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Research Paper

Postfledging habitat selection and survival of Henslow's Sparrow: management implications for a critical life stage

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ABSTRACT. Conserving populations of species that rely on rare habitat requires that managers understand which habitat characteristics will best support population growth across multiple life stages. For songbirds, management is most often aimed at nesting adult habitat associations. However, habitat that meets adult requirements may not be similarly suited to requirements for other life stages. Henslow's Sparrow (*Centronyx henslowii*) is a tallgrass prairie songbird listed as threatened or endangered in 13 states. We examined survival and habitat selection of Henslow's Sparrow during the postfledging period. During the nesting seasons in 2015 and 2016, we attached radio transmitters to 46 nestlings in a tallgrass prairie and modeled their survival and habitat selection as a function of habitat characteristics. Thirty-five percent of fledglings survived until two weeks postfledge. Survival was negatively associated with areas of sumac (*Rhus copallinum*) cover, positively associated with years since last burn, and decreased as the breeding season progressed. Snakes were the most common predator of fledglings. Independent fledglings used habitat that was different than that used by adults and dependent fledglings, with habitat used during the independent period having lower litter cover and increased forb cover compared to points used during the dependent period. During the dependent period, points used by fledglings were a mean distance of 40 m (± 11 SD) from the natal nest. Following independence, points used by fledglings were 236 m (± 89 SD) from the natal nest. Henslow's Sparrow populations may benefit from removal of encroaching sumac in tallgrass prairie, and from consideration of the varying habitats used by the species during different life stages.

Sélection d'habitat après l'envol et survie chez le Bruant de Henslow: répercussions sur l'aménagement à un stade critique du cycle vital

RÉSUMÉ. Pour assurer la conservation de populations d'espèces qui dépendent de milieux rares, les gestionnaires doivent comprendre quelles caractéristiques influent positivement sur la croissance des populations au cours des divers stades du cycle vital. Dans le cas des oiseaux chanteurs, l'aménagement est souvent orienté sur les adultes nicheurs et leurs habitats. Toutefois, les milieux qui conviennent aux adultes ne sont pas nécessairement les mêmes que ceux qui sont utilisés durant les autres stades du cycle vital. Le Bruant de Henslow (*Centronyx henslowii*), oiseau chanteur de milieux de prairie à grandes graminées, figure sur la liste des oiseaux menacés ou en voie de disparition dans 13 États. Nous avons examiné la survie et la sélection d'habitat chez le Bruant de Henslow durant la période suivant l'envol des jeunes. Durant les saisons de nidification de 2015 et 2016, nous avons fixé des émetteurs radio sur 46 oisillons dans une prairie à grandes graminées et avons modélisé leur survie et leur sélection d'habitat en fonction des caractéristiques d'habitat. Trente-cinq pourcent des jeunes ayant pris leur envol ont survécu jusqu'à deux semaines après l'envol. Le taux de survie était associé négativement avec les secteurs de sumac (*Rhus copallinum*), positivement avec les années suivant le dernier brûlis, et diminuait au fur et à mesure que la saison de nidification progressait. Les serpents étaient le prédateur le plus commun des jeunes oiseaux. Les jeunes oiseaux indépendants ont utilisé des habitats différents de ceux utilisés par les adultes et les jeunes dépendants; les milieux fréquentés durant la période d'indépendance présentaient moins de litière et plus de plantes herbacées non graminéennes comparativement aux endroits utilisés durant la période de dépendance. Durant cette dernière, les endroits utilisés par les jeunes étaient à une distance de 40 m (± 11 écart type) du nid d'origine. Une fois indépendants, les jeunes ont utilisé des endroits situés à 236 m (± 89 écart type) du nid. Les populations du Bruant de Henslow pourraient profiter de l'élimination des empiètements de sumac dans les prairies à grandes graminées, et de la prise en compte des habitats variés qu'utilise l'espèce durant les différents stades du cycle vital.

Key Words: *Ammodramus henslowii*; *Centronyx henslowii*; demographic; habitat; Henslow's Sparrow; postfledging; shrubs; survival; tallgrass prairie

INTRODUCTION

Estimates of demographic parameters at every life stage are vital to our understanding of the factors that most influence populations of rare or declining songbirds (Saether and Bakke 2000, Wisdom et al. 2000). The availability of high-quality habitat

may be a limiting factor for these species (Samson and Knopf 1994, Faaborg et al. 2010), which are often habitat specialists that rely on a narrow range of vegetative characteristics (Wiens 1969). Understanding the effects of changes in habitat condition on stage-specific demographic parameters can give insight into the

mechanisms driving population declines as well as suggest targeted management strategies designed to efficiently maximize population growth (Donovan and Thompson 2001, Johnson 2007).

Populations of grassland songbirds have declined because of habitat loss, fragmentation, and degradation (Askins et al. 2007). Over 90% of North American tallgrass prairie habitat has been converted to other uses (Samson and Knopf 1994), and as a result, management of remaining areas of tallgrass prairie is vital. Studies that have examined site-specific recruitment in grassland songbird populations have often focused on nest success. However, estimates of nest success are only one component of seasonal reproductive output (Thompson et al. 2001, Streby and Andersen 2011). Failure to estimate overall seasonal fecundity as well as postfledging survival may lead to biased population models and/or inaccurate conclusions about habitat quality (Nagy and Holmes 2004, Knutson et al. 2006). Furthermore, assumptions that breeding season habitat characteristics that lead to increases in abundances or survival during one life stage will be similarly suitable for other life stages may be inappropriate (Van Horne 1983, Vickery et al. 1992). Habitat used by nesting adults may not meet the needs of newly fledged offspring during the postfledging period, potentially resulting in lowered survival rates (e.g., Shipley et al. 2013).

