Diel fledging patterns among grassland passerines: Relative impacts of energetics and predation risk

Authors: Ribic, Christine A., Ng, Christoph S., Koper, Nicola, Ellison, Kevin, Pietz, Pamela J., et al.

Source: The Auk, 135(4) : 1100-1112

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-17-213.1

The Auk
Ornithological Advances

AmericanOrnithology.org

Volume 135, 2018, pp. 1100–1112
DOI: 10.1642/AUK-17-213.1

RESEARCH ARTICLE

Diel fledging patterns among grassland passerines: Relative impacts of energetics and predation risk

Christine A. Ribic,[1]* Christoph S. Ng,[2] Nicola Koper,[2] Kevin Ellison,[3] Pamela J. Pietz,[4] and David J. Rugg[5]

[1] U.S. Geological Survey, Wisconsin Cooperative Wildlife Research Unit, University of Wisconsin, Madison, Wisconsin, USA
[2] Natural Resources Institute, University of Manitoba, Winnipeg, Manitoba, Canada
[3] Northern Great Plains Program, World Wildlife Fund, Bozeman, Montana, USA
[4] U.S. Geological Survey (emeritus), Northern Prairie Wildlife Research Center, Jamestown, North Dakota, USA
[5] U.S. Forest Service, Research and Development, Madison, Wisconsin, USA
* Corresponding author: caribic@wisc.edu

Submitted November 6, 2017; Accepted July 3, 2018; Published September 12, 2018

ABSTRACT

The time of day that nestlings fledge from a nest is thought to be shaped by predation risk and energetics. To minimize predation risk, fledging is predicted to start as early in the day as possible so that nestlings can maximize time outside the nest to find a safe place to stay before nightfall. Fledging times are predicted to be tightly grouped and to not be affected by the number of nestlings, given that all nestlings are responding to the same relative risk of predation. Conversely, energetic considerations predict that fledging time of day should vary so that nestlings can maximize energy intake before having to forage for themselves. However, data to evaluate the relative importance of these drivers in grassland birds are scarce because of the difficulty of observing nestlings as they fledge. We used nest surveillance video from 178 nests to evaluate how the initiation and duration of fledging varied among 7 grassland passerine species, as well as by the number of nestlings in the nest and fledging date. Fledging initiation varied most strongly by species, with some effects of date. Across species, the median start time of fledging was 4.55 hr after sunrise. Fledging before the solstice started ~30 min earlier compared to fledging at or after the solstice. Fledging duration increased with number of nestlings in the nest and was spread over >1 day in 21% of nests. While our results primarily supported the hypothesis that fledging is motivated by energetic considerations, additional data on basic life history traits and behavior will be needed to fully understand how fledging grassland birds balance energetics against predation risk.

Keywords: behavior, energetics, fledging duration, fledging time, grassland birds, predation

Patrones diarios de abandono del nido entre paserinos de pastizal: Impactos relativos de consideraciones energéticas y del riesgo de depredación

RESUMEN

Se piensa que la hora del día a la que los volantones abandonan el nido está modelada por el riesgo de depredación y por consideraciones energéticas. Para minimizar el riesgo de depredación, se predice que el abandono del nido se iniciará lo más temprano posible durante el día para que los volantones maximicen el tiempo afuera del nido para encontrar un lugar seguro donde quedarse antes del anochecer. Se predice que los tiempos de partida están fuertemente agrupados y no son afectados por el número de volantones, ya que todos ellos responden al mismo riesgo relativo de depredación. Por el contrario, las consideraciones energéticas predicen que la hora del día del abandono debería variar para que los volantones puedan maximizar el consumo de energía previo a tener que alimentarse por sí mismos. Sin embargo, los datos para evaluar la importancia relativa de estos factores en las aves de pastizal son escasos debido a la dificultad de observar a los volantones a medida que abandonan el nido. Usamos videos de vigilancia en 178 nidos para evaluar el número de volantones en el nido, la fecha de partida y cómo el inicio y la duración del período de abandono variaron entre siete especies de paserinos de pastizal. El inicio de la partida varió más fuertemente por especie, con algunos efectos de la fecha. Entre especies, la mediana de la hora de inicio de la partida fue 4.55 h luego del amanecer. La partida del nido antes del solsticio comenzó ~30 min más temprano comparada con la partida en o luego del solsticio. La duración de la partida aumentó con el número de volantones en el nido y se extendió por más de un día en 21% de los nidos. Mientras que nuestros resultados apoyaron principalmente la hipótesis de que la partida del nido está motivada por consideraciones energéticas, se necesitarán datos adicionales sobre los rasgos básicos de la historia de vida y de comportamiento para entender completamente cómo las aves de pastizal que abandonan el nido balancean las consideraciones energéticas frente al riesgo de depredación.

Palabras clave: aves de pastizal, comportamiento, consideraciones energéticas, depredación, duración del emplumamiento, hora de partida del nido

INTRODUCTION

Fledging behavior is one of the least understood aspects of the breeding ecology of birds (Johnson et al. 2004); more work has been conducted on cavity-nesting passerines (Skutch 1953, Lemel 1989, Nilsson 1990, Johnson et al. 2004, 2013, Schlicht et al. 2012) than on cup-nesting passerines (Pietz et al. 2012a, Chiavacci et al. 2015). Most grassland birds are ground nesters whose cup-style nests are relatively well concealed, making direct observation difficult (e.g., Potter 1974, Smith and Merkt 1980). But with the development of video surveillance systems for use in grasslands (Ribic et al. 2012b), we can begin to quantify fledging behavior in grassland birds.

The literature presents a variety of ideas regarding what motivates the decision to fledge from a nest, particularly from an energetics or development perspective. Johnson et al. (2004), in a survey of the literature, describes 4 potential motivators for fledging: parental manipulation (e.g., reducing feeding rates or amounts to motivate nestlings to leave), threshold size (i.e. minimum nestling development requirements have been met), nestling competition (e.g., nestling leaves first to get more food by intercepting parent), and inclusive fitness (i.e. more developed nestlings defer fledging in order to give their less developed nestmates an opportunity to grow enough for successful fledging). Others have suggested that fledging reflects a balance between predation risk and energy needs (Lemel 1989); avoiding in-nest predation risk may be a driver for minimizing the length of the nestling period (Remeš and Matysioková 2016). There are, however, relatively few hypotheses regarding the effect that avoiding predation might have on the time of day at which a fledgling leaves the nest. This may be due to the fact that the species that have been studied are primarily cavity-nesting birds where predation risk in the nest is low (e.g., Lemel 1989). Studying cup-nesting passerines in shrubs, which are subject to higher predation risk (e.g., Thompson 2007), Chiavacci et al. (2015) proposed that nestlings act to minimize their postfledging predation risk by leaving the nest early in the day to maximize time to find a place safe from predation outside the nest before dark, assuming that predation risk outside the nest is due to nocturnal predators; Chiavacci et al. (2015) labeled this the "maximum time hypothesis."

While these hypotheses are usually applied to understanding the time at which individual nestlings fledge when there are multiple nestlings in a nest, the hypotheses might also provide insight into duration of fledging (an emergent property of the nest). While fledging duration is often assumed to span a single daylight period, there appears to be a subset of nests in which fledging spans multiple days (Lemel 1989, Nilsson 1990, Johnson et al. 2004, 2013, Schlicht et al. 2012). Johnson et al. (2004, 2013) suggested that for nests with a fledging duration of 2 days, the first nestling to fledge may have been accidentally pushed out by a parent or sibling. However, Chiavacci et al. (2015) also found that a small but significant proportion of fledging durations spanned 2 days, indicating that the pattern may not be accidental.

