ResearchGate

See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/272819660

Habitat use and movement patterns by dependent and independent Grasshopper Sparrows during the post-fledging period

Article in Journal of Field Ornithology · March 2015

DOI: 10.1111/jofo.12085

CITATION		READS	
1		35	
3 autho	rs:		
	Daniel M. Small		Peter J. Blank
	Washington College	\sim	14 PUBLICATIONS 106 CITATIONS
	12 PUBLICATIONS 12 CITATIONS		SEE PROFILE
	SEE PROFILE		
Ga	Bernard Lohr		
S	University of Maryland, Baltimor		

42 PUBLICATIONS 754 CITATIONS

SEE PROFILE

All content following this page was uploaded by Peter J. Blank on 09 June 2016.

The user has requested enhancement of the downloaded file.

Habitat use and movement patterns by dependent and independent juvenile Grasshopper Sparrows during the post-fledging period

Daniel M. Small,^{1,4} Peter J. Blank,² and Bernard Lohr³

¹Chester River Field Research Station, Washington College, 101 South Water Street, Chestertown, Maryland 21620, USA ²Department of Zoology, University of Wisconsin, 436 Birge Hall, Madison, Wisconsin 53706, USA

³Department of Biological Sciences, University of Maryland Baltimore County, 1000 Hilltop Circle, Baltimore, Maryland 21250, USA

Received 4 May 2014; accepted 28 November 2014

ABSTRACT. The post-fledging period is a critical life stage for young grassland birds. Habitat selection by recently fledged birds may differ from that of adults and may change as juveniles transition from the care and protection of parents to independence. To describe patterns of habitat selection during these important life stages, we studied habitat use by juvenile Grasshopper Sparrows (*Ammodramus savannarum*) in a Conservation Reserve Program grassland in Maryland. We used radio-telemetry to track daily movement patterns of two age classes of Grasshopper Sparrows during the post-fledging period. Sparrows were classified as either dependent (<32-d-old) or independent (\geq 32-d-old). We characterized the vegetation at 780 vegetation plots (390 plots where birds were located and 390 paired random plots). Microhabitats where dependent birds were found had significantly more bare ground, litter, and plant species richness than paired random plots. In addition, dependent birds were found in plots used by independent birds. Plots where independent birds were located also had significantly more bare ground than random plots. Dependent birds are less able to escape from predators because their flight feathers are not fully grown so they may benefit from remaining in areas of greater vegetation cover. However, juveniles transitioning from dependence to independence must forage on their own, possibly explaining their increased use of more open areas where foraging may be easier. To properly manage habitat for grassland birds, management strategies must consider the changing needs of birds during different stages of development. Our results highlight the importance of diverse grassland ecosystems for juvenile grassland birds during the transition to independence.

RESUMEN. El uso del hábitat y patrones de movimiento por dependientes e independientes Ammodramus savannarum floridanus jóvenes en el período después de dejar el nido

El período después de dejar el nido es una etapa crítica de la vida de las aves jóvenes de pastizal. Selección de hábitat por aves que recién dejaron el nido pueden diferir en el uso del hábitat de los adultos y puede cambiar a medida cuando los jóvenes pierden la atención y protección de los padres en la transición a la independencia. Para describir los patrones del selección de hábitat durante las etapas importantes de la vida, se estudió el uso del hábitat por Ammodramus savannarum floridanus jóvenes en un pastizal Conservation Reserve Program en Maryland, EEUU. Ŝe utilizó la radio telemetría para rastrear los patrones de movimiento diario de dos clases de edad de Á. savannarum floridanus durante el período después de dejar el nido. Gorriones fueron clasificados como dependientes (< 32 días de vida) o independientes (≥ 32 días de edad). Hemos caracterizado la vegetación en 780 parcelas de vegetación (390 parcelas donde se encontraban las aves y 390 emparejados parcelas al azar). Los micro hábitats, donde se encontraron las aves dependientes, tenían significativamente más suelo desnudo, hojarasca, y un mayor riqueza de especies de plantas en comparación con las parcelas al azar pareados. Además, las aves dependientes fueron encontrados en las parcelas con menos suelo desnudo, más cobertura de pasto de temporadas calientes, mas cobertura de vegetal, y más cobertura de hierbas en comparación con las parcelas utilizadas por las aves independientes. Las parcelas donde se encontraron las aves independientes también tenían el suelo significativamente más desnudo que las parcelas al azar. Aves dependientes tienen menos capacidad de escapar de los depredadores porque sus plumas de vuelo no se han desarrollado completamente, entonces los aves dependientes se puedan beneficiarse de quedar en las zonas de mayor cobertura vegetal. Sin embargo, los jóvenes en transición de la dependencia a la independencia deben alimentarse de manera independiente, lo cual quizá explique el incremento del uso de las zonas más abiertas donde el forrajeo puede ser más fácil. Para gestionar adecuadamente el hábitat para las aves de pastizal, las estrategias de gestión deben

