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Research Paper

## Age-specific effects on reproductive performance of grassland songbirds nesting in agricultural habitats

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**ABSTRACT.** Clutch size and number of young fledged has been shown to increase with female age until approximately mid-life, when reproductive performance declines. We used a long-term dataset (2002–019) to investigate age-specific effects on reproductive parameters of known-age female Savannah Sparrows (*Passerculus sandwichensis*, n = 60), and Bobolinks, (*Dolichonyx oryzivorus*, n = 75) breeding in managed hayfields and pastures in Shelburne and Hinesburg, Vermont, USA. Female Savannah Sparrows (age 1 to 6 years) showed evidence of reproductive senescence with the number of young fledged peaking at 2 years of age and declining in older age classes. Additionally, daily nest survival was strongly and negatively affected by female age. The effect of age on Bobolink reproductive performance was weak. We found an increase in the number of eggs laid from 1 to 2 years of age, no age effect on number of nest attempts or number of young fledged, and a weak, negative effect of age on daily nest survival. We found no support for an effect of grassland management treatment on daily nest survival, which may have been a result of unequal distribution of nesting attempts across treatment types. However, species-specific responses to hay harvest may have affected the relationship between age and reproductive performance. Savannah Sparrows re-nest rapidly and frequently after nest loss due to haying, which may constrain long-term investment in reproduction. In this highly managed system, older females may allocate less energy toward reproduction than younger females, potentially shifting those resources to behaviors that support annual survival. By contrast, Bobolinks may not invest as heavily in reproduction, generally re-nesting only once after nest failure and have a truncated breeding season because of their long fall migration to South America. Consequently, their reproductive success may not vary as strongly with age.

### Effets spécifiques de l'âge sur les performances de reproduction d'oiseaux chanteurs de prairies nichant en milieu agricole

**RÉSUMÉ.** Il a été démontré que la taille de la ponte et le nombre de jeunes à l'envol augmentent avec l'âge de la femelle jusqu'en milieu de vie environ, moment où la performance reproductive se met à diminuer. Nous avons utilisé un jeu de données s'échelonnant sur plusieurs années (2002-19) pour étudier les effets spécifiques de l'âge sur les paramètres de reproduction de Bruants des prés (*Passerculus sandwichensis*, n = 60) et de Goglus des prés (*Dolichonyx oryzivorus*, n = 75) nichant dans des champs de foin et des pâturages aménagés à Shelburne et à Hinesburg, au Vermont, États-Unis. Les Bruants des prés femelles (âgées de 1 à 6 ans) ont montré des signes de sénescence reproductive, le nombre de jeunes à l'envol atteignant un pic à 2 ans et diminuant dans les classes d'âge supérieures. De plus, le taux de survie quotidien du nid était fortement et négativement affecté par l'âge des femelles. L'effet de l'âge sur la performance de reproduction du Goglu des prés était faible. Nous avons constaté une augmentation du nombre d'œufs pondus de 1 à 2 ans, aucun effet de l'âge sur le nombre de tentatives de nidification ou le nombre de jeunes à l'envol, et un effet négatif faible de l'âge sur le taux de survie quotidien du nid. Nous n'avons trouvé aucun indice confirmant l'existence d'un effet du type d'aménagement des prairies sur le taux de survie quotidien des nids, ce qui pourrait être le résultat d'une répartition inégale des tentatives de nidification selon les types d'aménagement. Cependant, les réactions spécifiques des espèces à la récolte du foin peuvent avoir affecté la relation entre l'âge et la performance de reproduction. Les Bruants des prés re-nichent rapidement et fréquemment après la perte de leur nid consécutive à la récolte du foin, ce qui peut limiter leur investissement à long terme dans la reproduction. Dans ce système de milieux grandement aménagés, les femelles plus âgées allouent sans doute moins d'énergie à la reproduction que les femelles plus jeunes, déplaçant peut-être ces ressources vers des comportements qui soutiennent la survie annuelle. En revanche, les Goglus des prés n'investissent peut-être pas autant dans la reproduction, ne re-nichent généralement qu'une seule fois après l'échec du nid et ont une saison de reproduction tronquée en raison de leur longue migration automnale vers l'Amérique du Sud. Par conséquent, leur succès de reproduction ne varie peut-être pas aussi fortement avec l'âge.