The postfledging period is the time after passerines leave the nest but before they disperse in the fall (Cox et al. 2014, Naef-Daenzer and Gruebler 2016). This period can be further divided into the dependent and independent postfledging period. During the dependent period, fledglings often have low flight power and are directly dependent on adults for provisioning and habitat selection. At the onset of the independent period, adult provisioning ceases and fledglings use their increased flight power to leave the natal territories. Recent research focusing on survival of grassland birds during the dependent period has shown that this may be a time of high mortality (Yackel Adams et al. 2006, Berkeley et al. 2007, Suedkamp Wells et al. 2007, Fisher and Davis 2011, Hovick et al. 2011). Because of limited battery life for transmitters that can be fit to small songbirds, few researchers have followed fledglings into the independent period. However, those studies that have examined this period have shown that fledglings may use habitat with different vegetative characteristics than those utilized by nesting adults (Vitz and Rodewald 2010, Dittmar et al. 2014, Small et al. 2015). If this is the case, then management that focuses on providing habitat suited to adults may not meet the needs of fledglings, thereby potentially limiting productivity.

We examined postfledging survival, movement, and habitat selection of Henslow's Sparrow (*Centronyx henslowii*, formerly *Ammodramus henslowii*), an obligate grassland bird listed as threatened or endangered in 13 states and Canada (Cooper 2012). Henslow's Sparrow's nesting habitat is characterized by a well-developed litter layer, dense grass cover, vertical standing dead grass, and a low cover of woody vegetation (Wiens 1969, Zimmerman 1988, Herkert 1994, Winter 1999). The interruption of natural disturbance regimes, including periodic fire, can lead to increased woody vegetation that may result in increased presence of potential predators, thereby lowering nest success for

grassland birds (With 1994, Klug et al. 2010, Graves et al. 2010). However, frequent fires or heavy grazing that might limit woody vegetation, also eliminate the litter layer that Henslow's Sparrow depends on for nesting. As a result, Henslow's Sparrow population densities are especially sensitive to fire and grazing management practices at the highly dispersed and fragmented sites where this species is still found (Hunter et al. 2001, Herkert 2002, Herse et al. 2017).

Several studies have examined factors influencing nest success and habitat use for adult Henslow's Sparrow (Zimmerman 1988, Herkert 1994, Winter 1999, Monroe and Ritchison 2005, Graves et al. 2010, Jaster et al. 2014). However, survival and habitat use during other potentially important life-stages remain unexamined. We used radio telemetry to examine survival and habitat use during the postfledging period in a tallgrass prairie in southwest Missouri. Our objectives were to (1) quantify survival during the postfledging period as a function of habitat variables, (2) identify specific causes of mortality, (3) measure movement of fledglings during both the dependent and independent postfledging periods, and (4) examine the characteristics of habitat used by fledglings.

METHODS

Field methods

We studied Henslow's Sparrows at Prairie State Park in southwest Missouri, a 1200 ha native tallgrass prairie remnant maintained by rotational burning conducted at four year intervals. Burn unit area at the time of our study ranged from 26 to 71 ha with an average of 56 ha \pm 17 sd. Approximately two-thirds of the park was grazed by ~84 bison (*Bison bison*) during our study. Dominant plants included native warm season grasses, such as big bluestem (*Andropogon gerardii*) and Indian grass (*Sorghastrum nutans*), as well native forbs, predominantly represented by the Asteraceae and Fabaceae families. Woody vegetation, predominantly winged sumac (*Rhus copallinum*), has invaded large sections of the site, forming a gradient from areas free of woody vegetation, to areas with isolated clumps, to areas that might more appropriately be classified as shrubland than prairie. Bison are stocked at ~12 ha per animal and have free range of large sections of the park but tend to concentrate in certain areas. Within these areas, grazing has created heterogeneous patches of vegetation structure. These grazed areas consisted of contrasting patches of short cropped grass with low litter interspersed with areas of high forb cover as well as ungrazed areas of tall grass with deep litter (*personal observation*).

Beginning on 16 April in both 2015 and 2016 we observed adult behavior for signs of nest initiation such as alarm calls issued by territorial males and nesting material carried by females. We then used these behavioral cues to locate nests. We observed likely areas using a portable blind to pinpoint the nest location and minimize disturbance to the vegetation caused by extended searching. The blind was set between 10 and 20 m from the likely nest location. If alarm calls did not cease within 10 minutes, the blind was either repositioned or observation was terminated. If the female did not return in 40 minutes, the blind was removed. This method was not used during wet, cold, or extreme heat conditions to avoid increasing the risk of nest failure.

The first nests were found on 7 May and 2 May in 2015 and 2016, respectively. Once located, nest locations were recorded using Garmin GPSMap 64 handheld units (Garmin Ltd, Olathe, Kansas). A flag was placed 5 m to the south of the nest, and a 5 mm piece of black electrical tape was placed on a piece of grass directly over the nest. This tape was virtually invisible from a distance, but allowed quick relocation of cryptic nests and minimized disturbance during nest checks.

During the month of May in both study years we attached transmitters to 20 females for a related study. These females were followed throughout the breeding season, and their nests were located using transmitter signals. Once located, all nests were monitored every 3–4 days until fledging (Martin and Geupel 1993).

We attached a Lotek NTQB-2 Nanotag (Lotek Wireless Inc, Newmarket, Ontario) to nestlings on day 8 or 9 posthatch using the figure-eight, leg-loop harness method (Rappole and Tipton 1991). In our experience, nestlings fledged from undisturbed nests by day 9 posthatch. Our method resulted in the immediate fledging of all the nestlings. However, by waiting until just prior to the point that nestlings would fledge naturally, we were able to eliminate uncertainty over fledge status and minimize the negative effects of premature fledging (Streby et al. 2013). Our goal was to tag one nestling per nest but we tagged two nestlings at 12 nests and three nestlings at two nests because low nest survival rates limited our pool of available nests (Young 2017). Each nestling was weighed and fit with a U.S. Geological Survey aluminum band. Transmitters weighed 0.40–0.50 g and nestlings weighed on average $9.63 \text{ g} \pm 0.53 \text{ SD}$ at the time of transmitter attachment. After the transmitter was attached, all nestlings were placed back in the nest cup. Application of transmitters to individual nestlings took less than two minutes, and total time from removal to replacement of the brood was less than 10 minutes.

