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RESEARCH ARTICLE

Post-fledging habitat use in the Dickcissel

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ABSTRACT

Effective habitat management requires understanding habitat needs across a species' life history stages. In songbirds, management of breeding habitat is generally focused on the pre-nesting and nesting stages, while habitat use during the critical post-fledging stage remains understudied and is seldom a target for management. In 2014 and 2015, we documented post-fledging habitat use of Dickcissels (*Spiza americana*) in central Illinois, USA. We examined vegetation characteristics used by fledglings and how fledgling survival varied with habitat use. We also compared fledgling habitat use to nesting site habitat. Fledgling Dickcissels used areas with vegetation that was overall denser and more concealed than at random locations. Fledglings preferentially selected dense vegetation after fledging (days 1–3 post-fledging), and then used even denser vegetation once they became more mobile (days 4–11 post-fledging). Fledglings that used comparatively denser habitat were more likely to survive the critical part of the post-fledgling period (days 0–3 post-fledging), but not during subsequent parts of the post-fledging period (>3 days post-fledging). Habitat characteristics preferred by fledglings did not differ from those preferred by females for nest sites. Our results suggest that dense vegetation is needed for fledglings until they develop adequate mobility to evade predators. Furthermore, our finding of a positive association between fledgling survival and denser habitat during, but not after, the critical part (days 0–3) of the post-fledging period identifies an important window for management to increase fledgling survival. Management for dense habitat, however, must be appropriately timed not to disturb adults, nests, and young, immobile fledglings.

Keywords: conservation, Dickcissel, fledging, habitat, micro-habitat, post-fledging, songbird

Uso del Hábitat Post-emplumamiento en *Spiza americana*

RESUMEN

En manejo efectivo del hábitat requiere entender las necesidades de hábitat a través de las etapas de la historia de vida de una especie. En las aves canoras, el manejo del hábitat reproductivo se enfoca generalmente en las etapas de pre-anidación y anidación, mientras que el uso del hábitat durante la etapa crítica de post-emplumamiento sigue siendo poco estudiado y es raramente un objetivo de manejo. En 2014 y 2015, documentamos el uso del hábitat post-emplumamiento de *Spiza americana* en el centro de Illinois, EEUU. Examinamos las características de la vegetación usadas por los volantones y cómo la supervivencia de los volantones varió con el uso del hábitat. También comparamos el uso del hábitat de los volantones con el hábitat del sitio de anidación. Los volantones de *S. americana* usaron áreas con vegetación que fue en general más densa y más cerrada que la de lugares al azar. Los volantones seleccionaron preferencialmente vegetación densa luego de emplumar (días 1–3 post-emplumamiento), y luego usaron vegetación incluso más densa una vez que se volvieron más móviles (días 4–11 post-emplumamiento). Los volantones que usaron comparativamente hábitat más denso tuvieron mayor probabilidad de sobrevivir la parte crítica del período post-emplumamiento (días 0–3 post-emplumamiento), pero no durante las partes subsecuentes del período de post-emplumamiento (>3 días post-emplumamiento). Las características del hábitat preferidas por los volantones no difirieron de las preferidas por las hembras para los sitios de anidación. Nuestros resultados sugieren que los volantones necesitan vegetación más densa hasta que desarrollan una movilidad adecuada para evadir a los depredadores. Más aún, nuestro hallazgo de una asociación positiva entre la supervivencia de los volantones y el hábitat más denso durante, pero no luego, de la parte crítica (días 0–3) del período de post-emplumamiento identifica una ventana importante de manejo para aumentar la supervivencia de los volantones. El manejo para un hábitat denso, sin embargo, debe ser temporalizado apropiadamente para no alterar a los adultos, los nidos y los juveniles volantones inmóviles.

Palabras clave: Ave canora, Conservación, Emplumamiento, Hábitat, Micro-hábitat, Post-emplumamiento, *Spiza americana*

INTRODUCTION

Species' habitat needs often vary within and among life history stages. Thus, for conservation to be effective, management must integrate knowledge of species' habitat needs for all phases of their life cycles (Norris and Marra 2007). In songbirds, habitat management and conservation has focused primarily on the nesting phase, while one of the most critical phases—the post-fledging period—remains comparatively understudied (Maness and Anderson 2013, Cox et al. 2014, Remeš and Matysioková 2016). Often defined as the time between when a nestling leaves the nest and when it migrates or disperses, the post-fledging period is associated with high rates of mortality, particularly during the first days after fledging when juveniles are still in early stages of development (Anders et al. 1998, Vega Rivera et al. 1998, Berkeley et al. 2007, Vitz and Rodewald 2011, Naef-Daenzer and Gruebler 2016). As fledgling survival is thought to play a critical role in avian population dynamics (Anders et al. 1997, Anders and Marshall 2005, Cox et al. 2014, Jenkins et al. 2016), insuring suitable post-fledging habitat is available for juvenile birds should be a management priority.

