate land-use-related productivity effects, 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 (Supporting Table S2). Clutch size ($R^2 = 0.001$, $t = 0.348$, $p = 0.728$) and brood size ($R^2 = 0.037$, $t = -1.528$, $p = 0.132$) were not significantly correlated with clutch initiation date (Julian date). However, number of fledglings per nest was significantly correlated with the clutch initiation date with a weak negative trend ($R^2 = 0.12$, $t = -2.211$, $p =$ **0.033**). When accounting for clutch initiation date, the number of fledglings per nest was still non-significant between AG and non-AG sites ($F_{1,35} = 0.175$, $p = 0.678$).

Nestling body mass at 7 days old was also not significantly different on AG sites compared to non-AG sites (Supporting Table S3, Fig. 3). Tarsus length was a good predictor of body mass ($R^2 = 0.20$, $t = 4.477$, $p \leq$ **0.001**). When accounting for tarsus length, the body condition (residual body mass) of 7-day old nestlings was also not significantly different between nestlings hatched on AG sites compared to non-AG sites (Supporting Table S3). Although the observed body mass ($t = 5.166$, $p \leq$ **0.001**) and body condition ($t = 2.850$, $p =$ **0.006**) of 7-day old nestlings were significantly different between male and female nestlings (n = 28 females, 40 males), there was no difference in body condition between land-use types after accounting for sex (Supporting Table S3, Fig. 3).

A general linear model to examine body condition ($R^2 = 0.22$, $F_{4,53} = 3.513$, $p =$ **0.013**) determined that sex of nestlings ($F_{1,53} = 5.914$, $p =$ **0.018**), and total arthropod biomass ($F_{1,53} = 4.331$, $p =$ **0.042**) were a significant predictors, but land-use type (AG vs. non-AG: $F_{1,53} = 0.870$, $p = 0.355$) and brood size ($F_{1,53} = 1.447$, $p = 0.234$) were not significant predictors.

Irrespective of land-use type, nestling body condition was not correlated with surviving the fledgling period during the first 9 days after leaving the nest ($R^2 = 0.03$, Wald = 0.560, $p = 0.454$) or for the 3-week fledgling period ($R^2 = 0.05$, Wald = 1.042, $p = 0.307$).

Thirty-four 7-day old nestlings were sampled for CORT on the non-AG sites (16 in 2016, 18 in 2017) and 13 nestlings were sampled on the AG sites (8 in 2016, 5 in 2017). In 2016, there was no significant interactions between CORT levels and land-use type ($R^2 = -0.05$; land-use type: $F_{1,21} = 0.01$, $p = 0.912$; stress response: $F_{1,21} = 1.19$, $p = 0.286$; land-use type*stress response: $F_{1,21} = 0.01$, $p = 0.926$;

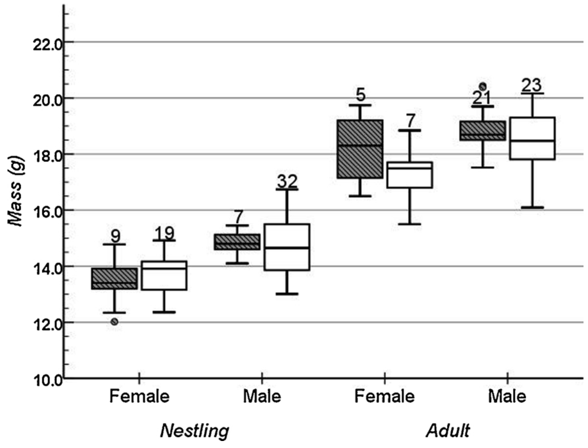

Fig. 3. Nestling and Adult Body Mass. Median (+/- minimum and maximum quartiles) body mass of 7-day old nestlings and adults, between sex and land-use types: agriculture (hatched gray bars) and non-agricultural (open bars). Samples sizes displayed above error bars. Sex of nestlings determined through DNA analysis of blood, and sex of adults determined by presence of physical breeding characteristics.