Fledglings were located daily during the dependent period, which we defined as the period during which the fledglings were under direct parental care. During this time, evidence for adult care included alarm calls when researchers approached the territory, observations of feeding, and adults flushing from fledgling locations. For the majority of fledglings, this period ended by day 21 postfledging. After fledglings left the natal territory and adult care ceased, we considered the fledglings independent. During the independent period, locations were recorded every two to three days until the transmitter battery died or the fledgling died or left the study site. Transmitter batteries lasted over 40 days and had an effective range of ~300 m. For the purpose of vegetative analyses (below), we considered the dependent period to consist of locations starting on the day after the transmitter was attached (day 1) through the day that adult care was assumed to have ceased. We assessed the dependent status of fledglings by recording adult behavior during daily locations. Once adults no longer issued alarm calls or were in the vicinity of fledglings for three consecutive daily locations we assumed that fledglings were independent. The date of independence for that fledgling was then recorded as the date of the first location where adults were not present.

We did not attempt to locate fledglings early in the morning while the grass was wet, on rainy days, or when bison were in the area. During the first five days postfledging, fledglings did not fly when

approached by researchers. In an effort to avoid stepping on immobile fledglings, we took multiple bearings to determine their location. At least two GPS points were taken ~10 m from the localized transmitter signal and compass bearings were recorded at as close to 90 degree angles as possible. Fledgling positions were later triangulated using the package “SigLoc” in program R (Berg 2015). If adults were with the fledgling or issuing alarm calls, we assumed the fledgling was alive. If the fledgling had not moved from the previous day, we searched the vegetation for visual confirmation of status. After five days, fledglings flushed from the vegetation and flew a distance of < 10 m when researchers approached. At this time we recorded a single GPS location at the point where the fledgling initially flushed. If the fledgling did not flush we recorded the patch of vegetation where the signal was strongest. If the fledgling had not moved from the day before, or adults issuing alarm calls were not present, we attempted to flush the fledgling. If the fledgling did not flush, we searched for signs of mortality. Mortality was assumed if we found a transmitter with signs of predation such as feathers or body parts in the area or marks on the transmitter. Often, mortality could be assigned by tracking the signal to a live snake or a transmitter covered in snake feces. Mortality was also assumed if there was no signal on the territory prior to the point that a fledgling would have achieved independence. If a transmitter was found with no signs of predation we assumed that these transmitters had fallen off and these fledglings were right censored during analysis, following the standard protocol for incorporating individuals of uncertain fate in survival analysis (Klein and Moeschberger 2006).

We were able to estimate survival for a subset of fledglings without transmitters because 20 adult females per year were fitted with radio transmitters. When the nest of a tagged female successfully fledged before we could attach transmitters to nestlings, we monitored fledgling status using adult behavior. Adults became visibly agitated and issued alarm calls when researchers approached areas occupied by fledglings during the dependent period. By continuing to locate tagged females every three to four days after successful fledging of a brood, we could assess whether any fledglings survived based on adult behavior and observations of fledglings with adults. Females gave alarm calls when flushed in the presence of dependent fledglings. Males gave alarm calls from the ground or a perch when workers entered the territory containing any dependent fledglings. We used the number of nestlings alive at the last nest check as the number successfully fledged. If adults stopped issuing alarm calls or reinitiated nesting before fledglings could have reached independence, we assumed no fledglings had survived. If adults were seen caring for fledglings or issuing alarm calls on or past 18 days postfledging, we assumed that at least one fledgling had reached independence unless we could visually confirm the survival of multiple offspring. We chose 18 days because of the fact that all recorded mortality events of tagged fledglings occurred during the first 14 days of the dependent period and the majority of tagged individuals became independent between days 19 and 21. We then totaled the number of untagged nestlings that fledged as well as the minimum and maximum that could have survived and report this range of survival estimates. These data were not included in our estimates of fledgling survival. Instead, we compared these estimates of untagged fledglings to estimates of tagged fledglings to look for any large effects of transmitters on survival.

We measured vegetation composition and structure for each fledgling occupied-location during both the dependent and independent periods, as well as at paired random points. Random points were generated in QGIS (version 2.14.3, QGIS Development Team 2016) using a random number to indicate a bearing from the previous day's location and were placed at a distance equal to the distance moved from that previous location to the occupied point of interest. Random points were not placed within 5 m of another point, either occupied or random, to avoid point overlap.

At each point, we estimated the percent covers of grass, forbs, litter, lodge, and woody vegetation within a 2.5-m radius of either the occupied or random point. We defined lodge as the prostrate dead grass material consisting of previous year's growth and litter as decomposing vegetative duff directly adjacent to the ground. The functional biological importance for this species is that lodge served as a substrate and/or cover for nests, and the space between litter and lodge provided cover for both fledglings and adults. Vegetation cover was visually estimated within a 2.5-m radius of either the occupied or random point in 5% increments. Total estimates of cover across cover variables were not constrained to 100%. Cover estimates were recorded for each of four quadrants within the 2.5-m circle based on cardinal directions and then averaged. We also measured litter depth and grass and forb height at the point where 80% of the vegetation biomass was below the measured point by visual estimate (Fisher and Davis 2010). Occupied points were not measured if they were within 5 m of a previously measured point to minimize any effects of lack of independence among points. Observers were trained to visually estimate cover variables in a manner that was consistent with the lead author in order to minimize variation in estimates between observers.

We examined the effect of habitat characteristics on survival at the scales of the nest and the territory because the exact location of a fledgling's death was never known. Nest-scale habitat represented vegetation cover and height estimates for grass, forbs, litter, lodge, and woody vegetation measured at random points within ~50 m of the natal nest. We calculated mean cover and height values for the random points generated to assess habitat selection (see above). We combined our set of random point measurements with habitat measurements at the nest to represent habitat characteristics for the area most frequently used by newly fledged birds during the first 14 days postfledging (Berkeley et al. 2007, Hovick et al. 2011). Vegetation around the natal nest was measured in the same manner and at the same scale as used and random points for fledglings. Measurements at the nest were made within 14 days of fledging.