The various hypotheses presented in the literature lead to different predictions about the time of day when the first nestling fledges (fledging initiation) and the time over which all nestlings fledge (fledging duration). Grassland birds are ground nesters, and their primary nest predators are generalists (Pietz et al. 2012b) that typically encounter nests by chance (Vickery et al. 1992, Heske et al. 1999). If birds optimize fledging time to minimize postfledging nocturnal predation risk, we would predict that all grassland species would follow similar patterns in fledging initiation to minimize this risk, and fledging duration should be short, because all nestlings should try to maximize daylight time to find a place outside the nest that is safe from predation at night. Fledging would also be predicted to start close to dawn each day to maximize time for fledglings to find safe shelter, regardless of the number of nestlings in the nest.

Energetics-related hypotheses suggest different predictions. There is little evidence that nestlings are fed at night (Slay et al. 2012), and energetics is related to body size (Weathers 1992), so nestlings from smaller-bodied species may be hungrier in the morning and more apt to leave the nest in search of the adult, leading to species variation in fledging initiation. In addition, fledging might be more likely to occur over an extended period (longer fledging durations) if some nestlings stay in the nest to obtain more food with lowered competition, particularly for nests with large numbers of nestlings. This expectation is based on Johnson et al.'s (2004) finding that in House Wrens (*Troglodytes aedon*), when parents are caring for fledglings and nestlings concurrently, there is no reduction in the frequency of parents feeding the nestlings, even though competition among nestlings has declined. The fledglings also experience less sibling competition before all of their siblings have fledged. Therefore, from an energetics perspective, fledging over multiple days could be advantageous.

Grassland birds nesting later in the breeding season can have lower nest success than birds nesting earlier in the season (Kershner et al. 2004a, Grant et al. 2005, Grant and Shaffer 2012). Fledging time, then, might also vary seasonally. If reduced nest success is due to increased predation later in the breeding season (e.g., Cox et al. 2013), fledging may start earlier in the day to ensure sufficient time to find a safe space in the face of heightened predation pressure. Alternatively, to the extent that renesting birds may be in poorer condition than earlier-nesting birds (Martin 1987), which might affect the parents' ability to care for nestlings, fledging from nests that were started later in the breeding season may start earlier in the day, as nestlings leave the nest to minimize competition from siblings.

To our knowlege, inclusive fitness and parental manipulation hypotheses have not received any attention in relation to time of day of fledging; those concepts have been used to understand what day, rather than what time of day, fledging should occur. Furthermore, discussions of inclusive fitness generally arise in the context of substantially older (i.e. larger) nestlings potentially staying in the nest longer than necessary, thereby providing their siblings an opportunity to develop enough to fledge successfully. Grassland passerines, however, do not appear to exhibit the type of asynchronous hatching (Pietz et al. 2012a) that would lead to strong age and development hierarchies that may be present in the cavity-nesting species for which possible inclusive fitness-oriented behavior has been considered (Johnson et al. 2004).

Given this paucity of data regarding the fledging behavior of grassland passerines, the variety of drivers proposed in the literature, and the support for different drivers provided by different studies, our objectives were to (1) determine the timing of fledging initiation and any variation due to species, number of nestlings, or date within the breeding season; (2) determine the proportion of nests that fledged over multiple days and compare fledging initiation of nests where fledging spanned multiple days to that of nests where fledging spanned a single day; (3) determine fledging duration and any variation with species, number of nestlings to fledge, and date within the breeding season; and (4) examine our findings on grassland passerine fledging behavior with respect to the maximum time and energetics hypotheses, as described in the literature.

METHODS

We used video records from published grassland-bird nesting studies. Study sites were located in Alberta, Canada, near Brooks (50.5642°N, 111.8989°W); in North Dakota, USA, near Jamestown (46.9000°N, 98.7167°W), Woodworth (47.1333°N, 99.3000°W), and Upham (48.5833°N, 100.7333°W); in Minnesota, USA, near Crookston (47.7833°N, 96.6167°W); and in Wisconsin, USA, near Mt. Horeb (43.0167°N, 89.7500°W). Alberta nests were contributed by Bernath-Plaisted and Koper (2016) ($n = 11$; 2013–2014); North Dakota and Minnesota nests were contributed by Pietz and Granfors (2017) ($n = 52$; 1996–2001); Wisconsin nests were contributed by Renfrew et al. (2005), Ribic et al. (2012a), Ellison et al. (2013), and Byers et al. (2017) ($n = 143$; 1999–2011). Fledging behavior was recorded in grassy habitats composed of native mixed-grass prairie, continuously and rotationally grazed pastures, remnant tall-grass prairie, or warm-season and cool-season fields enrolled in the U.S. Department of Agriculture's Conservation Reserve Program.

We used only nests for which we knew the fates of all nestlings; we did not include nests that experienced forced fledging (human-induced or otherwise) or partial depredation or that hosted Brown-headed Cowbird (*Molothrus ater*) young. Fledging time was defined as the time at which the nestling left the nest and did not return; times were recorded to the nearest second. Fledging duration was defined as the time difference between the fledging times of the first and last nestlings to fledge, and thus applies only to nests with $\geq$2 nestlings.

Field Methods

Although each study used slightly different nest surveillance systems to answer different questions, the general design was similar across studies. Beginning in early to mid-May and ending in late July, nests were systematically searched for. Nests were typically found by rope dragging or systematic walking by 2–8 technicians. Cameras were set up during both incubation and nestling stages and remained in place for the duration of the nesting period. Nest cameras were chosen for their small size, weatherproof housing, and infrared light-emitting diodes to permit recording under low-light conditions. Nest cameras were set up 10–50 cm away from nests and, depending on the height of surrounding vegetation, sometimes raised $\leq$40 cm above the ground on a dowel. Cameras were connected by 25 m or 50 m cables to a battery and either a videocassette recorder (VCR) or digital video recorder (DVR). The VCR systems captured $\sim$4 images s^{-1} and required a daily videotape change and a battery change every 3–4 days. The DVR systems captured $\sim$30 images s^{-1} and required a battery and SD card change every 3–4 days.

Video Review

We watched date- and time-stamped video of 206 nests to determine exact fledging times. Digital video was watched using VideoLAN VLC Media Player or DivX Player. Fledging times were determined by examining the video systematically. Because nestlings often took brief trips outside the nest before fledging permanently, it was most efficient to work backwards from the final fledge and iteratively "rewind" the video until all the nestlings were present in the nest. In this way, the times of fledging could be determined by counting the increasing number of remaining nestlings.

Data Analysis

To adjust for latitudinal differences in sunrise across the studies, fledging times were translated to time relative to local sunrise in decimal hours. Times of local sunrise were determined from the U.S. Naval Observatory (2016). Local sunrise was used to define the new day, so negative times were possible (i.e. fledging could occur after local midnight but before local sunrise). We used local sunrise because adult grassland birds tend to become active (i.e. leave the nest) around that time (Slay et al. 2012). The fledging metrics we used were time that the first nestling left the nest (i.e. fledging initiation) and difference between the first and last nestling fledging times (i.e. fledging duration).