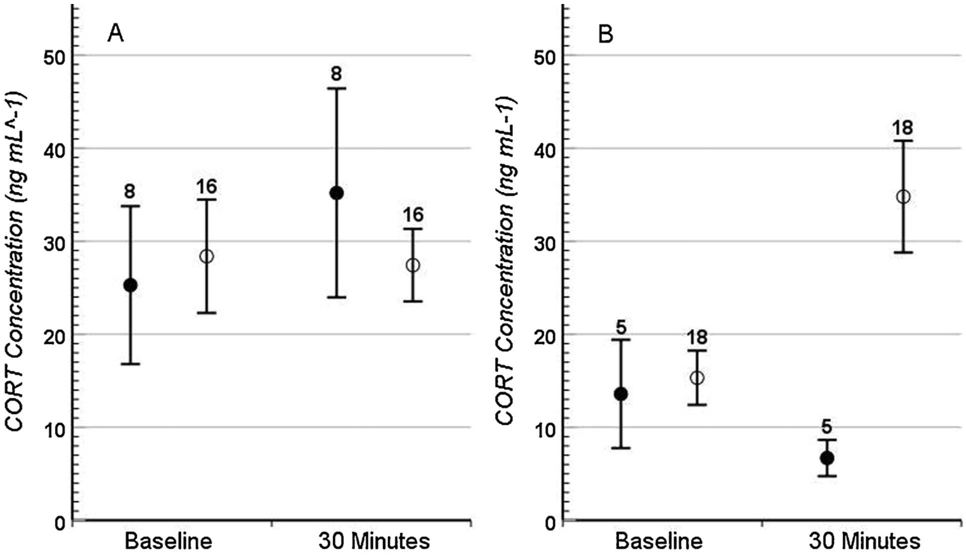

Fig. 4. Nestling Corticosterone Concentrations. Mean corticosterone (CORT) concentrations (+/- SE) in 7-day old nestlings on agricultural (black circles) and non-agricultural (open circles) sites between (A) 2016 and (B) 2017. Sample size displayed above error bars. Blood was sampled within 2–3 minutes of handling (baseline) and again after 30 min (acute restraint).

Fig. 4A). However, in 2017, land-use type and the interaction between land-use type and stress response were significant (R^2 = 0.45; land-use type: $F_{1,20}$ = 5.49, p = **0.037**; stress response: $F_{1,20}$ = 0.53, p = 0.475; land-use type*stress response: $F_{1,20}$ = 6.59, p = **0.016**), where nestlings on non-AG sites mounted a stress response to acute restraint, but nestlings on AG sites did not mount a stress response (Fig. 4B).

3.3. Arthropod abundance

The total dry biomass of arthropods was not significantly different between AG and non-AG sites over the nesting period (df = 53, U = 318, p = 0.364, Supporting Table S4) but was marginally associated with nestling body condition with a slight negative trend (R^2 = 0.06, t = -1.972, p = 0.053) and was a predictor of nestling body condition (see Section 3.2). 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 (Supporting Table S4). Homopterans are an important nestling food for Savannah Sparrows (Meunier and Bédard, 1984) and the biomass was significantly higher on non-AG sites (Supporting Table S4) but even so did not predict nestling body condition (R^2 = 0.02, t = -1.141, p = 0.258).

3.4. Adult body condition

Adult body mass in AG versus non-AG sites was similar for both males (df = 44, t = 1.028, p = 0.310) and females (df = 10, t = 1.301, p = 0.222; Fig. 3). Body condition was not significantly different between AG and non-AG sites for adult males (df = 41, t = -0.723, p = 0.474) nor for adult females (df = 10, t = -1.286, p = 0.228). Because males were caught over 2 months in the first year, and over one week in the second year of the study, we examined if date had an impact on adult male body condition and we found that day of the year (date of capture) and adult male body condition were not correlated (n = 44, R^2 = 0.01, t = 0.699, p = 0.489).

4. Discussion

4.1. Nesting success and fledgling survival

Although non-significant, the estimated nesting success from the daily survival rate model (11% on AG sites and 27% on non-AG sites) tended to be lower on agricultural sites suggesting that agricultural habitats are lower quality habitat. The most strongly supported model of nest daily survival rate included both nest age and land-use type, and the top 3 models included land-use type as a variable (cumulative weighting 0.55) which provides support for the prediction that nest survival will be lower on intensive agriculture. However, the constant model also had strong support, reflecting the relatively weak effect of land-use type on nest survival (ΔAIC = 1.39). Land-use type appeared to have a strong effect on nest survival, but larger sample sizes would be needed to support this conclusion and to better distinguish among the top models. The estimates of survival from both land-use types are similar to other studies of the same species in Vermont (7–48% in grazed pastures and hayfields: Perlut et al., 2006; Perlut and Strong, 2011) and New Brunswick (10–80% in non-agricultural sites: Dixon, 1978; Wheelwright and Schultz, 1994; Wheelwright et al., 2012).

Apparent nesting success was twice as high on non-agricultural (50%; 30 of 60) than agricultural sites (27%; 9 of 34), when both years were combined, and was almost entirely due to nest predation. Unlike in hayfields, nests in this study 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). Apparent nesting success was not used to test predictions because it is a biased estimate (Jehle et al., 2004). Almost all nests were found during the incubation stage on agricultural sites (31 of 34; 91%) whereas many nests were found during the nestling stage on the non-AG sites (19 of 60; 32%) and thus nests that were monitored on AG sites had far greater exposure. Monitoring predator identity and density at the local and landscape level would be important for understanding why Savannah Sparrow nesting success in this study was only moderately reduced when birds were nesting in narrow grassy laneways surrounded by monocultures versus grassland habitats.