Fledgling habitat may differ markedly from nesting habitat (differences in stage-specific habitat use; Jones and Bock 2005, King et al. 2006, Vitz and Rodewald 2010, Streby et al. 2013, Jenkins et al. 2016), which poses a challenge for land managers. Furthermore, fledglings may use a variety of habitats throughout the post-fledging period as they age and become more mobile (age-specific habitat use; e.g., Small et al. 2015, Jenkins et al. 2016). Thus, understanding differences in stage- and age-specific habitat use and consequences for individual survival (e.g., how age-specific post-fledging habitat use relates to fledgling survival) may be critical for conservation agencies as land management actions can be undertaken with the aim of improving songbird survival (Jenkins et al. 2016). Unfortunately, there remains a paucity of studies comparing nesting and age-specific post-fledging habitat use in songbirds (Cox et al. 2014, Small et al. 2015).

We examined associations between habitat use, survival, and age of fledgling Dickcissels (*Spiza americana*) in central Illinois, USA. An obligate grassland specialist (Temple 2002), Dickcissels are part of a grassland bird community experiencing the steepest population declines of any group of birds in recent decades (Brennan and Kuvlesky 2005, Sauer et al. 2017). Thus, a more complete understanding of stage- and age-specific habitat needs in grassland species such as the Dickcissel may be critical for conserving imperiled grassland birds. Specifically, the objectives of our study were to (1) compare habitat use of fledglings to (a) available habitat and (b) nesting sites from which fledglings originated, and (2) examine age-

specific post-fledging habitat use in the context of fledgling mobility and survival.

METHODS

Focal Species and Study Sites

In 2014 and 2015, we studied Dickcissels on 2 grassland sites of 129.5 ha and 259 ha ~15 km apart in central Illinois, USA. Converted from agricultural lands roughly 10 years ago, the grasslands are part of the State Acres for Wildlife Enhancement program in Illinois and have been managed by the Illinois Department of Natural Resources (with complete burns every 3 years during March, and mowing and spraying of herbicides in May). Each grassland consists of a mosaic of warm- and cool-season grasses and native forbs (*Sorghastrum nutans*, *Andropogon gerardi*, *Elymus canadensis*, *Solidago* spp., *Ambrosia* spp., and *Symphyotrichum pilosum*) along with exotic invasives (*Bromus inermis*, *Setaria* spp., *Medicago sativa*, *Cirsium arvense*), and wetland areas (1–2 small, <2 ha, pond[s]). Both grasslands are surrounded by agricultural lands, which rotate corn and soybeans.

Capturing and Marking Nestlings

From May through August of 2014 and 2015, we located Dickcissel nests by systematically searching vegetation and observing behavioral cues of adults. We visited nests every 3–6 days, and every 1 or 2 days as fledging approached. On the day of fledging (day 7 or 8 post-hatching), we captured nestlings and banded them with a metal U.S. Geological Survey leg band and a unique combination of plastic color bands. Additionally, we attached a 0.7-g radio-transmitter with a 12 cm whip antenna and 42–60 days of battery life (Lotek, Newmarket, Ontario, Canada, and DJC Corporation, Fisher, Illinois, USA) to 1–3 randomly selected nestlings per brood. We attached transmitters using an adult-size backpack (determined via Naef-Daenzer 2007) with figure-eight leg harness constructed with elastic beaded cord (Rappole and Tipton 1991). To prevent the adult-size harness from falling off, we glued a synthetic fabric under each transmitter. This bit of fabric eventually fell off, or was preened off by fledglings (T. Jones, personal observations) as they grew. Our transmitter/harness design weighed approximately 3–5% of fledgling body mass. We radio-tagged more than one nestling from some broods because past rates of nest predation on Dickcissels indicated that the number of nests fledging young would be insufficient if we selected only one individual per nest (Berkeley et al. 2007, Suedkamp Wells et al. 2007).