We restricted analysis to species that had $\geq$10 observed nests. This resulted in a usable set of 7 species that made up 86% of the 206 nests: Bobolink ($n = 46$), Eastern Meadowlark ($n = 43$), Savannah Sparrow ($n = 26$), Clay-colored Sparrow ($n = 22$), Grasshopper Sparrow ($n = 14$), Song Sparrow ($n = 14$), and Chestnut-collared Longspur ($n = 13$). The remaining 28 nests were from 10 other species. Summary statistics are presented in Appendix Tables 5 and 6; for scientific names of species, see Appendix Table 5. The derived dataset containing data for all species is available in Ribic et al. (2018).

Using linear models, we evaluated how species, number of nestlings in the nest, and time within the breeding season affected fledging initiation or fledging duration. Species was a fixed factor. Number of nestlings in the nest varied from 1 to 6. To adjust for latitudinal differences in day length among the study sites, time within the breeding season was defined as solstice day length minus fledging day length. To differentiate fledging that occurred before and after the solstice, we multiplied the difference by -1 if fledging occurred prior to the solstice.

We included 2 other variables as alternates for species: average fledging mass (g) and average proportion of adult mass at fledging. None of the studies weighed nestlings; therefore, average fledging mass (g), average adult mass (g), and average proportion of adult mass at fledging were taken from the Birds of North America species accounts (Vickery 1996, Arcese et al. 2002, Wheelwright and Rising 2008, Grant et al. 2012, Jaster et al. 2012, Bleho et al. 2015, Renfrew et al. 2015). If average proportion of adult mass at fledging was not reported in those accounts, we derived it from average fledging and adult masses. The bird mass data can be found in Appendix Table 7.

Fledging initiation occurred across the 24 hr daily cycle, and time of day functions like degrees on a circle, so fledging initiation was a circular statistic. Therefore, we used a regression model of a circular response in relation to linear explanatory variables (Fisher 1993). Specifically, fledging initiation was transformed to radians, and a von Mises distribution was used for the error structure (Fisher 1993). Fledging duration is a time difference, which allowed us to use an ordinary least squares regression model. We used a linear model and a Gaussian error structure with a natural log transformation of fledging duration (i.e. fledging duration is log-normally distributed). Standard design matrices were used to model species effects. Because there might be a nonlinear response of the fledging metrics to day length, we also considered a polynomial function for fledging day length.

Because all 3 explanatory variables (species, number of nestlings, and fledging day length) could potentially affect the fledging metrics, we considered all combinations of variables for the set of a priori models for a total of 11 models (including fledging day length as a polynomial). We performed model selection using Akaike's Information Criterion corrected for small sample size ($\mathrm{AIC_c}$) and considered all models within 2 $\mathrm{AIC_c}$ units of the minimum $\mathrm{AIC_c}$ model to be competitive (Burnham and Anderson 2002). We calculated Akaike weights (w_i) and evidence ratios (w_1/w_i, where model 1 is the min$\mathrm{AIC_c}$ model and i indexes the rest of the models in the set; Burnham and Anderson 2002) to compare models in the competitive set. We also calculated relative variable importance over the entire set of models (Burnham and Anderson 2002) to determine which of the explanatory variables were most important. To understand how the different explanatory variables affected the fledging metric, we used the minimum $\mathrm{AIC_c}$ model to predict the fledging metrics over the observed range of each explanatory variable while holding the values for the other explanatory variables constant (Shaffer and Thompson 2007). Recall that when describing the effect of a particular, or focal, variable in a multivariable model, the nonfocal explanatory variables need to be held constant as the value of the focal explanatory variable changes. For our analyses, when variables were nonfocal, their values were, for example, species = Bobolink, number of nestlings in the nest = 4, and day length = 0 (i.e. fledging day was the solstice), average fledging mass = 15.4 g, and average proportion of adult mass at fledging = 0.762.

For nests that fledged over multiple days ("multiday nests"), we asked whether the first nestling to leave the multiday nest left later in the day compared to single-day nests. To answer this question, we reran the analysis of fledging initiation using only nests with $\geq$2 nestlings to fledge (i.e. those nests with the potential to be multiday nests) and added a variable for multiday nests. We also asked whether nestlings within the same multiday nest that fledged on different days (hereafter "subsequent-day nestlings") fledged at the same time of day as the first nestling out of those nests. We answered that question by taking the difference between the 2 times (paired by nest) and used a linear model to determine whether the intercept was different from zero.

Because existing hypotheses regarding fledging initiation ignore multiday nests, we planned to conduct additional analyses if multiday nest effects were found in the preceding analyses. This additional exploratory analysis would use the model results from the reduced

TABLE 1. Minimum AIC$_c$ model and models within 4 AIC$_c$ units for fledging initiation of 7 passerine species that nest in grasslands (n = number of nests, K = number of model parameters, w_i = Akaike weight, and evidence ratio = w_1/w_i, where model 1 is the minAIC$_c$ model and i indexes the rest of the models in the set). Poly(variable, 2) indicates the use of a quadratic function; species is a coded variable to represent the specific species of grassland bird; time within the breeding season is solstice day length minus fledging day length, with negative values indicating that fledging occurred prior to the solstice; and number of nestlings is the number of nestlings in the nest.

Model	n	K	ΔAIC$_c$	w_i	Evidence ratio
Species + poly(time within the breeding season, 2) + number of nestlings	178	11	0[a]	0.340	
Species + poly(time within the breeding season, 2)	178	10	0.75	0.234	1.45
Species	178	8	1.68	0.147	2.32
Species + number of nestlings	178	9	1.98	0.126	2.69
Species + time within the breeding season	178	9	3.36	0.063	5.37
Species + time within the breeding season + number of nestlings	178	10	3.58	0.058	5.83

[a] Lowest value of AIC$_c$ = –178.41.

dataset to explore whether multiday fledging might affect the modeling results from the full dataset. Because only nests with more than one nestling can fledge over multiple days, the multiday nest indicator and number of nestlings are correlated. We could use models with the 2 variables combined and separated to assess the relative impacts of the individual variables. In particular, when 2 related variables that are individually significant are placed in a combined model, generally either (1) both variables lose significance because they are explaining the same thing, and explanatory power is now shared between the 2 variables; (2) both variables become more significant because, while related, they explain different parts of the response (so, with both in the model, variance is further reduced, increasing significance); or (3) one variable remains significant and the other becomes insignificant. We thus expected AIC$_c$ model selection to provide reliable inferences about the relative strength of the 2 variables.

All analyses were computed using R 3.3.3 (R Core Team 2016); circular statistics analyses were computed with R package "circular" (Pewsey et al. 2013). Coefficient values are reported ± SE.

RESULTS

Fledging Initiation

Fledging time of the first nestling to leave the nest was influenced by species, time during the breeding season the nestling fledged, and how many nestlings were in the nest (Table 1). The model with average fledging mass instead of species was 14.4 AIC$_c$ units away from the minAIC$_c$ model, and the minAIC$_c$ model was 1,366× better than the average fledging mass model, indicating that fledging time variation by species was not explained by mean mass of the species' nestlings. Similarly, the model with fledging mass as a proportion of adult mass instead of species was 19.7 AIC$_c$ units away from the minAIC$_c$ model, and the minAIC$_c$ model was 18,769× better than the proportion of adult mass model. Therefore, we do not consider the mass models further.

Of the 3 explanatory variables in the minAIC$_c$ model (Table 1), species was most important (relative variable importance = 0.99). Fledging day length as a polynomial term was a better explanatory variable (relative importance value = 0.59) than fledging day length as a linear term (relative importance value = 0.13). Number of nestlings had a relative importance value of 0.54.