Key Words: *age; Bobolink; grassland; life history; passerine; reproduction; Savannah Sparrow; senescence*

## INTRODUCTION

Quantifying age-specific variation in demographic parameters is critical to understanding population dynamics and the evolution of life-history traits. In birds, life history traits are generally

distributed across a fast-slow life history axis, with annual reproductive success and adult mortality rate being directly proportional to one another (Ricklefs 1977, 2000). For species on the fast end of the life history axis, estimating age-specific

demographic parameters can be challenging because of high natal dispersal and low apparent survival rates, particularly with migratory species (e.g., Fay et al. 2020).

In this study, we quantified age-specific components of annual reproductive success in two species of migratory passerines that exhibit short natal dispersal distances in our study system. Previous studies have shown two general patterns in age-specific reproductive variation. First, an increase in reproductive success with age results from greater breeding experience, acquisition of higher quality territories, or physiological maturation (e.g., Balbotin et al. 2007, Bouwhuis et al. 2009, Brown and Roth 2009, Amininasab et al. 2017). Older females may lay more eggs and fledge more young (Wheelwright and Schultz 1994, Robertson and Rendell 2001) and feed nestlings at greater rates (Geslin et al. 2004) than younger females. At the population level, selection pressures acting on individuals with lower fitness can also drive the expression of this pattern (Nol and Smith 1987). Second, a number of studies document senescence in annual reproductive success (Rose 1990, Ricklefs 1998, Møller and De Lope 1999, Holmes et al. 2003). There are several theories that describe potential causes of senescence, primarily the somatic damage incurred from the costs of survival and prior reproductive efforts and the accumulation of genetic mutations that express later in life (Partridge and Barton 1993).

Trade-offs between survival and reproductive effort are readily apparent across the fast-slow life history axis. For passerines at the fast end of life history axis, age-specific variation in reproductive success is challenging to quantify as individuals attempt to maximize lifetime reproductive success over short lifespans. However, single species studies have shown age-dependent declines in both annual reproductive success and survival, suggesting that at least for older age classes there is not a trade-off between reproduction and survival (Keller et al. 2008, Brown and Roth 2009). Other studies of passerines have shown that although short-lived species are physiologically capable of successful reproduction early in life, other factors may interact with reproductive physiology, such as habitat quality, foraging efficiency (Desrochers 1992), and ability to attract mates (Enstrom 1993), resulting in lower reproductive success in younger age classes.

Environmental factors may also create selection pressures that interact with age-specific demographic parameters. Predation risk and competition have been shown to accelerate declines in reproductive success with age (Balbotin and Møller 2015). Overall low rates of reproductive success for birds breeding in the eastern United States are suspected to be a result of the negative effects of predation and brood parasitism resulting from grassland habitat fragmentation (Robinson et al. 1995, Herse et al. 2020). Clark and Martin (2007) suggested that greater investment in adult survival (versus investment in low or unpredictable reproductive success) should lead to greater population growth rates through selection for increased iteroparity for these populations. Although trade-offs may occur as a result of environmental selection pressures, other studies have shown that the results are not age-specific. In Yellow-eyed Penguins (*Megadyptes antipodes*), researchers found no effect of investigator disturbance on lifetime reproductive success in birds in different age categories (Stein et al. 2017). Older Shags

(*Phalacrocorax aristotelis*) had greater reproductive success than younger individuals regardless of environmental conditions, suggesting age-specific differences in brood rearing capacity were insensitive to extrinsic factors. In our study system, the timing and intensity of hay harvests and grazing is known to negatively affect reproductive success (Perlut et al. 2006, 2011); however, we do not know if, or how, age might interact with an individual's ability to adapt and respond to agricultural management.