Radio-tracking

We used a receiver and a three-element Yagi antenna to locate fledglings every 1–3 days during the first week post-

fledging, and once every 1–5 days during subsequent weeks until fledglings left the study sites, died, or until the transmitter's battery died. Fledgling locations were marked by tying a small piece of flagging directly above or below (within 10 cm) where each fledgling was perched. At younger ages (days 0–7 post-fledging), fledglings appeared to freeze when we would approach, remaining completely still even when we went to tie flagging. At older ages (days 7+ post-fledging) fledglings would remain still until we were on top of them, at which point they would flush and/or run away. Fortunately, such behaviors allowed us to detect and document where fledglings were originally perched (within 10 cm) prior to our presence. To avoid the potential for predators to be attracted to the fledglings, after marking the location we continued walking in the same direction in which we approached fledglings to avoid leaving a dead-end trail for predators to cue into. When we were unable to detect a signal near a fledgling's last documented location, we searched the adjacent habitat (<400 m radius) for at least 30 min in an attempt to pick up a signal. We georeferenced all fledgling locations (2–4 m error; GPSMAP64, Garmin, Olathe, Kansas, USA) so we could return to the area, find the flagging, and center vegetation measurements on the fledgling's location.

Characterization of Habitat

We sampled vegetation using 1-m² quadrats (Small et al. 2015) at each fledgling location, at a random location associated with each fledgling location, and at the nest site from which each fledgling originated. Random plots were located in a random direction (0–360°), within 15 m of fledgling locations for those ageing from 1 to 3 days after fledging, within 25 m for 4–11 days after fledging, and within 50 m of fledgling locations for 12+ days after fledging; directions and distances to random plots were generated using a random number generator in Microsoft Excel (Version 2013). Following Fisher and Davis (2011), this approach adjusts for the increasing mobility of fledglings with age and reflects increased access to habitat. Though sampling vegetation in this way may increase spatial autocorrelation, our method makes more sense ecologically as it allowed us to compare “used” vs. “available” habitat within range of a fledgling's mobility, rather than sampling vegetation >50 m away, far beyond the reach of poorly volant young fledglings. For each plot, we estimated mean vegetation height (estimated to the nearest 5 cm), total percent cover of vegetation (i.e. “canopy cover”), vegetation-height density (averaging 4 Robel pole values made 1 m from each location at 1 m above the ground in each cardinal direction; variation of methods in Robel et al. 1970), and percent concealment of the fledgling/nest (we estimated how much of the bird would have been concealed if it were still perched next to the flagging from each point a Robel sample was taken, and

from directly above). For nest sites we used the actual nest to estimate concealment. For random points, we estimated concealment at a height matching that of the bird at the original location. Vegetation was sampled after fledglings left the general area (range: 1–21 days), with paired plots collected on the same day.

Fledgling Fate

We assigned each fledgling one of 3 fates: (1) survived = fledgling lived until it dispersed; (2) died = fledgling was found dead with the transmitter still attached, its transmitter was found next to remains or had obvious signs of damage caused by a predator (e.g., tooth or beak marks, harness material chewed through), we tracked its signal back to a predator, or its transmitter signal was lost prior to ages at which the fledgling could leave the area or disperse; or (3) unknown = for any reason we felt unsure that a fledgling had died or moved off when a signal was lost or transmitter was found on the ground. Fates were determined using hand-tracking, visual observations, and automated radio-telemetry system data (Jones et al. 2017).

Data Analyses

We examined habitat use via 2 separate methods: (1) using each of our collected vegetation parameters in univariate models, and (2) examining all vegetation parameters in a more holistic approach by using a principal components analysis (PCA; Proc Factor, SAS Institute 1990). Except for concealment, all vegetation parameters were correlated ($p < 0.01$ and $r > 0.12$) and thus we used PCA to reduce the dimensionality of vegetation characteristics down to 2 new overarching variables. To compare habitat characteristics between fledgling and random locations and between fledgling and nest locations, we first determined the difference between paired plots for each vegetation variable (including factors derived from our PCA). Using the difference as a response variable, we tested whether differences in vegetation parameters of paired plots were equal to zero during days 1–3, 4–11, and 12+ post-fledging (age classes that best predict Dickcissel post-fledging survival in our study system; Jones et al. 2017; Proc Glimmix, SAS Institute 1990). If the intercept of a model was significantly different from zero ($p \leq 0.05$), then differences in the vegetation parameter between paired locations were considered significant. We included nest ID and bird ID as random factors to account for non-independence between members of the same brood and multiple observations from the same individual.