We estimated the effects of territory-scale features on fledgling survival by measuring the total shrub cover area within a 100-m radius of the nest, as well as recording burn status of the field. We classified burn status as 1, 2, or 3 growing seasons since the last burn based on management maps provided by the park. Shrub areas were defined as woody clumps (most commonly winged sumac but also *Rubus* spp.) that were tall or taller than the surrounding grasses and forbs and covered > 50% of a given area at least 2 m x 2 m in size. Shrub area was digitized manually in the field by creating polygon shape files using a handheld Trimble Juno SB (Trimble Inc., Sunnyvale, California) to map individual

shrub areas. These data were transferred to QGIS and the total shrub area within the nest territory was summed. We selected a scale of a 100-m radius centered on the nest because this encompassed the area used by fledglings during the dependent period.

Analyses

We measured daily movements of fledglings and daily displacement from the nest using GPS locations of fledglings. Daily movements were measured in QGIS by recording the distance moved between consecutive days. Displacement from the nest was measured for every occupied-location point. To avoid pseudoreplication of movement and displacement data in cases where we monitored multiple fledglings in a brood, we averaged daily movement and displacement by brood. The average daily movement and displacement across all monitored broods was then calculated for each day across both the dependent and independent period.

We examined habitat selection during both the dependent period and the independent period using a resource selection function (RSF; Manly et al. 2002, Johnson et al. 2006). The vegetative characteristics of used points were compared to those of random points using generalized linear regression mixed effect models with nest ID as a random effect. We fit a set of univariate and multivariate models composed of vegetation variables measured at a 2.5-m radius around fledgling locations. In total, we fit 39 models including a null model that contained only the intercept as well as two global models; one composed of litter variables and one composed of vegetative cover and height variables. The response variable was coded as "0" for random points and "1" for used points. Model sets were separately ranked for both the independent and dependent periods using AIC adjusted for small sample size (AIC_c; Burnham and Anderson 2002).

We also compared habitat used by fledglings during the dependent period to habitat used during the independent period. We again used the same 39 logistic regression mixed models with a random effect of nest ID. The response variable was coded as 0 if a point was used by a dependent fledgling and 1 if a point was used by an independent fledgling. Models were ranked using AIC_c.

Estimates of fledgling survival were produced using a Kaplan-Meier survival analysis in program R using the package "survival" (Therneau 2019). This analysis measures survival time from a start point to a mortality event by a specified interval. We used days as our interval with our start point being the attachment of transmitters. In this case, survival estimates for "day 1" estimate the average survival from the time of transmitter attachment until the fledglings were located the next day. Individuals were right censored if fate could not be determined because of either researcher error or the transmitter falling off. For this and all subsequent analyses we combined years because a log rank test did not support a difference between the two yearly survival curves ($chisq = 1.9$, $p = 0.169$, see Results). We did not mark fledglings from territories that had been used the previous year, and there was no overlap between years in marked adults whose nests we monitored.

We estimated fledgling daily survival as a function of both nest-scale vegetation cover variables and territory-scale habitat variables using generalized linear mixed models with a binomial

distribution fit using package “lme4” in program R (Bates et al. 2015). A random effect of nest ID was included to account for multiple fledglings from a single nest and for repeated locations within the same territory. All explanatory variables were scaled and centered to aid in convergence of models. We measured the effects of nest-scale vegetation on fledgling survival by fitting the set of 39 models described above using mean values generated from random and nest point cover and height values for the area used by fledglings. The effects of territory-scale habitat characteristics on fledgling survival were assessed by fitting a set of eight models that contained combinations of the variables shrub cover, burn status, and study day. Study day was defined by a sequential series of numbers starting with 1 May as “1” for both years to coincide with the observed breeding season. These territory-scale models were applicable to assessing the effect of habitat on survival during the dependent period because fledglings stayed within the 100-m radius of the nest for which we measured shrub cover during this time.

We constrained our analysis of the effects of habitat on survival to the first 14 days of the dependent postfledging period, when all observed predation-related mortality occurred to meet the assumption of normality and thus reduce potential bias in the resulting parameter estimates. Candidate model sets were ranked separately using AIC_c . We report parameter estimates for all variables contained in top models as well as variables from models $< 2 \Delta AIC_c$ from the top model unless the variable was uninformative *sensu* Arnold (2010). Additionally, we only report estimates for variables if 85% bootstrapped confidence intervals for the estimate do not overlap zero. We used 85% confidence intervals to better align with AIC model selection criteria so that potentially informative variables were not discarded (Arnold 2010). All analyses were conducted in program R version 3.3.1 (R Core Team 2016).