We studied a marked population of known-age females of two passerines, Savannah Sparrows (*Passerculus sandwichensis*) and Bobolinks (*Dolichonyx oryzivorus*), to investigate the effect of age on the reproductive effort and success in managed hayfields and pastures. We assessed the number of nest attempts, eggs laid, and young fledged, as well as daily nest survival (DNS) of known-age females. We hypothesized that the reproductive performance, as well as daily nest survival, would increase with increasing age, until approximately mid-life. As a result of intense selection pressure from hay harvest practices, which increases reproductive effort (Perlut et al. 2006), we predicted that these species would show declines in reproductive success in later age classes.

## METHODS

### Study area

We conducted our research in the Champlain Valley of Vermont, USA, an area that contains ~146,000 ha of managed grassland (National Agricultural Statistics Service 2010). The Champlain Valley is located in Bird Conservation Region 13, which includes 15% of the global population of Bobolinks (Renfrew et al. 2019). Our study sites consisted of privately owned hayfields and pastures in Shelburne (44.3806° N, 73.2276° W) and Hinesburg (44.3292° N, 73.1107° W), Vermont. Our study fields were in five treatment types: traditional early-hayed fields ("early-hayed", n = 2) were cut between 16 May and 11 June and generally again 35 to 52 days later, grassland bird incentive fields ("early-delay", n = 2) were cut before 29 May and had a 65-day window between the first and second cuts, middle-hayed fields ("middle-hayed", n = 5) were hayed between 21 June and 11 July, late-hayed fields ("late-hayed", n = 10) were cut after 15 July, typically after most birds have ended their reproductive season, and rotationally grazed pastures ("grazed", n = 4; Perlut et al. 2006, 2011; additional details on field management and vegetation characteristics).

### Field methods

From 2002 to 2019, we used mist-nets to capture and band breeding adults on all study fields starting in mid-May. Field sizes ranged from 13.2 to 38.3 ha; mean 21.1 ha. We spent 1–2 full days mist-netting (30–35 12 m mist nets per day) from 0400 to 1300 at each site to catch as many adults as possible. Adults were banded with a unique combination of three color bands and one U.S. Geological Survey (USGS) metal band. We identified each birds' sex, collected a blood sample from the brachial vein, and took standard morphological measurements. We searched each study field for nests every one to two days throughout the breeding season. Nests were located either through behavioral observations or by opportunistically flushing incubating females off nests (Perlut et al. 2006). We identified the adults associated with each nest by resighting color-banded individuals or by catching

unbanded birds near the nest. Any unbanded bird associated with a nest were banded following our method. We monitored nests at least every one to two days until they fledged or failed. Nestlings were banded at day five or six with one metal USGS band on the right leg. This population had a high rate of natal philopatry and first year apparent survival (Cava et al. 2016, Fajardo et al. 2009, Perlut and Strong 2016). These philopatric individuals provided us with a known-age population, as neither species can be aged reliably by plumage (Pyle 1997).

## Data analysis

From 2002 to 2019, we compiled the reproductive effort and success for every known-age female detected on the study site, which included number of nest attempts, eggs laid, and young fledged per breeding season ( $n = 60$  Savannah Sparrows and  $n = 75$  Bobolinks). These data included all known re-nesting attempts. The number of breeding seasons recorded for each female ranged from one to five (Savannah Sparrow  $\bar{x} = 1.43$ ; Bobolink  $\bar{x} = 1.41$ ). Consequently, our data were too sparse to estimate apparent survival rates. To analyze whether the number of nest attempts, eggs laid, or young fledged varied with female age, we ran two-way ANOVA tests in PROC MIXED (SAS Institute, Cary, North Carolina, USA). We included year as a fixed effect to control for year-to-year variation in reproductive effort and success and, female band number as a random effect (some individuals had  $> 1$  year of data), and because of limited sample size, pooled all birds  $\geq 5$  years of age into a single age cohort. If models identified significant differences among age classes, we then compared the means of each pair of age classes with a Tukey's test.