To examine how habitat use changed as fledglings became older and more mobile, we used generalized linear mixed models with distance from the nest as the response variable and fledgling age as the independent variable (Proc Mixed, SAS Institute 1990). As in the analysis of

TABLE 1. Principal component analysis (PCA) of habitat characteristics reflecting vegetation structure of 1-m² sampling plots in grasslands of central Illinois, USA, 2014–2015.

PCA analysis	Factor 1: Vegetation density	Factor 2: Overall concealment	Factor 3
Eigenvalue	2.17	0.99	0.67
Variance explained	54.2%	25.0%	16.6%
Loadings			
Concealment (%)	0.21	0.96	−0.19
Cover (%)	0.69	0.14	0.71
Vegetation height-density (dm)	0.91	−0.11	−0.07
Height (cm)	0.91	−0.21	−0.23

habitat use, we included nest ID and bird ID as random factors.

We examined fledgling habitat use and fledgling survival via generalized linear mixed models (Proc Glimmix, SAS Institute 1990). We used a binomial distribution and logit link function with fledgling fate (binary, died or survived) as the response variable and a vegetation variable as the independent variable (a separate model for each parameter). As in other analyses, we included nest ID and bird ID as random factors. Fledglings with unknown fates ($n = 1$) were not included in our survival analyses. We present results as Beta estimate (β) \pm standard errors (SE).

RESULTS

We measured habitat characteristics at a total of 698 points: 323 fledgling locations (4.97 ± 0.38 locations per fledgling), 323 random locations, and 52 nest locations from 60 different fledglings. We examined associations amongst habitat characteristics and fledgling survival for a total of 59 individuals (52 broods). We sampled habitat use from 59 fledglings, ages 1–3; 49 fledglings, ages 4–11; and 31 fledglings, ages 12 or older. We documented fledgling distances from nest from 66 fledglings. Although we tracked the survival of 104 fledglings, we were unable to collect vegetation and location data for all individuals due to early fledgling death and logistical constraints.

Our principle component analysis identified 2 factors that distinguished among the vegetation variables. The first factor explained 54% of the sample variation (eigenvalue = 2.17) and average height, cover, and vegetation-height density values all loaded strongly and positively into the factor (Table 1); we called the factor “vegetation density” (i.e. vegetation that is taller, horizontally and vertically more dense). The second factor explained 25% of sample variation (eigenvalue = 0.99) and was composed primarily of our concealment parameter; we called the factor “overall concealment.” The remaining factors produced by the PCA

had eigenvalues less than 1 and were not used in our analyses (Table 1).

Younger fledglings (age classes 1–3 and 4–11 post-fledging) used areas with vegetation that were denser and more concealed compared to random areas (Table 2). Of the 3 primary variables making up the vegetation density factor, vegetation-height density was the most important, followed by vegetation height, with both variables exhibiting greater values than in random areas (Table 2). Furthermore, 4–11-day-old fledglings used even denser vegetation compared to when they were younger (days 1–3; Table 2). We found no differences in vegetation density between fledgling and nest locations for all fledgling age classes, but nests were located in vegetation that was more concealed and had more cover compared to sites used by young fledglings (days 1–3 post-fledging; Table 3).

We found no association between fledgling survival and individual vegetation characteristics for all age groups (average height, $P = 0.12$, $P = 0.39$, $P = 0.25$; cover, $P = 0.07$, $P = 0.10$, $P = 0.69$; concealment, $P = 0.56$, $P = 0.97$, $P = 0.67$; vegetation height-density, $P = 0.10$, $P = 0.15$, $P = 0.34$; days 1–3, 4–11, and 12+, respectively). When characteristics were considered as PCA factors, however, fledgling survival was positively associated with vegetation density during days 1–3 ($\beta = 0.82 \pm 0.40$, $P = 0.05$; Figure 1), but not during the rest of the post-fledging period (days 4–11, $P = 0.12$; days 12+, $P = 0.34$) nor with overall concealment for all age classes (days 1–3, $P = 0.74$; days 4–11, $P = 0.84$; days 12+, $P = 0.53$). Fledgling distance from nest was positively associated with fledgling age ($\beta = 5.69 \pm 0.48$, $P < 0.001$; Figure 2), suggesting that older fledglings were more mobile and had access to larger areas of habitat.