RESULTS

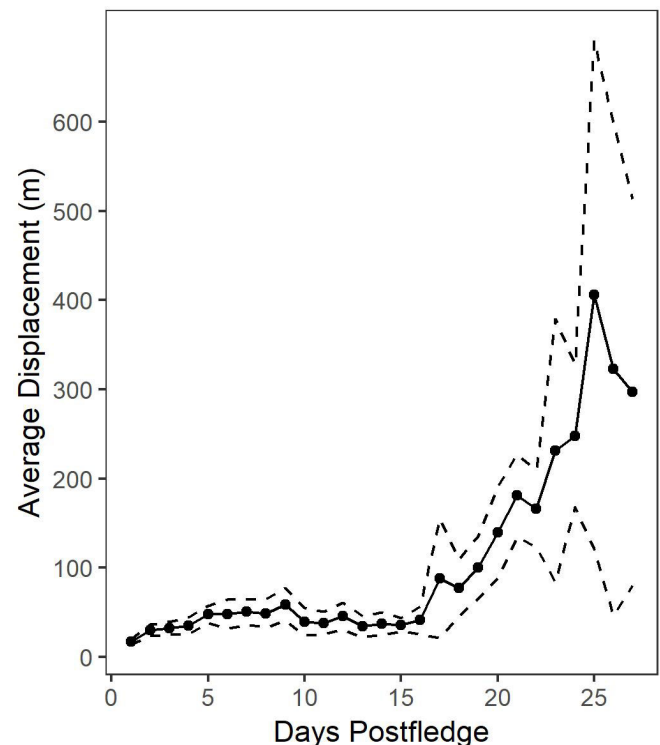
In 2015 we attached transmitters to 21 nestlings, and three of these were right censored. In 2016, we placed transmitters on 25 nestlings with three being right censored, for a total of 46 fledglings tracked for 514 observation days across the two seasons. Three of the censoring events occurred because transmitters fell off. The remaining three were censored because mortality appeared to result from the tracking process. In two cases we found fledglings with the transmitter antennae entangled in vegetation. Entanglement has since been reported from a study of fledglings of another grassland species (van Vliet and Stutchbury 2018). To prevent further instances of tangling, we clipped the antennae from 15 cm to 8 cm. This reduced signal strength, but appears to have prevented further tangling events. Because fledglings were located daily and because we searched the vegetation when there was no apparent movement from the preceding day, we are confident that these tangling incidents were isolated events. The third case of mortality resulted from a fledgling being accidentally stepped on during the tracking process.

Habitat use

During the dependent period, all fledglings stayed within a 100-m radius of the natal nest with an average displacement of 40 m (± 11 SD) during the first 14 days postfledge (Fig. 1). Average movement between daily locations was 36 m (± 12 SD; Fig. 2)

during the first 14 days postfledge. Daily locations of siblings from nests in which we tagged multiple nestlings were on average 22 ± 11 m apart during the first 5 days postfledge. At the onset of the independent period (median = day 19 postfledge, min = day 16, max = day 23) fledglings made large movements outside of the natal territory. We followed nine independent fledglings for a total of 113 observation days. Average displacement from the natal nest during the independent period was 236 m (± 89 SD) and average movement between daily locations during the independent period was 90 m (± 19 SD).

Fig. 1. Average daily displacement of Henslow’s Sparrow (*Centronyx henslowii*) fledglings from the natal nest in Missouri, USA. Dashed lines represent 95% confidence intervals. Solid line is the absolute linear distance from the fledglings’ location to the natal nest averaged by day.



The top model for habitat use during the dependent period included a term for percent cover of woody vegetation (Table 1). Points used during the dependent period had a lower percent cover of woody vegetation than random points ($\beta = -0.16$, SE = 0.08, 85% CI = -0.30, -0.03). Model rankings for habitat use during the independent period (Table 1) indicate that fledglings are using habitat with shorter grass height ($\beta = -0.36$, SE = 0.17, 85% CI = -0.63, -0.11) and lower percent cover of woody vegetation ($\beta = -0.28$, SE = 0.17, 85% CI = -0.54, -0.03) than associated random points.

The best model describing habitat use differences between the dependent and independent periods included terms for forb and litter cover. The model had 86% of the overall AIC_c weight, no other model was within 2 AIC_c points of it, and the ΔAIC_c for

Table 1. Model-selection results for models describing habitat use by fledgling Henslow's Sparrows (*Centronyx henslowii*) during both the dependent and independent periods in Missouri, USA.

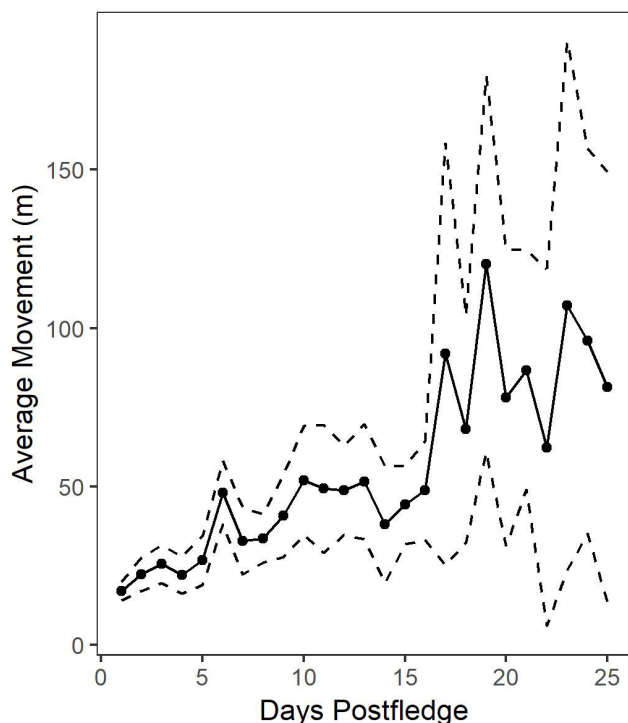
Model	Dependent Period			
	res.dev [†]	K [‡]	ΔAIC _c	w _i [§]
% Cover Woody	761.61	2	0.00	0.12
% Cover Woody + % Cover Grass	759.68	3	0.09	0.11
% Cover Woody + % Cover Forbs	760.91	3	1.32	0.06
% Cover Woody + % Cover Litter	761.08	3	1.49	0.06
Null	765.23	1	1.60	0.05
% Cover Woody + Grass Height	761.51	3	1.92	0.05
Model	Independent Period			
	res.dev	K	ΔAIC _c	w _i
Grass Height	205.88	2	0.00	0.11
Grass Height + % Cover Woody	204.17	3	0.38	0.09
Grass Height + Forb Height	204.50	3	0.70	0.08
Grass Height + % Cover Lodge	205.02	3	1.23	0.06
Grass Height + % Cover Forbs	205.59	3	1.80	0.05
% Cover Woody	207.68	2	1.81	0.05
Grass Height + Litter Depth	205.62	3	1.82	0.05
~				
Null	210.48	1	2.55	0.03

[†]Model residual deviance

[‡]Parameters in model

[§]Model weight

Fig. 2. Average movement from the previous day's location for Henslow's Sparrow (*Centronyx henslowii*) fledglings in Missouri, USA. Dashed lines represent 95% confidence intervals. Movement is defined as the distance between daily locations on consecutive days averaged by day.