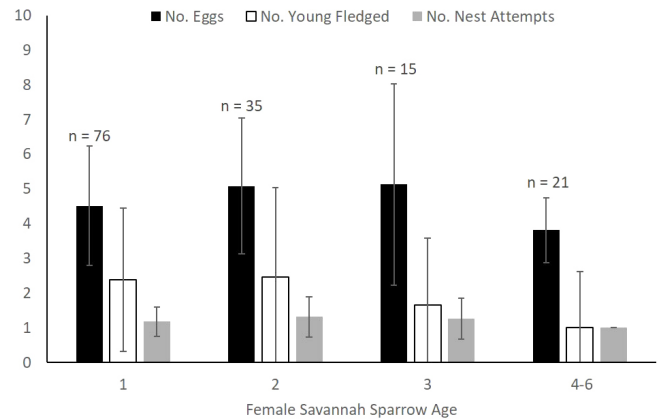
We ran daily nest survival models in program MARK (White and Burnham 1999, Dinsmore and Dinsmore 2007) to estimate variation in daily nest survival through additive and interactive models with the following factors: species, female, treatment (early-hayed, early-delay, middle-hayed, grazed, late-hayed) and age (1–7). Because of notable annual variation, we included year as a fixed effect and female as a random effect in all models. We included interactive models in order to test for variation between individuals varied over time and with treatment. We ranked models using the Akaike's Information Criterion adjusted for small sample sizes ( $AIC_c$ ). We considered strongly supported models to have a  $\Delta AIC_c$  of  $< 2$  and moderately supported models to have a  $\Delta AIC_c$  between 2–4 (Anderson 2008). We interpreted biological significance within the top ranked models ( $\Delta AIC_c \sim 2$ ) by examining beta values and their associated 95% confidence intervals. We considered factors whose 95% confidence interval did not cross zero as biologically significant.

## RESULTS

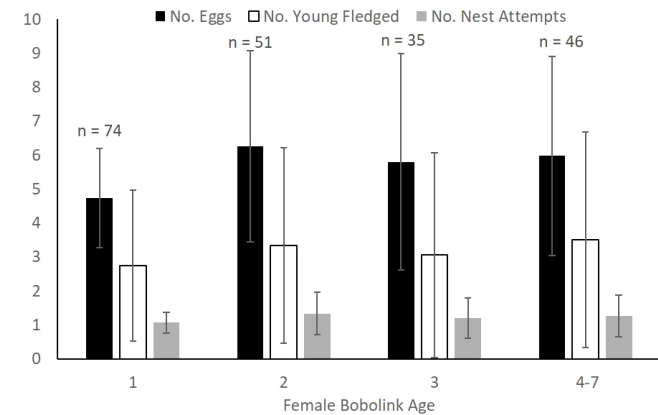
For Savannah Sparrows, when controlling for year effects, the number of young fledged ( $F_{3,56} = 7.18$ ,  $p = 0.008$ ) was greatest in years 1 and 2 and declined in later age classes (ages 1 and 4+ [ $t = 2.63$ ,  $p = 0.01$ ] and 2 and 4+ [ $t = 2.48$ ,  $p = 0.01$ ] differed significantly). The number of eggs laid ( $F_{3,56} = 0.51$ ,  $p = 0.476$ ) and number of nest attempts ( $F_{3,56} = 1.00$ ,  $p = 0.302$ ) did not vary with age (Fig. 1). For Bobolinks, after controlling for year effects, the number of eggs laid ( $F_{3,71} = 6.91$ ,  $p = 0.009$ ) peaked at 2 years of age (ages 1 and 4+ [ $t = 2.64$ ,  $p = 0.01$ ], 1 and 3 [ $t = 2.07$ ,  $p = 0.04$ ], and 1 and 2 [ $t = 3.32$ ,  $p < 0.01$ ] differed significantly), but

the number of nest attempts ( $F_{3,71} = 3.45$ ,  $p = 0.065$ ) and total number of young fledged ( $F_{3,71} = 2.10$ ,  $p = 0.149$ ) did not change with age (Fig. 2).