Average fledging initiation was spread out over the morning hours (Figure 1A). Clay-colored Sparrows started the earliest, at 3.33 hr after sunrise (coefficient = –0.32 ± 0.09), followed by Grasshopper Sparrows at 3.75 hr (coefficient = –0.21 ± 0.11). Species that started fledging the latest were Eastern Meadowlarks at 5.07 hr (coefficient = 0.15 ± 0.07), Song Sparrows at 5.24 hr (coefficient = 0.20 ± 0.12), and Chestnut-collared Longspurs at 5.84 hr after sunrise (coefficient = 0.40 ± 0.14). Savannah Sparrows at 4.08 hr (coefficient = –0.12 ± 0.08) and Bobolinks at 4.15 hr (coefficient = –0.10 ± 0.07) were in between the other species.

Fledging before the solstice started earlier in the day than fledging at or after the solstice (polynomial relationship: linear term coefficient = 0.45 ± 0.18; square term coefficient = –0.42 ± 0.19; Figure 1B). Nests that started to fledge before the solstice (when day length was 10 min shorter) were predicted to start fledging 3.82 hr after sunrise, compared to 4.15 and 4.39 hr for nests that started to fledge at the solstice and after the solstice (when day length was 10 min shorter), respectively. Fledging initiation started later if there were more nestlings in the nest (coefficient = 0.06 ± 0.01; Figure 1C). A single nestling was predicted to fledge at 3.52 hr after sunrise, compared to 4.36 hr for the first fledged from a nest with 5 nestlings.

Fledging over Multiple Days

There were 165 nests with ≥2 nestlings that fledged. Fledging spanned 1 day for 79% of these nests, 2 days for 18% of these nests, and 3 days for 3% of these nests (Table

TABLE 2. Number of nests, categorized by number of days over which fledging occurred, for 7 passerine species that nest in grasslands. For scientific names of species, see Appendix Table 5.

Species	Nests with multiple nestlings	Fledging period			Proportion multiple nests
		1 day	2 days	3 days	
Bobolink	41	36	4	1	0.122
Eastern Meadowlark	38	31	6	1	0.184
Savannah Sparrow	25	20	4	1	0.200
Clay-colored Sparrow	21	14	7	0	0.333
Grasshopper Sparrow	14	9	4	1	0.357
Chestnut-collared Longspur	13	9	3	1	0.308
Song Sparrow	13	11	2	0	0.154
Total	165	130	30	5	0.212

2). One-third of the nests of Grasshopper Sparrows, Chestnut-collared Longspurs, and Clay-colored Sparrows fledged over multiple days (Table 2). Combined over all species, the proportion of multiday nests increased with number of nestlings, ranging from a low of 13% for nests with 2 nestlings to 31% for nests with 5 nestlings (rho = 0.995, $P = 0.004$).

In this reduced dataset, first nestlings to leave multiday nests left later in the day than first nestlings from single-day nests (Table 3; multiday fledge indicator coefficient = 0.50 ± 0.09). The first nestling to leave a multiday nest was predicted to leave at 6.09 hr after sunrise, compared to 4.20 hr for the first nestling from a single-day nest. The multiday indicator variable (relative variable importance = 1.0) was just as important as species (relative variable importance = 1.0). While fledging day length as a polynomial maintained its importance in this reduced dataset (relative variable importance = 0.49), number of nestlings did not (relative importance value = 0.28).

The minAIC$_c$ model for nests with more than one nestling included the multiday nest indicator but not the number of nestlings (Table 3). Having both variables in the model reduced the model's explanatory power (Table 3), which suggests that the effect of number of nestlings on fledging initiation found using the full dataset might be due to the presence of multiday nests, which start fledging later in the day than single-day nests. When the models were run on the full dataset, the minAIC$_c$ model included only species, polynomial of fledging day length, and multiday indicator (AIC$_c$ = –202.41; multiday fledge indicator coefficient = 0.52 ± 0.09). Adding number of nestlings to this model resulted in a decrease in explanatory power (AIC$_c$ = –201.11; multiday fledge indicator coefficient = 0.49 ± 0.09; number of nestlings coefficient = 0.03 ± 0.03), indicating an overfit. The model with the multiday nest indicator (instead of number of nestlings) was better (~24 AIC$_c$ units lower) than the minAIC$_c$ model that included number of nestlings in Table 1. This indicates that substantially more of the variation in fledging initiation for the full dataset was explained by whether the nest was a multiday nest rather than by number of nestlings.

In addition, for multiday nests, the first nestling to leave the nest left later in the day than the nestlings that left first on the subsequent days. Subsequent-day nestlings left the nest, on average, 3.09 hr after sunrise ($n = 37$), earlier in the day than the nestling that first fledged from that nest the prior day (difference intercept = –5.19 ± 0.72 hr).

TABLE 3. Minimum AIC$_c$ model and models within 4 AIC$_c$ units for fledging initiation of nests with 2 or more nestlings to fledge, for 7 passerine bird species that nest in grasslands (n = number of nests, K = number of model parameters, w_i = Akaike weight, and evidence ratio = w_1/w_i, where model 1 is the minAIC$_c$ model and i indexes the rest of the models in the set). Poly(variable, 2) indicates the use of a quadratic function; species is a coded variable to represent the specific species of grassland bird; time within the breeding season is solstice day length minus fledging day length, with negative values indicating that fledging occurred prior to the solstice; number of nestlings is the number of nestlings in the nest; and multiday nest indicator is defined as 1 for nests taking >1 day to fledge all nestlings and 0 otherwise.

Model	n	K	ΔAIC$_c$	w_i	Evidence ratio
Species + poly(time within the breeding season, 2) + multiday nest indicator	165	11	0 [a]	0.345	
Species + multiday indicator	165	9	0.64	0.251	1.37
Species + poly(time within the breeding season, 2) + number of nestlings + multiday nest indicator	165	12	1.73	0.146	2.37
Species + time within the breeding season + multiday nest indicator	165	10	2.10	0.121	2.86
Species + number of nestlings + multiday nest indicator	165	10	2.70	0.089	3.86
Species + time within the breeding season + number of nestlings + multiday nest indicator	165	11	4.00	0.047	7.39

[a] Lowest value of AIC$_c$ = –182.87.