DISCUSSION

Our results suggest that fledgling Dickcissels used habitat nonrandomly, preferring comparatively denser and more concealing vegetation during the first 11 days after leaving the nest. The main threats to juvenile Dickcissels during the post-fledging period are predation (mainly by snakes) and exposure to the elements (Berkeley et al. 2007, Suedkamp Wells et al. 2007, Jones et al. 2017). Consequently, use of denser areas by fledglings may aid their survival by providing better cover from predators and refuge from heat or rain (Anders et al. 1998, King et al. 2006, Cox et al. 2014). Indeed, we found a positive relationship between vegetation density and Dickcissel fledgling survival (days 1–3), suggesting that fledglings moved to areas that aided their survival. The primary benefit of dense vegetation in our study system was likely concealment from predators—the primary source of fledgling mortality (Jones et al. 2017)—though we also documented cases where fledgling death was likely due to

TABLE 2. Differences in vegetation density and overall concealment (Table 1) and the characteristics comprising the 2 factors between fledgling and paired random locations during days 1–3, 4–11, and 12+ post-fledging.

Vegetation characteristic	Fledgling locations		Random locations		Mean difference fledgling – random		<i>t</i>	<i>P</i>
	Mean	SE	Mean	SE	SE (diff)			
Days 1–3 post-fledging								
Vegetation density	–0.11	0.10	–0.28	0.10	0.19	0.06	3.08	0.02
Overall concealment	0.15	0.08	–0.09	0.08	0.24	0.09	2.72	0.03
Average height (cm)	57.86	2.41	53.66	2.49	3.84	1.74	2.21	0.06
Total cover (%)	73.02	2.09	72.16	2.13	0.86	1.53	0.56	0.59
Concealment (%)	78.00	2.02	70.56	2.20	7.66	2.28	3.36	0.01
Vegetation height-density (dm)	3.82	0.21	3.41	0.22	0.40	0.17	2.43	0.04
Days 4–11 post-fledging								
Vegetation density	0.34	0.09	–0.07	0.09	0.40	0.07	5.35	0.00
Overall concealment	0.11	0.08	–0.33	0.09	0.44	0.08	5.63	<0.01
Average height (cm)	66.73	2.55	60.07	2.52	7.06	1.83	3.85	0.01
Total cover (%)	78.75	1.50	73.99	1.93	4.76	1.73	2.76	0.04
Concealment (%)	79.21	1.74	66.28	2.25	13.42	2.01	6.68	0.00
Vegetation height-density (dm)	5.05	0.28	3.98	0.22	1.12	0.25	4.43	0.01
Days 12+ post-fledging								
Vegetation density	0.18	0.12	–0.00	0.10	0.18	0.08	2.42	0.25
Overall concealment	–0.56	0.14	–0.87	0.14	0.30	0.10	2.91	0.21
Average height (cm)	65.80	3.17	60.69	2.95	5.08	2.26	2.25	0.27
Total cover (%)	76.16	2.15	76.71	1.99	–0.46	2.06	–0.22	0.86
Concealment (%)	61.22	3.34	51.20	3.53	9.89	2.72	3.64	0.17
Vegetation height-density (dm)	4.88	0.33	4.21	0.28	0.69	0.27	2.55	0.24

hypothermia or heatstroke associated with heavy rainfall and/or drastic changes in temperature. Thus, consistent with past post-fledging studies on grassland (e.g., Kershner et al. 2004, Jones and Bock 2005, Berkeley et al. 2007, Suedkamp Wells et al. 2008, Fisher and Davis 2011, Small

et al. 2015) and forest-dwelling songbirds (Anders et al. 1998, King et al. 2006, Rush and Stutchbury 2008), our observations suggest that fledglings prefer denser vegetation that provides concealment from predators and refuge from adverse environmental conditions.

TABLE 3. Differences in vegetation density and overall concealment (Table 1) and the characteristics comprising the 2 factors between fledgling and nest locations during days 1–3, 4–11, and 12+ post-fledging.