**Fig. 1.** Number of eggs (mean  $\pm$  SD), number of young fledged (mean  $\pm$  SD), and number of nest attempts (mean  $\pm$  SD) of female Savannah Sparrows (*Passerculus sandwichensis*) ranging from ages 1 to 6, with ages 4 to 6 pooled (for age 4,  $n = 11$ ; age 5,  $n = 4$ ; age 6,  $n = 6$ ).



**Fig. 2.** Number of eggs (mean  $\pm$  SD), number of young fledged (mean  $\pm$  SD), and number of nest attempts (mean  $\pm$  SD) of female Bobolinks (*Dolichonyx oryzivorus*) ranging from ages 1 to 7, with ages 4 to 7 pooled (for age 4,  $n = 18$ ; age 5,  $n = 15$ ; age 6,  $n = 8$ ; age 7,  $n = 5$ ).



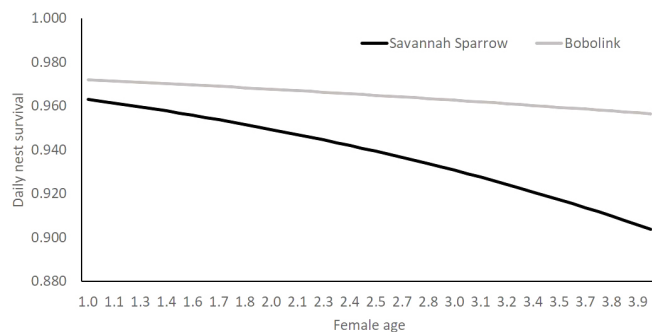
The age\*female interaction model best explained variation in Savannah Sparrow daily nest survival ( $w_i = 0.41$ ; Table 1; Table 2 sample sizes of age by treatment type). Further, age was an additive or interactive factor in the top three models, which cumulatively accounted for 86% of the model weight. The beta value for age ( $-2.48$ ; 95% CI:  $-2.58 - -2.38$ ) in the top ranked model was biologically significant. Estimates of daily nest survival for Savannah Sparrows decreased from 0.963 to 0.904 between ages of 1 to 4 years. Extrapolated over the 24-day nesting cycle for Savannah Sparrows, nest success was 41% and 9% for 1 and 4-year-old females, respectively.

**Table 1.** Program MARK additive (+) and interactive (\*) daily nest survival models with the factors species, treatment (early-hayed, early-delay, middle-hayed, grazed, late-hayed) and age (1–7). Akaike’s Information Criterion adjusted for small sample sizes (AICc) and the Akaike weight ( $w_i$ ) were used to rank the models. † indicates models with  $\Delta AIC_c < 2.0$ .

Model	No. Par	Bobolink ( <i>Dolichonyx oryzivorus</i> )			Savannah Sparrow ( <i>Passerculus sandwichensis</i> )		
		AICc	$\Delta AIC_c$	$w_i$	AICc	$\Delta AIC_c$	$w_i$
age	3	307.4	0.00	0.27†	277.7	0.71	0.29†
null	2	307.6	0.25	0.24†	280.8	3.76	0.06
age*female	4	307.8	0.38	0.22†	277.0	0.00	0.41†
age^2	4	308.9	1.52	0.13†	279.2	2.12	0.14
female	3	309.6	2.26	0.09	282.8	5.78	0.02
treatment	5	312.0	4.61	0.03	283.8	6.73	0.01
treatment+age	6	312.9	5.50	0.02	281.1	4.06	0.05
treatment+female	6	314.0	6.64	0.01	285.8	8.76	0.01
treatment*female	10	316.6	9.21	0.00	289.8	12.75	0.00
treatment*age	10	319.9	12.50	0.00	286.2	9.20	0.00