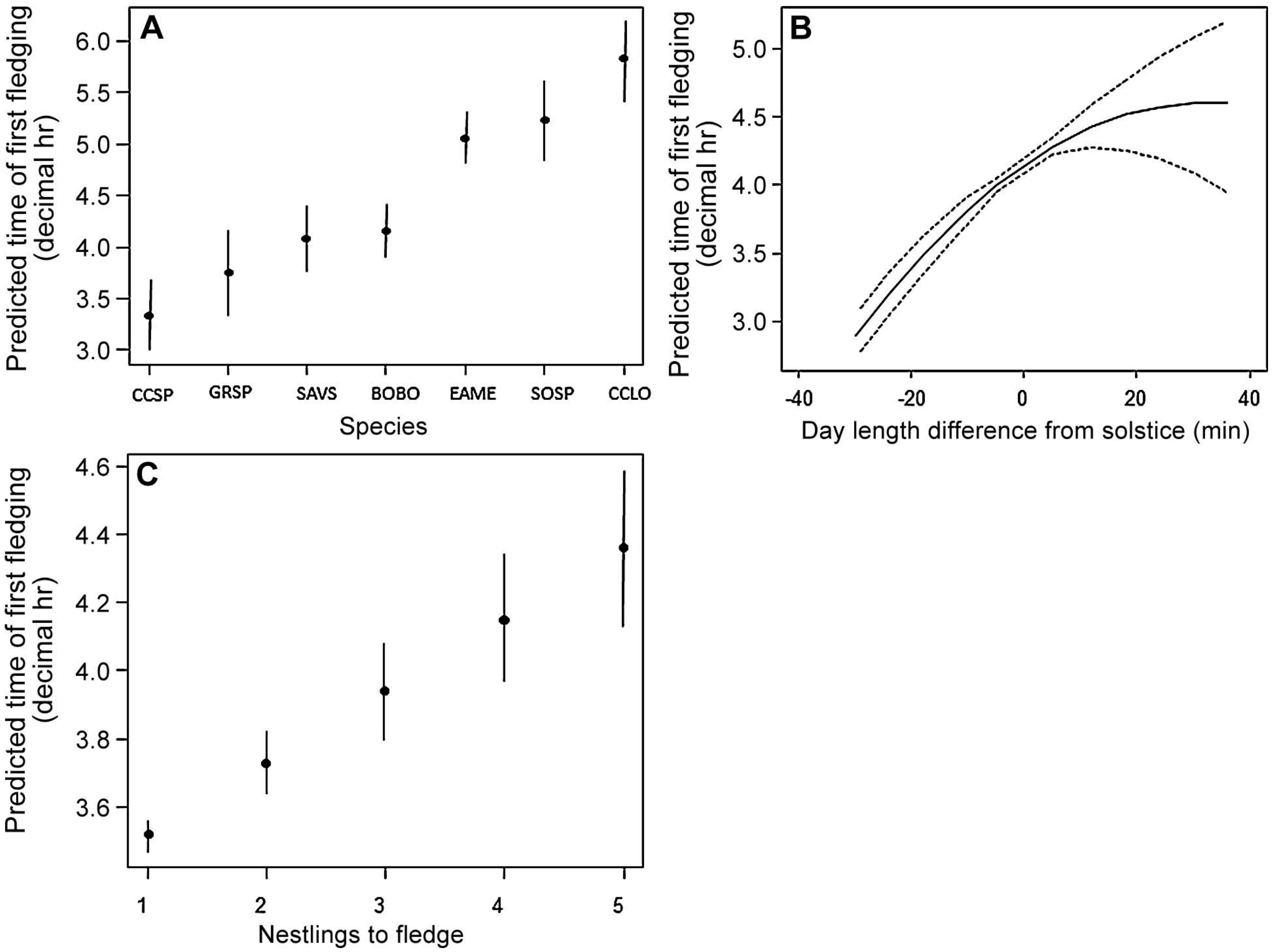

FIGURE 1. Predicted relationships between fledging initiation and (**A**) species, (**B**) time within the breeding season, and (**C**) number of nestlings in the nest, using the minimum AIC model based on data from 7 passerine species that nest in grasslands. Predicted time is in relation to local sunrise. Abbreviations: CCSP = Clay-colored Sparrow, GRSP = Grasshopper Sparrow, SAVS = Savannah Sparrow, BOBO = Bobolink, EAME = Eastern Meadowlark, SOSP = Song Sparrow, and CCLO = Chestnut-collared Longspur. For scientific names of species, see Appendix Table 5. Time within the breeding season is the difference in day length between the day of fledging and local solstice.

Fledging Duration

Fledging duration was influenced by number of nestlings to fledge and by fledging day length (Table 4). The most important explanatory variable was number of nestlings (relative variable importance = 1.0). Fledging day length as a linear term was a better explanatory variable (relative variable importance = 0.43) than fledging day length as a polynomial (relative importance value = 0.23). Species had a relative importance value of 0.34.

Fledging duration increased with increasing number of nestlings (coefficient = 0.82 ± 0.21). Predicted fledging duration for nests with 2 nestlings was 0.25 hr, whereas predicted fledging duration for nests with 5 nestlings was 2.98 hr. For fledging day length (coefficient = 1.24 ± 0.62), nests initiating fledging before the solstice (when day length was 10 min shorter) were predicted to have a fledging duration of 0.88 hr, compared to 1.44 hr for nests initiating fledging after the solstice (when day length was 10 min shorter).

DISCUSSION

We found that fledging initiation varied by species, time within the breeding season, and whether nests fledged over multiple days. We also found that nests with more nestlings had longer fledging durations and took longer to fledge later in the breeding season. These results are generally more consistent with hypotheses regarding energetic drivers of fledging, rather than maximizing time to avoid predation risk for grassland songbirds. However, while our results did not support the maximum time hypothesis, this does not imply that predation risk is not a driver in another context that we did not test. In addition,

TABLE 4. Minimum AIC_c model and models within 4 AIC_c units for fledging duration for 7 passerine species that nest in grasslands (n = number of nests, K = number of model parameters, w_i = Akaike weight, and evidence ratio = w_1/w_i, where model 1 is the minAIC_c model and i indexes the rest of the models in the set). Poly(variable, 2) indicates the use of a quadratic function; species is a coded variable to represent the specific species of grassland bird; time within the breeding season is solstice day length minus fledging day length, with negative values indicating that fledging occurred prior to the solstice; and number of nestlings is the number of nestlings in the nest.

Model	n	K	ΔAIC_c	w_i	Evidence ratio
Number of nestlings + time within the breeding season	165	4	0[a]	0.332	
Number of nestlings + species	165	8	0.97	0.204	1.63
Number of nestlings + poly(time within the breeding season, 2)	165	5	1.07	0.194	1.71
Number of nestlings	165	3	1.88	0.129	2.56
Number of nestlings + species + time within the breeding season	165	10	2.42	0.099	3.35

[a] Lowest value of $AIC_c = 787.64$.

some observations could not be understood through the mechanisms presented in the literature for either driver.

For fledging initiation, the grassland bird species in our study fell along a continuum from sunrise to late morning. From the supplemental material of Chiavacci et al. (2015), shrub-nesting bird species may demonstrate a similar continuum for fledging initiation, with Field Sparrows (*Spizella pusilla*) starting earliest (average of 1.94 hr from start of civil twilight) and Gray Catbirds (*Dumetella carolinensis*) starting latest (average of 7.64 hr from start of civil twilight). Chiavacci et al. (2015) did not report on how much species variability was associated with fledging initiation for shrub-nesting birds, but a regression analysis of their supplemental material indicates that nest height explained about a third of the variability in fledging initiation; the variability left unexplained would have been part of the random effect for species, indicating that species might vary in fledging initiation.

The underlying mechanism for the observed species differences in our study is unclear. Average fledging mass and fledging mass as a proportion of adult body mass (as taken from the literature) did not explain variation in fledging initiation in our study. This may be due to the relatively short period nestlings are in the nest in northern latitudes (Remeš and Matysioková 2016), causing nestlings across relatively synchronously hatching species, such as the grassland species in our study, to be at similar developmental stages when they fledge; thus, controlling for adult mass results in little variation in fledging mass proportions among the species. It may be that individual variation in mass is a more important consideration than species averages. Studies of Great Tits (*Parus major*; Lemel 1989) and Marsh Tits (*P. palustris*; Nilsson and Svensson 1993) found that individual nestling mass and wing development were good predictors of fledging time. The effect of nestling development on timing of fledging in grassland bird species needs further investigation.