To our knowledge, this is the first study to examine the fledgling survival of grassland songbirds on intensive agriculture in North America. The apparent fledgling survival (over 3 weeks) was 21% on agricultural sites and 35% on non-agricultural sites. There was only weak evidence for land-use effect on fledgling survival, as the third most supported model for daily survival rate included age of the fledgling and land-use type (model weight = 0.13). This weak trend may be explained due to low statistical power because fewer nestlings were tagged on agricultural sites (n = 14) than on non-agricultural sites (n = 34). The probability of surviving increases the longer the fledgling is out of the nest which is consistent with the literature (Cox et al., 2014). Very few studies have investigated fledgling survival in agricultural areas. Survival of fledgling White-throated Robins (*Turdus assimilis*) in Costa Rica was lower on coffee plantations compared to pastures (Cohen and Lindell, 2004). We could not quantify cause of death for fledglings in our study because it is difficult to attribute mortality to predation versus scavenging/decomposition after starvation or exposure when tracking every 3–5 days. Often the highest mortality risk 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). Quantifying 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. There may be 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 for several weeks (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.

4.2. 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 (e.g., Tiainen et al., 1989; Ghilain and Bélisle, 2008). However, in this study, with failed nests removed, the clutch size, brood size and number of fledglings per successful nest was not different between the two land-use types. This indicates that Savannah Sparrow parents apparently do not face food limitations in agriculturally intensive areas which is consistent with the lack of differences in insect abundance between land-use types in our study. This result is consistent with many species in Europe, for which clutch size was not impacted by agricultural intensification (Galbraith, 1988; Tiainen et al., 1989; Brickle et al., 2000; 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. Total arthropod biomass was not significantly different between agricultural and non-agricultural sites and did not predict nestling body condition but could be investigated more extensively in future research. Certain orders of insects and arachnids were different between the two types of sites (Supporting Table S2) 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 (Boatman et al., 2004; Morris et al., 2005). 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), Barn Owl nestlings in Switzerland (Almasi et al., 2015), and Tree Swallows in Saskatchewan (Michelson et al., 2018). It is possible for nestling body mass to not be impacted from low food supply in the local habitat if the parental effort is increased to sustain nestling growth (Tremblay et al., 2005; Lee et al., 2016) and potentially the differences in Savannah Sparrow densities between sites in our study may have been a result of access to food resources.

Nestling corticosterone levels can be a useful measure of habitat quality in some species, such as Barn Owls, which have elevated baseline corticosterone levels in intensive agricultural areas (Almasi et al., 2015). However, we did not find elevated baseline levels on agricultural sites, but interestingly we did find evidence of a modified HPA axis where CORT levels did not increase after handling in nestlings raised on agricultural sites. Our results partially support our predictions and the ceiling hypothesis (Pakkala et al., 2016) because plasma CORT levels significantly increased in response to 30 min acute restraint in nestlings on non-agricultural sites whereas there was no significant increase in plasma CORT in nestlings from agricultural sites in 2017. However, there was a significant effect of year since this pattern was not evident in 2016. The interannual differences may be explained by improvements in sampling methods after the first year of the study such as increased proficiency with blood sample collection, including more rapid placement onto ice in the field, indeed the degree of hemolysis was qualitatively less in 2017. Further, CORT levels in nestlings can be highly variable even within the 3-minute sampling time (for baseline levels) and time of day (Newman et al., 2017; Small et al., 2017), and baseline glucocorticoids can also be influenced by many factors such as habitat, sex, age and life history stages and thus can be complicated to use for assessing environmental conditions (Madliger and Love, 2016). Ideally, sampling windows within a day and season should be narrow to reduce temporal variability in CORT among samples (Newman et al., 2017), however, this presents serious logistical problems in a landscape-level study such as ours with large travel distances between sites. Our results from 2017 indicate that measuring nestling CORT levels may be a useful tool for understanding habitat quality and stress for nestling Savannah Sparrows in agricultural landscapes. CORT treatment during the nestling period affects juvenile pre-migratory movements, indicating that early exposure to CORT can carry over to affect subsequent life stages (Pakkala et al., 2016). Additionally, adult CORT levels may be more reliable for assessing habitat quality in songbirds (e.g., Done et al., 2011; Walker et al., 2015) and thus, future research should also investigate corticosterone levels of adult Savannah Sparrows in relation to agricultural intensification.

4.3. Adult body condition

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). However, in Saskatchewan, adult Tree Swallows had both higher body mass and body condition on grassland sites compared to agricultural sites (Michelson et al., 2018). 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., 2006). 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) and in this study, we found no negative impact of intensive agriculture on adult Savannah Sparrows.

4.4. Conclusion

Although intensive agricultural habitats differ greatly 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. 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 (Firbank, 2005; Kleijn et al., 2011). For Savannah Sparrows in this study, where we compared two extremes in habitat, we found a negative impact of agricultural intensification on nesting success and a change in nestling physiology but there was surprisingly little evidence of a negative impact on fledgling mortality, clutch and brood size, body condition of both adults and nestlings and insect abundance. 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 and fledgling survival results indicate that a larger and longer-term study is needed to determine whether nest predation and fledgling mortality are consistently higher in agricultural sites, and if so what the long-term impact of this would be on regional population declines.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2019.106696.

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