Variation in Bobolink DNS was best explained by the age model ( $w_i = 0.29$ ); however, the beta value for age (-0.17; 95% CI: -0.367 - 0.009) in the top ranked model was not biologically significant. Age was an additive or interactive factor in three of the top four Bobolink models (all with  $\Delta AIC_c < 2.0$ ); however, only the age model had greater support than the null model. For Bobolinks, estimates of daily nest survival decreased from 0.972 to 0.956 between the ages of 1 and 4 years (Fig. 3). Extrapolated over Bobolink’s 25-day nesting cycle, nest success was 49% and 33% for 1 and 4-year-old females, respectively. Grassland management treatment did not appear until the 5<sup>th</sup> and 6<sup>th</sup> ranked models for Savannah Sparrows and Bobolinks, respectively (all models with treatment had  $\Delta AIC_c > 4.0$ ).

**Fig. 3.** Daily nest survival decreases with age for Savannah Sparrows (*Passerculus sandwichensis*) and Bobolinks (*Dolichonyx oryzivorus*) breeding in hayfields and pastures in the Champlain Valley of Vermont, USA. Age was not biologically significant for Bobolinks, as the SE was 0.009.



## DISCUSSION

We found mixed support for age-specific variation in reproductive performance in Savannah Sparrows and Bobolinks. For Savannah Sparrows, the most compelling evidence was that age was included in the three most highly supported models of daily nest survival. The significant negative beta in the age model is suggestive of senescence in daily nest survival. Similarly, the number of young

fledged per female decreased after year 2. The relatively strong support for the age\*female interaction model indicates significant individual variation in daily nest survival, which is likely influencing the lack of age-specific differences in number of eggs laid and number of nesting attempts.

For Bobolinks, the evidence for age-specific variation in reproductive performance was less definitive. The best supported model describing daily nest survival was age, with a non-significant negative beta. However, we found nearly equal support for the null model and the age\*female model, suggesting substantial variation among individuals. We found significant age-specific variation in the number of eggs laid per year, increasing from year 1 to year 2 and declining in later age classes. The number of nesting attempts and the number of young fledged per year showed no variation with age. These patterns show weak support for greater reproductive potential after year 2, but limited support for reproductive senescence.

In a literature review of age-specific reproductive performance, Sæther (1990) found that for passerines, first-time breeders generally initiated breeding later in the nesting season and had smaller clutch sizes, but with mixed results for hatching and fledging success. In general, across all taxa, females > 1 year of age had greater reproductive performance. We only documented this pattern for number of eggs laid by female Bobolinks. For species that are on the fast end of the life history axis, evidence for continued decline in reproductive performance after the first breeding attempt is limited. In most studies, declines in reproductive parameters have not been documented until substantially later in life: Song Sparrows (*Melospiza melodia*) after year 7 (Keller et al. 2008), female Florida Scrub-Jays (*Aphelocoma coerulescens*) after year 9 (Wilcoxon et al. 2013), Wood Thrush (*Hylocichla mustelina*) after year 4 (Brown and Roth 2009), female Tree Swallows (*Tachycineta bicolor*) after year 4 (Robinson and Rendell 2001), and Hihi (*Notiomystis cincta*) after year 4 (Low et al. 2007). By contrast, our results showed limited support for a curvilinear relationship between age and daily nest survival. However, Gustafsson and Pärt (1990) found Pied Flycatchers (*Ficedula albicollis*) that did not breed in their first year laid larger clutches later in life. And, in an island population of Savannah Sparrows, Wheelwright and Schultz

**Table 2.** Contingency table of samples per species (n = 2) per treatment (n = 5) used in program MARK daily nest survival models. Bobolink, *Dolichonyx oryzivorus*; Savannah Sparrow, *Passerculus sandwichensis*.