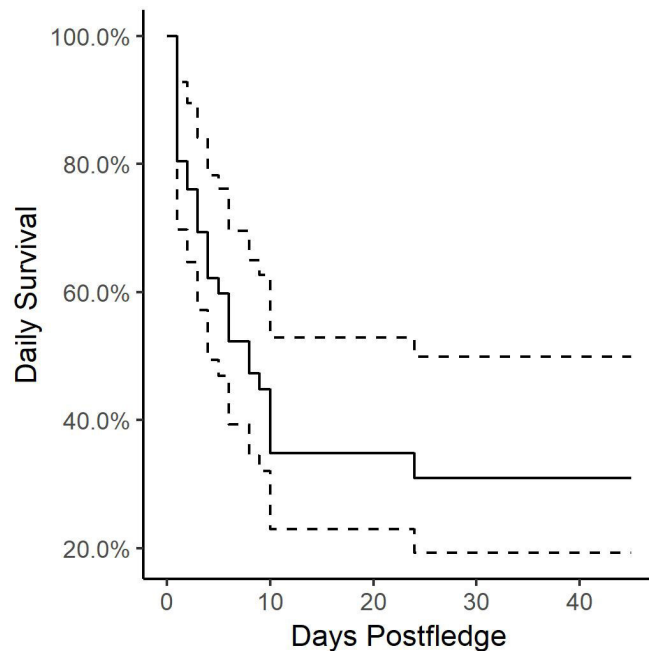
the null was 26.13. Points used during the independent period had a higher percent cover of forbs ($\beta = 0.59$, SE = 0.18, 85% CI = 0.28, 0.95) and a lower percent cover of litter ($\beta = -0.67$, SE = 0.21, 85% CI = -1.03, -0.39) than points used during the dependent period.

Survival

Survival at 14 days in 2015 was 0.255 ± 0.106 SE (95% CI 0.113, 0.577). Four monitored fledglings survived until the independent period. In 2016, survival at 14 days was 0.421 ± 0.101 (95% CI 0.263, 0.673), and eight monitored fledglings survived to independence. Combining both years, survival at 14 days was 0.349 ± 0.074 (95% CI 0.230, 0.529; Fig. 3). All recorded mortality occurred within the first 10 days postfledging except for one fledgling that was found dead from a nonpredation event on day 24 postfledging, possibly due to excessive heat. For seven successful nests at which we continued to monitor adult behavior without tagged fledglings, only two (28.6%) successfully raised at least one fledgling to independence. We estimate that these seven nests produced 23 fledglings and at least three but no more than seven fledglings achieved independence, suggesting that the overall survival rate for untagged fledglings was between 0.13 and 0.30.

We documented 29 mortality events. Fifteen mortalities (51.7%) were attributed to snake predation. We visually confirmed predation of two fledglings by eastern yellow-bellied racers (*Coluber constrictor*), which was also the most common species that we observed at the site. The speckled kingsnake (*Lampropeltis getula holbrookii*) was also a visually confirmed predator of one fledgling, as well as the only visually confirmed predator of nests. Two predation events were attributed to mammals based on marks on the transmitter and condition of the remains. Two predation events were attributed to birds because the transmitter was found

Fig. 3. Cumulative daily survival probability for Henslow's Sparrow (*Centronyx henslowii*) fledglings in 2015 and 2016 in Missouri, USA. Dashed lines represent 95% confidence intervals.



suspended in vegetation > 1 m tall. We could not determine the cause of death for seven mortality events. Three fledglings were found buried by burying beetles but the cause of death could not be determined.

A priori correlation scores and an a posteriori variance inflation factor (VIF) test (< 1.5 for all predictor variables) of our top territory-scale model found no evidence of multicollinearity between predictor variables. We monitored 15 fledglings in areas burned 1 season ago, 17 in areas burned 2 seasons ago, and 14 in areas 3 years postburn. Habitat characteristics at the territory scale (100-m radius) influenced survival, with substantial support for the global model. The best model describing the effects of territory-scale habitat characteristics on fledgling survival included terms for shrub area, burn, and day of the season. The model had 87% of the overall AIC_c weight, no other model was within two AIC_c points, and the ΔAIC_c for the null was 10.82. Survival decreased as shrub area increased ($\beta = -1.11$, SE = 0.34, 85% CI = -1.76, -0.69; Fig. 4). The parameter estimate for 2nd year postburn indicated increased survival ($\beta = 1.56$, SE = 0.62, 85% CI = 0.72, 2.80), and the estimate for 3rd year postburn also indicated increased survival ($\beta = 2.65$, SE = 0.85, 85% CI = 1.60, 4.69; Figs. 4 and 5) compared to areas 1 year postburn. Estimated effects of ordinal date showed that probability of survival decreased as the season progressed ($\beta = -1.00$, SE = 0.39, 85% CI = -1.79, -0.47; Fig. 5). Model-based predictions of cumulative survival across the first 14 days of the fledging period (when almost all mortality occurred) suggest that survival was substantially higher in patches with reduced shrub densities and greater time since fire as well as earlier in the season. The null was

the top-ranked model in the nest-site vegetation analysis, indicating that there were no effects of nest-scale vegetation cover or litter characteristics on fledgling survival (Table 2).

Fig. 4. Predicted daily survival of Henslow's Sparrow (*Centronyx henslowii*) fledglings during the first 14 days postfledge in Missouri, USA. Survival is predicted in relation to shrub area within 100 m of the nest and growing seasons since last burn; (a) 1 growing season, (b) 2 growing seasons, and (c) 3 growing seasons. Shaded areas represent 85% confidence intervals.