Vegetation characteristic	Fledgling locations		Nest locations		Mean difference fledgling – nest		<i>t</i>	<i>P</i>
	Mean	SE	Mean	SE	SE (diff)			
Days 1–3 post-fledging								
Vegetation density	–0.11	0.10	–0.01	0.09	–0.11	0.10	–1.18	0.27
Overall concealment	0.15	0.08	0.45	0.05	–0.31	0.11	–2.78	0.02
Average height (cm)	57.86	2.41	55.82	2.42	1.55	2.60	0.60	0.57
Total cover (%)	73.02	2.09	77.01	1.93	–5.03	2.11	–2.38	0.05
Concealment (%)	78.00	2.02	84.41	1.24	–6.57	2.81	–2.34	0.05
Vegetation height-density (dm)	3.82	0.21	4.03	0.21	–0.27	0.22	–1.22	0.26
Days 4–11 post-fledging								
Vegetation density	0.34	0.09	–0.04	0.08	0.28	0.15	1.83	0.12
Overall concealment	0.11	0.08	0.43	0.05	–0.32	0.13	–2.49	0.06
Average height (cm)	66.73	2.55	55.33	2.03	9.30	3.40	2.74	0.04
Total cover (%)	78.75	1.50	76.44	1.72	0.43	3.08	0.14	0.89
Concealment (%)	79.21	1.74	84.10	1.25	–4.92	3.15	–1.56	0.18
Vegetation height-density (dm)	5.05	0.28	3.99	0.19	0.91	0.41	2.21	0.08
Days 12+ post-fledging								
Vegetation density	0.18	0.12	–0.08	0.09	0.24	0.18	1.34	0.41
Overall concealment	–0.56	0.14	0.52	0.06	–1.09	0.18	–6.24	0.10
Average height (cm)	65.80	3.17	53.28	2.21	12.64	4.12	3.07	0.20
Total cover (%)	76.16	2.15	76.86	2.15	–0.23	4.27	–0.05	0.97
Concealment (%)	61.22	3.34	85.68	1.33	–24.78	4.19	–5.91	0.11
Vegetation height-density (dm)	4.88	0.33	3.83	0.19	0.89	0.44	2.00	0.30

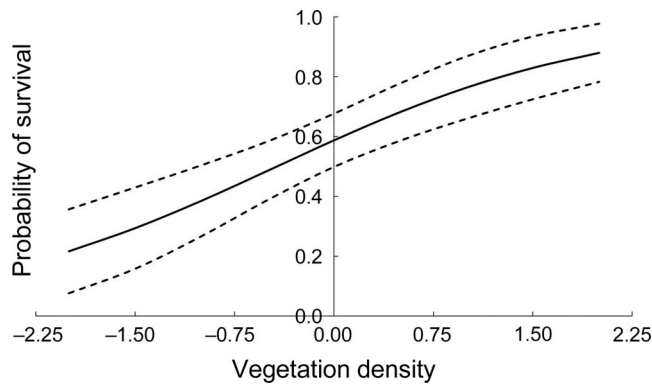


FIGURE 1. Association between vegetation density used by Dickcissel fledglings ($n = 59$) and fledgling survival (\pm SE) during days 1–3 post-fledging in grasslands of central Illinois, USA, 2014–2015. Vegetation density is a principal components factor composed primarily of average height, total cover, and vegetation height-density, with more positive values representing areas with taller, thicker vegetation that provides more cover for birds.

Our findings suggest that age-specific mortality pressures may ultimately drive age-specific habitat use in fledgling Dickcissels. Dickcissel nestlings fledge at relatively early developmental stages, probably in response to high nest predation rates (Berkeley et al. 2007, Suedkamp Wells et al. 2007, Jones et al. 2017), and consequently are relatively immobile as young fledglings. Once out of the nest, they require denser vegetation to hide and reduce their risk of post-fledging predation. Only when fledglings are much older and more mobile (more capable of evading predators) do they begin to use more open areas. Given documented variation in nest predation risk and development at fledging within and among avian species (Martin 2015, Lloyd and Martin 2016, Jones et al. 2017), future research should examine interspecific variation in post-fledging habitat use in the context of avian life histories, particularly nest predation risk and developmental stage at fledging.

Fledglings of Dickcissels and other grassland species do not appear to use markedly different habitat from nest sites chosen by their parents (e.g., Fisher and Davis 2011); however, this lack of a nest-to-post-fledging shift in habitat use is in direct contrast to what has been observed in many forest species (e.g., Anders et al. 1998, King et al. 2006, Rush and Stutchbury 2008, Streby and Anderson 2013; but see Jenkins et al. 2016). Past research suggests that fledglings for most songbird species prefer and benefit from using denser habitats (Cox et al. 2014). Thus, a nest-to-post-fledging shift in habitat use may be related to nest site characteristics. For instance, grassland species such as the Dickcissel place nests in denser, more complex, and well-concealed areas (Winter 1999) similar to those preferred by fledglings, while forest species such as the