Age	Early-hayed		Early-delay		Middle-hayed		Grazed		Late-hayed	
	Bobolink	Savannah Sparrow	Bobolink	Savannah Sparrow	Bobolink	Savannah Sparrow	Bobolink	Savannah Sparrow	Bobolink	Savannah Sparrow
1	0	6	7	14	9	2	3	4	20	19
2	0	6	5	8	4	1	0	0	11	9
3	1	2	5	2	2	1	0	0	6	4
4+	0	1	3	4	4	2	0	0	10	1

(1994) showed a general (non-significant) decrease in clutch size after year 2. Thus, trade-offs between first-year breeding and annual survival could be a strategy to maximize lifetime reproductive success in our study system. Although our sample consisted of known-aged birds, we did not necessarily document all nesting attempts as these species do show short-distance breeding dispersal (Fajardo et al. 2009). Consequently, reproductive histories are incomplete for some individuals in our sample. Anthropogenic habitat management can alter the trade-off between reproduction and survival. Mauritius Kestrels (*Falco punctatus*) that experienced a greater degree of forested land modified to agriculture as nestlings, had greater investment in reproduction early in adult life, followed by a sharp decline (Cartwright et al. 2014). This change in life history, as a response to a managed natal environment, shows adaptation to increase one's fitness by allocating more energy and resources to reproduction early in life, thereby compensating for the greater mortality risk associated with those less favorable environmental conditions.

In our study, daily nest survival models that included management treatment received almost no support for either species. This was somewhat surprising as Perlut et al. (2006) found that field treatment was the primary driver of reproductive success in our study system. Both Savannah Sparrow and Bobolink females nesting on early-hayed fields fledged significantly fewer young than those on grazed pasture, middle-, or late-hayed fields. Additionally, field treatment had an impact on reproductive effort as Savannah Sparrows laid more eggs and built more nests on early-hayed fields than any of the other treatment types (Perlut et al. 2006). Our sample of known-aged individuals was not evenly distributed across treatment types (Table 2), which may at least partially explain why we found limited support for treatment on age-specific reproduction. In both species, approximately 73% of nests were in either late-hayed fields or grassland bird incentive fields; for both species, reproductive success is higher on these two treatments as compared to grazed, early-hayed and middle-hayed fields (Perlut et al. 2011). Consequently, only ~27% of nests were in treatment types that would encompass the lower range of variation in daily nest survival. However, Fay et al. (2020) analyzed seven populations of Winchats (*Saxicola rubetra*) from the UK to Russia and found no evidence of reproductive senescence for this species, which is also subject to disturbance through agricultural management practices and is a long-distance migrant. The authors concluded that stochasticity in nest success caused by mowing and predation may have precluded documenting an effect of age on reproductive success.

Differences in life history strategies may have influenced the patterns in age-specific reproductive performance in our two study species. Savannah Sparrows show greater nest site fidelity and shorter breeding dispersal distances than Bobolinks (Fajardo et al. 2009). Further, Savannah Sparrows reneest frequently: over a four-year period, over 50% of breeding birds laid two clutches, 25% laid three clutches, 12% laid four clutches, and a few laid a fifth clutch (Perlut et al. 2006). Over the same period, < 10% of female Bobolinks laid a second clutch. This variation in annual potential fecundity is likely related to the substantially longer migration distances of Bobolinks, which necessitate a shorter breeding season (Renfrew et al. 2013). These disparate patterns of reproductive effort are the most likely explanation for the stronger decrease in reproductive performance in older age classes of Savannah Sparrows, such that individuals who make more breeding attempts at a younger age may make fewer at an older age. However, these species are confronted with an array of grassland management treatments in this study system, and other physiological stressors may affect their long-term reproductive potential. Further analyses including other factors on reproduction, such as male age, male-female interactions, age-related parasite loads, and other environmental conditions, will widen the lens by which we understand Savannah Sparrow and Bobolink life histories. Likewise, we encourage further studies of how these species respond to other human-mediated structures and habitats like wind turbines, harvesting and chemical use on grain fields, energy exploration, and airport management (Kalyn Borgard et al. 2014, Iglay et al. 2017, Raynor et al. 2017), many of which may affect their different stages of their annual life cycle.

Responses to this article can be read online at:  
<https://www.ace-eco.org/issues/responses.php/2090>

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care was approved under the University of New England IACUC protocol number UNE010-2009, and banding under U.S. federal permit 17610#23540.

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