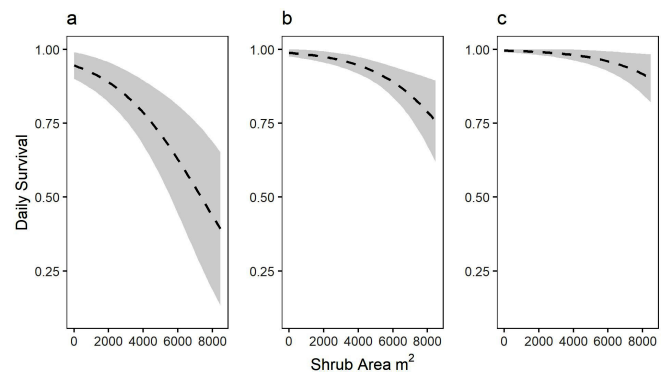
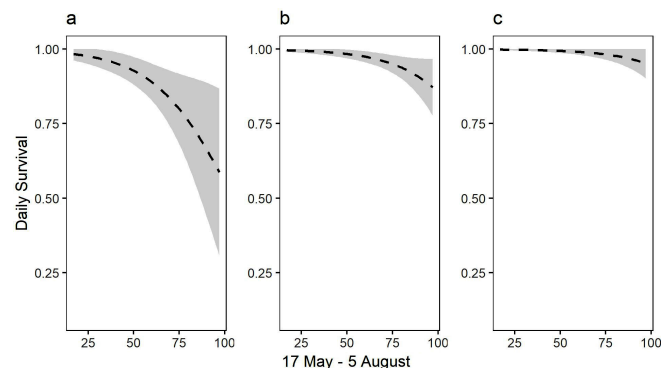


Fig. 5. Predicted daily survival of Henslow's Sparrow (*Centronyx henslowii*) fledglings during the first 14 days postfledge in Missouri, USA. Survival is predicted in relation to time of year and growing seasons since last burn; (a) 1 growing season, (b) 2 growing seasons, and (c) 3 growing seasons. Shaded areas represent 85% confidence intervals.



DISCUSSION

Understanding habitat selection and its implication for survival at all life stages is required to optimize management for rare and declining species. Here, we observed stage-specific habitat selection by fledgling Henslow's Sparrows, as well as substantial effects of habitat characteristics on fledgling survival, which suggests that opportunities exist for managers to directly affect the demography of this rare grassland bird.

During the dependent period, fledglings used an area (~1.5 ha) that was substantially larger than the ~0.29 hectare nesting

Table 2. Model selection results for models describing the effects of nest-scale habitat characteristics on fledgling survival of Henslow's Sparrows (*Centronyx henslowii*) during the first 14 days postfledge in Missouri, USA.

Model	res.dev [†]	K [‡]	ΔAIC _c	w _i [§]
Null	122.92	2	0.00	0.09
Forb height	125.54	3	0.23	0.08
% Cover lodge + Forb height	128.90	4	0.88	0.06
Grass height	125.77	3	1.20	0.05
% Cover lodge	124.21	3	1.30	0.05
% Cover woody	123.44	3	1.70	0.04
Litter depth	123.29	3	1.77	0.04

[†]Model residual deviance

[‡]Parameters in model

[§]Model weight

territory size we estimated by spot-mapping adults during concurrent work (*unpublished data*), as well as previously published estimates using similar methods (Wiens 1969, Jaster et al. 2013). Spot-mapping can sometimes underestimate the area of habitat used by adults (Streby et al. 2012), but our observations of fledglings entering neighboring territories with active nests confirms that young birds quickly moved outside the area defended by singing males. We observed no antagonism between adults feeding fledglings and singing males from adjacent nesting territories. Once fledglings were independent, reneating adults returned to their original nest territories. This expansion of the area that has classically been thought of as “territory size” may be an important aspect of area requirements for this species and one that managers may need to consider. Displacement from the nest during the dependent period for Henslow's Sparrow was approximately the same as that reported for Grasshopper Sparrows (*Ammodramus savannarum*; Hovick et al. 2011), a similarly sized species. Larger grassland species move greater distances from the nest during this period, with Dickcissels (*Spiza americana*) moving 63–205 m (Berkeley et al. 2007, Nooyen 2016) and Eastern Meadowlarks (*Sturnella magna*) moving ~100–500 m from the nest (Kershner et al. 2004).

Nearly all of the fledgling mortality we observed occurred during the dependent period, underscoring the need for management of this life stage. Cumulative survival was lower than estimates found for other tallgrass prairie species. Grasshopper Sparrows in Iowa were found to have a cumulative survival probability at 14 days postfledge of ~0.55 (Hovick et al. 2011), and cumulative survival of Dickcissels in eastern Nebraska was estimated to be 0.60 for one study (Berkely et al. 2007), and 0.70 for another (Nooyen 2016). Survival of Henslow Sparrow fledglings improved after the first seven days postfledge, and we saw little evidence of a spike in mortality at the onset of independence, a pattern seen in some forest birds (Anders et al. 1997). Instead, eight of nine fledglings that we followed past independence survived to at least day 35 postfledging. The only mortality event observed during the independent period was not a result of predation and occurred during an extended period of high temperatures with no rain.

Survival for fledglings without transmitters was similar to rates found for fledglings with transmitters, suggesting that the use of

transmitters that are ~5% of body mass at the time of attachment did not lead to a large effect on survival. Previous studies of passerine postfledging survival have not detected an effect of transmitters on postfledging survival (Powell et al. 1998, Rae et al. 2009), but the two cases of antenna entanglement we encountered prior to shortening antennas, and a subsequent report of entanglement of radio tagged Savannah Sparrow fledglings (van Vliet and Stutchbury 2018), suggest that care must be taken considering transmitter antenna length when studying grassland birds. We found that clipping antennas to 8 cm provided adequate signal strength while preventing entanglement.