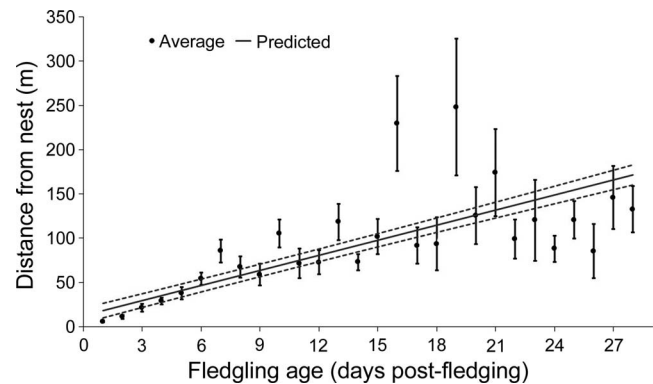


FIGURE 2. Average (\pm SE) and predicted (\pm SE) distance of Dickcissel fledglings ($n = 66$) from their nest site by age (days post-fledging) in grasslands of central Illinois, USA, 2014–2015. Distances from nest sites were based on locations of hand-tracked fledglings with predicted distances derived from a generalized linear mixed model.

Ovenbird place nests in open understories, requiring fledglings to move to denser vegetation (King et al. 2006). Variation in species stage-specific habitat use does not appear to depend on fledgling habitat selection, but rather on adult nest site selection.

Conservation Implications

The post-fledging stage is a vulnerable period for fledgling Dickcissels, highlighted by high fledgling mortality rates in the immediate days after fledging (“critical period”; Berkeley et al. 2007, Suedkamp Wells et al. 2007, Jones et al. 2017). Survival during this critical period, also known as the “post-fledging bottleneck” (Naef-Daenzer and Gruebler 2016), is therefore likely to play a critical role in influencing dynamics of Dickcissel populations. Our finding of a positive association between fledgling survival and denser habitat during, but not after, this bottleneck identifies an important area in which management can potentially mitigate population declines in grassland birds by increasing fledgling survival. Use of management techniques such as burning, herbicides, and/or mowing that can increase the density of vegetation may improve survival rates of fledglings (Suedkamp Wells et al. 2008) as well as attract settlement and nesting of adults (Berkeley et al. 2007). The use of such techniques, however, must be appropriately timed (e.g., late winter or early spring before birds arrive) so as not to disturb and/or cause mortality to adults, nests, and young, immobile fledglings (e.g. Davis et al. 2016).