While it appeared that single nestlings fledged earlier than the first nestlings from nests with multiple nestlings, this relationship was driven by nestlings from nests that fledged over multiple days. Chiavacci et al. (2015) did not find that the number of nestlings affected the fledging initiation for their shrub-nesting species, but they did not investigate differences between single-day and multiday nests. We found that nests containing multiple nestlings had 2 patterns of fledging—over a single day or over multiple days—and that the frequency of nests fledging over multiple days increased as the number of nestlings increased. Multiday fledging is more consistent with an energetics-based understanding of fledging than with maximizing time to reduce predation risk. Under the threshold size hypothesis, when there are multiple nestlings, it takes longer (i.e. more foraging trips) for the parents to feed the nestlings enough to pass the nestlings' energetics threshold, which leads to fledging starting later in the day. As fewer nestlings remain in the nest on subsequent days, remaining nestlings may obtain their minimum required energy much earlier, and this may explain the much earlier start to fledging on the second day.

Previous qualitative observations of grassland-nesting passerines have found that fledging can occur over >1 day (e.g., Song Sparrow; Smith and Merkt 1980), but quantification has been lacking. Our estimate that ~20% of nests fledge over multiple days is consistent with studies of shrub-nesting (Chiavacci et al. 2015) and cavity-nesting birds (Johnson et al. 2004, 2013, Schlicht et al. 2012). While cavity-nesting birds have the danger of falling from the nest, which may result in multiday fledging by accident (Johnson et al. 2004, 2013), grassland passerines nest on the ground, and nestlings can simply return to the nest if pushed out. Such behavior would be consistent with our observations of various nestlings leaving and returning to the nest several times before fledging. The fledging time difference we observed for multiday nests in our ground-nesting grassland species (i.e. first nestling leaves later in the day than the nestling that fledges first the next day) is consistent with Johnson et al.'s (2013) observations of Mountain Bluebirds (*Sialia currucoides*).

We know of no other study that has evaluated explanatory variables to account for variation in fledging duration. In our study, number of nestlings in the nest affected how long fledging takes. The patterns we found suggest that individual nestlings may maximize time in the nest to obtain more energy as sibling competition declines. We suggest that long fledging durations, including fledging over multiple days, may be a strategy for balancing energetic considerations (more food to reach threshold size) with predation risk (being attacked in the nest).

Although there is evidence for other aspects of fledging ecology changing as the breeding season advances (e.g., compression of the postfledging period to independence; Bustamante and Hiraldo 1990), we know of no other study that has considered how fledging initiation or duration might vary in relation to time within the breeding season. We found that nestlings started to fledge earlier in the day and that fledging duration was shorter in the early part of the breeding season. Additional study investigating changes in grassland birds' nesting ecology over the breeding season would be helpful to confirm these patterns and understand the drivers in a larger context.

Overall, in grassland birds, given the current hypotheses regarding fledging time, we found more support for the idea that the act of fledging is influenced by energetics rather than the time maximization hypothesis related to predation risk. In some respects, it is not surprising that the time maximization hypothesis is not highly predictive for grassland birds. The hypothesis is based on the importance of nocturnal predation as a driver; while nocturnal nest predation does occur, the major predators of grassland bird nests are diurnal (Pietz et al. 2012b). Grassland birds face high predation (often >60%) in the nest (e.g., Martin 1995), but diurnal predators will be active when the nestlings fledge during the day. The majority of fledgling grassland birds die in the first week out of the nest (e.g., Kershner et al. 2004b, Yackel Adams et al. 2006, Berkeley et al. 2007, Suedkamp-Wells et al. 2007, Hovik et al. 2011, Giovanni et al. 2015), and survival can be extremely low during that time (<20%; Yackel Adams et al. 2006). This implies that nestling grassland birds are likely moving from a high-risk environment into another high-risk environment.

It seems likely that nestlings balance 2 competing demands in deciding when to fledge. On one hand, it is advantageous to the nestling to remain in the nest as long as possible to maximize development and thereby reduce postfledging predation risk (Remeš and Matysioková 2016). On the other hand, in the northern temperate grassland systems where our studies took place, nestlings need to leave the nest soon enough to learn the skills needed to survive and ultimately migrate south. For example, House Wrens in migratory areas fledge sooner than those in nonmigratory areas (Johnson et al. 2004). However, some of our observations could not be understood through the hypotheses presented in the literature, which suggests that the paucity of studies on this topic has left gaps in our conceptual understanding of fledging behavior. Also, numerous patterns that we explored have not previously been discussed in the literature, leaving us with a limited ability to generalize our observations to other systems. Clearly, there is much work to be done toward understanding the interplay between the evolutionary force of predation and the ecological force of energetics in affecting fledging and other aspects of the breeding ecology of birds (Ibáñez-Álamo et al. 2015), and the various strategies developed by passerines for resolving this interplay.

ACKNOWLEDGMENTS

We thank our research collaborators T. J. Anderson, C. Byers, J. Dadisman, H. Doyle, P. J. Gouse, T. A. Grant, M. J. Guzy, D. H. Johnson, S. L. Jones, E. M. Madden, J. L. Nack, R. B. Renfrew, D. W. Sample, D. Schneider, J. A. Shaffer, and M. Winter. We thank all the field technicians who helped collect the data used in this paper. Camera systems were built by J. Bernath-Plaisted, J. Christensen, J. Dadisman, K. S. Ellison, R. Fuhrman, D. K. Garcelon, and J. Yoo. We thank A. Pidgeon and B. Zuckerberg for comments on the manuscript. We thank the U.S. Forest Service for assistance with publication expenses. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Funding statement: No outside funding supported this manuscript. However, the U.S. Geological Survey had to approve the manuscript before publication.

Ethics statement: No new data were collected for this manuscript. However, the original projects were conducted in compliance with the Guidelines to the Use of Wild Birds in Research. Data collection for the projects in Wisconsin was done under protocols A01023, A01410, and A1210 approved by the Animal Care and Use Committee of the University of Wisconsin-Madison. Data collection for the project in Alberta was done under protocol F12-010/1 approved by the Animal Care and Use Committee of the University of Manitoba. Data collection for the projects in North Dakota and Minnesota was done under a protocol approved by internal memorandum of the Animal Care and Use Committee of the U.S. Geological Survey, Northern Prairie Wildlife Research Center.

Author contributions: C.A.R. conceived the idea of the paper. C.A.R., K.E., and D.J.R. formulated questions and hypotheses. C.A.R., C.S.N., N.K., and P.J.P. collected the data. C.A.R. and D.J.R. analyzed the data. C.A.R., D.J.R., and C.S.N. wrote the paper, with substantial edits from K.E., N.K., and P.J.P.

Data deposits: The derived dataset used in this study is deposited with the U.S. Forest Service Research Data Archive and can be accessed at https://doi.org/10.2737/RDS-2018-0001. The base data from North Dakota and Minnesota are deposited with ScienceBase and can be accessed at https://doi.

org/10.5066/F7V98780. At the time of this project, the base data from Alberta, Canada, and Wisconsin had not been published by the funders of the original projects (U.S. Fish and Wildlife Service and Wisconsin Department of Natural Resources for the Wisconsin projects; Natural Sciences and Engineering Research Council and Cenovus Energy for the Alberta projects).

LITERATURE CITED

Arcese, P., M. K. Sogge, A. B. Marr, and M. A. Patten (2002). Song Sparrow (*Melospiza melodia*), version 2.0. In Birds of North America Online (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.704

Berkeley, L. I., J. P. McCarty, and L. L. Wolfenbarger (2007). Postfledging survival and movement in Dickcissels (*Spiza americana*): Implications for habitat management and conservation. The Auk 124:396–409.