Survival of fledglings decreased as shrub area within 100 m of the nest increased. A concurrent study at this site observed a similar pattern for daily nest survival (Young 2017), and Graves et al. (2010) also found lowered daily nest survival as shrub area increased (but see Hill and Deifenbach 2013). These findings suggest that clumped areas of dense sumac within otherwise open tallgrass prairie habitat may be altering the predator community for Henslow's Sparrow, leading to increased predation rates for multiple reproductive stages. Snakes were the most common predator of fledglings, and the most commonly observed snake species at our site, eastern racer, has been shown to disproportionately utilize shrubby habitat within tallgrass prairies (Klug et al. 2010). Movements and home range of eastern racers are limited, with 50% core use areas in similar habitat found to be 1.8 ha (Klug et al. 2011). Increases in abundance or occupancy for a predator that concentrates its predation efforts within a relatively small area would increase the likelihood of predation for dependent fledglings in these areas, especially given the limited movement and flight capabilities of fledglings during the first week postfledge.

We observed higher fledgling survival in fields in which the last burn had been 2 and 3 growing seasons prior. Henslow's Sparrows avoid nesting in fields burned that year, presumably because of a lack of a dead vegetation (lodge) for use as a nesting substrate (Herkert 1994, Byers et al. 2017). As time since the last burn increases, the density of dead vegetation should increase in the absence of intensive grazing (Knapp and Seastedt 1986, Fuhlendorf 2009). During the first few days postfledging, when fledglings are most vulnerable, higher cover and depth of litter and lodge would presumably provide protection from predation. Fledglings were observed to hide under prostrate domes of dense lodge (*personal observation*). Snakes that search visually for prey, including eastern racers (Fitch 1963), would have to increase search effort (Stake et al. 2005). However, we found no support for an effect of fine-scale vegetative cover variables, including litter, on fledgling survival. This may be because there is relatively little variation in habitat used by fledglings. Alternatively, the predator community may be responding to habitat heterogeneity at a larger scale than that which was measured. The high prevalence of snake-associated mortality on fledglings suggests that further work is needed on the response of snakes to frequently used management tools. Little is known about the dynamics of grassland snake community response to burns (Wilgers and Horne 2006). One study found that eastern racer abundance responded negatively to burns of the year (Cavitt 2000), though this response was found to largely disappear by fall of the burn year (Setzer and Cavitt 2003).

Our finding that the probability of fledgling cumulative survival probability decreased as the season progressed may provide further evidence for complex interactions with a predator community dominated by snakes. Evidence suggests that snake activity may peak later in the season (Meshaka et al. 2008), and that temporal variations for nest success in songbirds can be tied to seasonal snake activity patterns (Sperry et al. 2008, Cox et al. 2013, DeGregorio et al. 2014). Taken together, data suggest that recently burned areas with high shrub cover will exhibit high fledgling mortality, especially later in the breeding season, because of snake activity and the vulnerability of fledglings with low flight power.

Once independent, fledglings typically moved 200–300 m away from nesting territories and selected habitats that differed from that used during the dependent period. Given high rates of predation by snakes during the dependent period, independent fledglings may be selecting different habitat characteristics to decrease this risk. For example, eastern racers preferentially use habitat with a dense litter layer and dense shrubs (Cavitt 2000, Klug et al. 2010), which is consistent with habitat that independent fledglings tended to avoid. In addition, newly independent juveniles must still contend with the rigors of preparing for and conducting migration, an event that may be the time of highest mortality for adults (Sillert and Holmes 2002). It is possible that habitat used during the independent period is providing food resources that may lead to improved fitness or survival. Our observation of differential use of habitat during the independent postfledging period, and any potential effects on survival during this period or fall migration, certainly deserves further study.

Management implications

Conservation of grassland specialists such as Henslow's Sparrow will require active management of remaining grasslands. Our findings indicate that dense cover of woody vegetation substantially lowers survival of fledglings and that fledglings avoided using areas containing woody vegetation during both the dependent and independent stages. These findings align with the tendency for breeding adults to avoid using habitat with dense woody vegetation (Zimmerman 1988, Winter 1999). Our findings suggest that removal of woody vegetation may help to improve population outcomes for Henslow's Sparrow at this site. However, breeding Henslow's Sparrow populations span a wide geographic range, occurring from northern tier states such as New York to as far south and west as Oklahoma. Within this range, variation in the predator community may alter the effects of habitat on Henslow's Sparrow reproductive success. For example, in areas occupied by Henslow's Sparrow in Minnesota and Wisconsin, mammals were found to be the primary nest predators (Ribic et al. 2012, Byers et al. 2017). In contrast, eastern racer, a species associated with shrubby habitat, was the most commonly identified predator of fledglings at our site. In the southwest portion of this species' range, our findings suggest that removal of woody vegetation may substantially improve reproductive outcomes and should be employed where management for Henslow's Sparrow is prioritized. Future studies examining the effects of shrub expansion on reproductive outcomes in other geographic regions would be beneficial.

Traditional management recommendations for Henslow's Sparrow have focused on providing large areas of unburned,

ungrazed grassland maintained with three to four year fire rotations (Herkert 2002). The result of these recommendations is likely to be a homogeneous vegetation structure suitable for adult nesting habitat. However, our results indicate that the characteristics of habitat used by independent fledglings at this site are inconsistent with habitat used by nesting adults. Nesting adult Henslow's Sparrows may use habitat that is structurally heterogeneous at scales larger than the nesting territory (Fuhlendorf et al. 2006). Therefore, a mosaic of burned, unburned, and lightly grazed areas that provide adequate nest habitat while accounting for relatively small fledgling movement distances may be ideal if the differential habitat use we observed for independent fledglings imparts some benefit. Future studies focused on the independent period will help to improve our understanding of stage-specific breeding season habitat use and its implications for populations of grassland birds.

Responses to this article can be read online at:
<http://www.ace-eco.org/issues/responses.php/1418>

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