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LITERATURE CITED

- Anders, A. D., D. C. Dearborn, J. Faaborg, and F. R. Thompson III (1997). Juvenile survival in a population of Neotropical migrant birds. *Conservation Biology* 11:698–707.
- Anders, A. D., J. Faaborg, and F. R. Thompson III (1998). Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. *The Auk* 115:349–358.
- Anders, A. D., and M. R. Marshall (2005). Increasing the accuracy of productivity and survival estimates in assessing landbird population status. *Conservation Biology* 19:66–74.
- 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.
- Brennan, L. A., and W. P. Kuvlesky, Jr. (2005). North American grassland birds: An unfolding conservation crisis? *Journal of Wildlife Management* 69:1–13.
- Cox, W. A., F. R. Thompson III, A. S. Cox, and J. Faaborg (2014). Post-fledging survival in passerine birds and the value of post-fledging studies to conservation. *Journal of Wildlife Management* 78:183–193.
- Davis, S. K., S. M. Ludlow, and D. G. McMaster (2016). Reproductive success of songbirds and waterfowl in native mixed-grass pasture and planted grasslands used for pasture and hay. *The Condor: Ornithological Applications* 118:815–834.
- Fisher, R. J., and S. K. Davis (2011). Post-fledging dispersal, habitat use, and survival of Sprague's Pipits: Are planted grasslands a good substitute for native? *Biological Conservation* 144:263–271.
- Jenkins, J. M. A., F. R. Thompson III, and J. Faaborg (2016). Contrasting patterns of nest survival and postfledging survival in Ovenbirds and Acadian Flycatchers in Missouri forest fragments. *The Condor: Ornithological Applications* 118:583–596.
- Jones, T. M., M. P. Ward, T. J. Benson, and J. D. Brawn (2017). Variation in nestling body condition and wing development predict cause-specific mortality in fledgling Dickcissels. *Journal of Avian Biology* 48:439–447.
- Jones, Z. F., and C. E. Bock (2005). The Botteri's Sparrow and exotic Arizona grasslands: An ecological trap or habitat regained? *The Condor* 107:731–741.
- Kershner, E. L., J. W. Walk, and R. E. Warner (2004). Postfledging movements and survival of juvenile Eastern Meadowlarks (*Sturnella magna*) in Illinois. *The Auk* 121:1146–1154.
- King, D. I., R. M. Degraaf, M. L. Smith, and J. P. Buonaccorsi (2006). Habitat selection and habitat-specific survival of fledgling Ovenbirds (*Seiurus aurocapilla*). *Journal of Zoology* 269:414–421.
- Lloyd, P., and T. E. Martin (2016). Fledgling survival increases with developmental time and adult survival across north and south temperate zones. *Ibis* 158:135–143.
- Maness, T. J., and D. J. Anderson (2013). Predictors of juvenile survival in birds. *Ornithological Monographs*, no. 78.
- Martin, T. E. (2015). Age-related mortality explains life history strategies of tropical and temperate songbirds. *Science* 349:966–969.
- Naef-Daenzer, B. (2007). An allometric function to fit leg-loop harnesses to terrestrial birds. *Journal of Avian Biology* 38:404–407.
- Naef-Daenzer, B., and M. U. Grübler (2016). Post-fledging survival of altricial birds: Ecological determinants and adaptation. *Journal of Field Ornithology* 87:227–250.
- Norris, D. R., and P. P. Marra (2007). Seasonal interactions, habitat quality, and population dynamics in migratory birds. *The Condor* 109:535–547.
- Rappole, J. H., and A. R. Tipton (1991). New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62:335–337.
- 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.
- Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationship between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* 23:295–297.
- Rush, S. A., and B. J. M. Stutchbury (2008). Survival of fledgling Hooded Warblers (*Wilsonia citrina*) in small and large forest fragments. *The Auk* 125:183–191.
- SAS Institute. 1990. *SASSTAT User's Guide*. SAS Institute, Cary, NC, USA.
- Sauer, J. R., K. L. Pardieck, D. J. Ziolkowski, Jr., A. C. Smith, M.-A. R. Hudson, V. Rodriguez, H. Berlanga, D. K. Niven, and W. A. Link (2017). The first 50 years of the North American Breeding Bird Survey. *The Condor: Ornithological Applications* 119:576–593.
- Small, D. M., P. J. Blank, and B. Lohr (2015). Habitat use and movement patterns by dependent and independent juvenile Grasshopper Sparrows during the post-fledging period. *Journal of Field Ornithology* 86:17–26.
- Streby, H. M., and D. E. Andersen (2013). Movements, cover-type selection, and survival of fledgling Ovenbirds in managed deciduous and mixed coniferous-deciduous forests. *Forest Ecology and Management* 287:9–16.
- Streby, H. M., J. M. Refsnider, S. M. Peterson, and D. E. Andersen (2013). Retirement investment theory explains patterns in songbird nest-site choice. *Proceedings of the Royal Society B* 281:20131834.
- Suedkamp Wells, K. M., M. R. Ryan, J. J. Millsbaugh, F. R. Thompson III, and M. W. Hubbard (2007). Survival of postfledging grassland birds in Missouri. *The Condor* 109:781–794.

- Suedkamp Wells, K. M., J. J. Millsbaugh, M. R. Ryan, and M. W. Hubbard (2008). Factors affecting home range size and movements of post-fledging grassland birds. *The Wilson Journal of Ornithology* 120:120–130.
- Temple, S. (2002). Dickcissel (*Spiza americana*). In *The Birds of North America* (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bna.703
- Vega Rivera, J. H., J. H. Rappole, W. J. McShea, and C. A. Haas (1998). Wood Thrush postfledging movements and habitat use in northern Virginia. *The Condor* 100:69–78.
- Vickery, P. D., J. R. Herkert, F. L. Knopf, J. Ruth, and C. E. Keller (2000). Grassland birds: An overview of threats and recommended management strategies. In *Strategies for Bird Conservation: The Partners in Flight Planning Process* (R. Bonney, D. N. Pashley, R. J. Cooper, and L. Niles, Editors). U.S. Department of Agriculture, Forest Service, RMRS-P-16. pp. 74–77.
- Vitz, A. C., and A. D. Rodewald (2010). Movements of fledgling Ovenbirds (*Seiurus aurocapilla*) and Worm-eating Warblers (*Helmitheros vermivorum*) within and beyond the natal home range. *The Auk* 127:364–371.
- Vitz, A. C., and A. D. Rodewald (2011). Influence of condition and habitat use on survival of post-fledging songbirds. *The Condor* 113:400–411.
- Walk, J. W., and R. E. Warner (2000). Grassland management for the conservation of songbirds in the Midwestern USA. *Biological Conservation* 94:165–172.
- Winter, M. (1999). Nesting biology of Dickcissels and Henslow's Sparrows in southwestern Missouri prairie fragments. *Wilson Bulletin* 111:515–526.