Bernath-Plaisted, J., and N. Koper (2016). Physical footprint of oil and gas infrastructure, not anthropogenic noise, reduces nesting success of some grassland songbirds. Biological Conservation 204:434–441.

Bleho, B., K. Ellison, D. P. Hill, and L. K. Gould (2015). Chestnut-collared Longspur (*Calcarius ornatus*), version 2.0. In Birds of North America Online (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.288

Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second edition. Springer, New York, NY, USA

Bustamante, J., and F. Hiraldo (1990). Factors influencing family rupture and parent–offspring conflict in the Black Kite *Milgrus migrans*. Ibis 132:58–67.

Byers, C. M., C. A. Ribic, D. W. Sample, J. D. Dadisman, and M. R. Guttery (2017). Grassland bird productivity in warm season grass fields in southwest Wisconsin. The American Midland Naturalist 178:47–63.

Chiavacci, S. J., M. P. Ward, and T. J. Benson (2015). Why fledge early in the day? Examining the role of predation risk in explaining fledging behavior. Behavioral Ecology 26:593–600.

Cox, W. A., F. R. Thompson III, and J. L. Reidy (2013). The effects of temperature on nest predation by mammals, birds, and snakes. The Auk 130:784–790.

Ellison, K. S., C. A. Ribic, D. W. Sample, M. J. Fawcett, and J. D. Dadisman (2013). Impacts of tree rows on grassland birds and potential nest predators: a removal experiment. PLOS One 8: e59151.

Fisher, N. I. (1993). Statistical Analysis of Circular Data. Cambridge University Press, New York, NY, USA.

Giovanni, M. D., L. A. Powell, and W. H. Schacht (2015). Habitat preference and survival for Western Meadowlark (*Sturnella neglecta*) fledglings in a contiguous prairie system. The Wilson Journal of Ornithology 127:200–211.

Grant, T. A., and R. W. Knapton (2012). Clay-colored Sparrow (*Spizella pallida*), version 2.0. In Birds of North America Online (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.120

Grant, T. A., and T. L. Shaffer (2012). Time-specific patterns of nest survival for ducks and passerines breeding in North Dakota. The Auk 129:319–328.

Grant, T. A., T. L. Shaffer, E. M. Madden, and P. J. Pietz (2005). Time-specific variation in passerine nest survival: New insights into old questions. The Auk 122:661–672.

Heske, E. J., S. K. Robinson, and J. D. Brawn (1999). Predator activity and predation on songbird nests on forest-field edges in east-central Illinois. Landscape Ecology 14:345–354.

Hovik, T. J., J. R. Miller, R. R. Koford, D. M. Engle, and D. M. Debinski (2011). Postfledging survival of Grasshopper Sparrows in grasslands managed with fire and grazing. The Condor 113:429–437.

Ibáñez-Álamo, J. D., R. D. Magrath, J. C. Oteyza, A. D. Chalfoun, T. M. Haff, K. A. Schmidt, R. L. Thomson, and T. E. Martin (2015). Nest predation research: Recent findings and future perspectives. Journal of Ornithology 156 (Supplement 1): 247–262.

Jaster, L. A., W. E. Jensen, and W. E. Lanyon (2012). Eastern Meadowlark (*Sturnella magna*), version 2.0. In Birds of North America Online (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.160

Johnson, L. S., R. M. Hebert, F. M. Napollillo, and A. Allen (2013). The process of fledging in the Mountain Bluebird. Journal of Field Ornithology 84:367–376.

Johnson, L. S., R. L. Rauch, and S. N. Dellone (2004). The process and causes of fledging in a cavity-nesting passerine bird, the House Wren (*Troglodytes aedon*). Ethology 110:693–705.

Kershner, E. L., J. W. Walk, and R. E. Warner (2004a). Breeding-season decisions, renesting, and annual fecundity of female Eastern Meadowlarks (*Sturnella magna*) in southeastern Illinois. The Auk 121:796–805.

Kershner, E. L., J. W. Walk, and R. E. Warner (2004b). Postfledging movements and survival of juvenile Eastern Meadowlarks (*Sturnella magna*) in Illinois. The Auk 121:1146–1154.

Lemel, J. (1989). Body-mass dependent fledging order in the Great Tit. The Auk 106:490–492.

Martin, T. E. (1987). Food as a limit on breeding birds: A life-history perspective. Annual Review of Ecology and Systematics 18:453–487.

Martin, T. E. (1995). Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65: 101–127.

Nilsson, J.-A. (1990). What determines the timing and order of nest-leaving in the Marsh Tit (*Parus palustris*)? In Population Biology of Passerine Birds: An Integrated Approach (J. Blondel, A. Gosler, J.-D. Lebreton, and R. McCleery, Editors). NATO Advanced Science Institute Series G: Ecological Sciences 24:369–379.

Nilsson, J.-A., and M. Svennson (1993). Fledging in altricial birds: Parental manipulation or sibling competition? Animal Behaviour 46:379–386.

Pewsey, R. A., M. Neuhäuser, and G. D. Ruxton (2013). Circular Statistics in R. Oxford University Press, Oxford, UK.

Pietz, P. J., and D. A. Granfors (2017). Fledging times of grassland birds in North Dakota and Minnesota. U.S. Geological Survey data release. https://doi.org/10.5066/F7V98780

Pietz, P. J., D. A. Granfors, and T. A. Grant (2012a). Hatching and fledging times from grassland passerine nests. Studies in Avian Biology 43:47–60.

Pietz, P. J., D. A. Granfors, and C. A. Ribic (2012b). Knowledge gained from video-monitoring grassland passerine nests. Studies in Avian Biology 43:3–22.

Potter, P. E. (1974). Breeding behavior of Savannah Sparrows in southeastern Michigan. Jack-Pine Warbler 52:50–63.

R Core Team (2016). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

Remeš, V., and B. Matysioková (2016). Survival to independence in relation to pre-fledging development and latitude in songbirds across the globe. Journal of Avian Biology 47:610–618.

Renfrew, R., C. A. Ribic, and J. L. Nack (2005). Edge avoidance by nesting grassland birds: A futile strategy in a fragmented landscape. The Auk 122:618–636.

Renfrew, R., A. M. Strong, N. G. Perlut, S. G. Martin, and T. A. Gavin (2015). Bobolink (*Dolichonyx oryzivorus*), version 2.0. In Birds of North America Online (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.176

Ribic, C. A., M. J. Guzy, T. J. Anderson, D. W. Sample, and J. L. Nack (2012a). Bird productivity and nest predation in agricultural grasslands. Studies in Avian Biology 43:119–134.

Ribic, C. A., P. J. Pietz, N. Koper, and C. S. Ng (2018). Fledging times of grassland birds. Forest Service Research Data Archive. https://doi.org/10.2737/RDS-2018-0001

Ribic, C. A., F. R. Thompson III, and P. J. Pietz (Editors) (2012b). Video surveillance of nesting birds. Studies in Avian Biology 43.

Schlicht, L. A., A. Girg, P. Loës, M. Valcu, and B. Kempenaers (2012). Male extrapair nestlings fledge first. Animal Behaviour 83:1335–1343.

Shaffer, T. L., and F. R. Thompson III (2007). Making meaningful estimates of nest survival with model-based methods. Studies in Avian Biology 34:84–95.

Skutch, A. F. (1953). Life history of the southern House Wren. The Condor 55:121–149.

Slay, C. M., K. S. Ellison, C. A. Ribic, K. G. Smith, and C. M. Schmitz (2012). Nocturnal activity of nesting shrubland and grassland passerines. Studies in Avian Biology 43:105–116.

Smith, J. N. M., and J. R. Merkt (1980). Development and stability of single-parent family units in the Song Sparrow. Canadian Journal of Zoology 58:1869–1875.

Suedkamp Wells, K. M., M. R. Ryan, J. J. Millspaugh, F. R. Thompson III, and M. W. Hubbard (2007). Survival of postfledging grassland birds in Missouri. The Condor 109: 781–794.

Thompson, F. R., III (2007). Factors affecting nest predation on forest songbirds in North America. Ibis 149:98–109.

U.S. Naval Observatory (2016). Sun or moon rise/set table for one year. http://aa.usno.navy.mil/data/docs/RS_OneYear.php

Vickery, P. D. (1996). Grasshopper Sparrow (*Ammodramus savannarum*), version 2.0. In Birds of North America Online (A. F. Poole and F. B. Gill, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.239

Vickery, P. D., M. L. Hunter, Jr., and J. V. Wells (1992). Evidence of incidental nest predation and its effects on nests of threatened grassland birds. Oikos 63:281–288.

Vickery, P. D., P. L. Tubaro, J. M. Cardosa da Silva, B. G. Peterjohn, J. R. Herkert, and R. B. Cavalcanti (1999). Conservation of grassland birds in the Western Hemisphere. Studies in Avian Biology 19:2–26.

Weathers, W. W. (1992). Scaling nestling energy requirements. Ibis 134:142–153.

Wheelwright, N. T., and J. D. Rising (2008). Savannah Sparrow (*Passerculus sandwichensis*), version 2.0. In Birds of North America Online (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.45

Yackel Adams, A. A., S. K. Skagen, and J. A. Savidge (2006). Modeling post-fledging survival of Lark Buntings in response to ecological and biological factors. Ecology 87:178–188.

APPENDIX TABLE 5. Summary statistics for fledging time of first nestling to leave the nest (i.e. fledging initiation) for 13 obligate grassland species, 2 facultative grassland species, and 2 generalist species. Summary statistics are given for species with ≥5 nests; otherwise the data are given. Decimal time is in relation to local sunrise. Categorization of species by habitat specialization is based on Vickery et al. (1999). Data for all species are in Ribic et al. (2018).

		Fledging initiation (decimal hour)					
Species	Nests	Circular mean	Resultant length [a]	Median	Interquartile range	Earliest	Latest
Obligate grassland birds							
Bobolink (*Dolichonyx oryzivorus*)	46	4.39	0.77	4.17	2.60–5.49	0.82	12.23
Eastern Meadowlark (*Sturnella magna*)	43	5.78	0.65	5.18	3.51–8.16	0.78	13.38
Savannah Sparrow (*Passerculus sandwichensis*)	26	4.36	0.61	4.55	2.71–5.56	−1.50	15.57
Grasshopper Sparrow (*Ammodramus savannarum*)	14	3.91	0.62	4.10	1.85–6.03	1.00	14.35
Chestnut-collared Longspur (*Calcarius ornatus*)	13	7.76	0.55	8.97	4.25–11.43	1.13	12.75
Henslow's Sparrow (*Ammodramus henslowii*)	7	3.58	0.55	2.88	2.00–6.40	0.27	13.25
Vesper Sparrow (*Pooecetes gramineus*)	2	4.6, 9.95					
Baird's Sparrow (*Ammodramus bairdii*)	1	8.97					
Dickcissel (*Spiza americana*)	1	1.13					
Horned Lark (*Eremophila alpestris*)	1	5.60					
Sedge Wren (*Cistothorus platensis*)	1	6.95					
Western Meadowlark (*Sturnella neglecta*)	1	4.58					
Sprague's Pipit (*Anthus spragueii*)	1	1.27					
Facultative grassland birds							
Clay-colored Sparrow (*Spizella pallida*)	22	2.75	0.74	2.57	1.17–4.14	−2.28	12.57
Field Sparrow (*Spizella pusilla*)	5	3.48	0.79	4.23	0.58–5.65	0.37	6.37
Generalists							
Song Sparrow (*Melospiza melodia*)	14	5.97	0.74	6.17	4.04–8.11	2.57	15.10
Common Yellowthroat (*Geothlypis trichas*)	8	3.98	0.59	2.75	1.88–7.23	0.80	10.85

[a] Measure of variation for circular statistics; measure is bounded between 0 and 1; values close to 1 indicate that the data are clustered around the mean.

APPENDIX TABLE 6. Summary statistics for fledging duration in 13 obligate grassland species, 2 facultative grassland species, and 2 generalist species from nests that had ≥2 nestlings. Summary statistics are given for species with ≥5 nests; otherwise the data are given. Categorization of species by habitat specialization is based on Vickery et al. (1999). Data for all species are in Ribic et al. (2018). For scientific names of species, see Appendix Table 5.

		Fledging duration (decimal hour)					
Species	Nests	Average	SD	Median	Interquartile range	Shortest	Longest
Obligate grassland birds							
Bobolink	41	3.99	8.10	0.82	0.17–3.74	0.03	40.82
Eastern Meadowlark	39	5.41	10.47	0.48	0.04–3.28	0	49.85
Savannah Sparrow	24	7.21	10.14	3.33	0.82–7.26	0.17	37.48
Grasshopper Sparrow	14	8.38	13.07	1.41	0.18–12.58	0	44.60
Chestnut-collared Longspur	13	10.07	13.33	4.23	0.62–16.55	0.005	45.49
Henslow's Sparrow	7	4.57	7.14	0.68	0.30–7.17	0.04	16.33
Vesper Sparrow	2	0.48, 23.77					
Baird's Sparrow	1	0.87					
Dickcissel	1	7.83					
Horned Lark	1	0					
Sedge Wren	1	0.03					
Western Meadowlark	1	0					
Sprague's Pipit	1	0.91					
Facultative grassland birds							
Clay-colored Sparrow	21	8.91	10.09	1.73	0.50–19.13	0	25.93
Field Sparrow	3	0.05, 0.07, 0.19					
Generalists							
Song Sparrow	13	4.49	1.89	6.82	0.33–3.66	0	22.73
Common Yellowthroat	6	0.20	0.10	0.24	0.07–0.17	0.04	0.69

APPENDIX TABLE 7. Average fledging mass, average adult mass, and average proportion of adult mass at fledging for 7 passerine birds that nest in grasslands. For scientific names of species, see Appendix Table 5.

Species	Average fledging mass (g)	Average adult mass (g)	Proportion adult body mass (g)	Source
Clay-colored Sparrow	10.3	12	0.858	Grant and Knapton 2012
Grasshopper Sparrow	10.1	17.5	0.576	Vickery 1996 [a]
Savannah Sparrow	15.4	20.1	0.766	Wheelwright and Rising 2008
Bobolink	21.6	31.2	0.692	Renfrew et al. 2015 [b]
Eastern Meadowlark	58.94	111.65	0.528	Jaster et al. 2012
Song Sparrow	17.8	20.8	0.856	Arcese et al. 2002
Chestnut-collared Longspur	15.1	19.8	0.762	Bleho et al. 2015

[a] We did not use *floridanus* adult mass average.

[b] We used averaged masses of breeding adult males and females.