⁴Corresponding author. Email: dsmall2@washcoll.edu

^{© 2015} Association of Field Ornithologists

tener en cuenta las cambiantes necesidades de las aves durante las diferentes etapas de desarrollo. Nuestros resultados resaltan la importancia de los diversos ecosistemas de pastizales para las aves jóvenes de pastizal durante la transición a la independencia.

Key words: Ammodramus savannarum, grassland birds, habitat restoration, habitat selection, radio telemetry

The post-fledging period, broadly defined as the time between when a bird leaves a nest and when it migrates or settles in a wintering area, is a critical life history phase and probably the most challenging time in a young bird's life (Berkeley et al. 2007, Suedkamp Wells et al. 2008, Anthony et al. 2013). It is also generally the least studied and least understood life stage in songbirds (Vega Rivera et al. 1998, Fisher and Davis 2011). This period includes a dependent stage, when juveniles still receive parental care, followed by an independent stage. To survive and achieve independence, juveniles must become self-sufficient at finding food and shelter and avoiding predators (Kershner et al. 2004, Berkeley et al. 2007, Hovick et al. 2011).

Characteristics of the vegetation of natal home ranges can influence survivorship of fledgling grassland birds. For example, Berkeley et al. (2007) found increased survivorship of fledgling Dickcissels (Spiza americana) that used areas with denser vegetation and greater forb cover. Juvenile grassland birds may seek out areas with greater plant species diversity and greater food availability (e.g., more invertebrates; Burger et al. 1990). Predation risk may also influence microhabitat use by juvenile birds (Pulliam and Mills 1977), which may explain the tendency of recently fledged Botteri's Sparrows (Aimophila botterii) to be found in taller vegetation than at nest sites (Jones and Bock 2005). Birds in areas with dense vegetation cover have been shown to be less vulnerable to predation (Watts 1990, Suedkamp Wells 2005). Thus, microhabitats used by dependent and independent juvenile birds for foraging and movement may affect daily survivorship (Suedkamp Wells et al. 2007).

Little is known about the post-fledging ecology of grassland birds, particularly grasslandobligate species. In addition, most research has focused on the dependent stage (Yackel Adams et al. 2006, Berkeley et al. 2007, Hovick et al. 2011), with few studies conducted during the independent stage (Kershner et al. 2004, Suedkamp Wells et al. 2008). These latter studies report increasing movement with increasing fledgling age, particularly for independent juveniles. However, no one to date has compared habitat use by dependent and independent grassland fledglings, or compared habitat use by fledglings at either stage to that of adults. Therefore, we examined microhabitat use by both dependent and independent juvenile Grasshopper Sparrows. Our objectives were to determine if birds selected specific microhabitats, and if habitat use changed during the transition from dependence to independence. We hypothesized that as juvenile Grasshopper Sparrows become independent their habitat requirements change, which may be an important factor influencing juvenile survival. Understanding the habitat preferences of juvenile grassland birds during these early life stages may provide important information about resource use by grassland birds, and can potentially inform land managers about the habitat requirements of grassland birds.

METHODS

We conducted our study on a 91.7-ha Conservation Reserve Program warm-season grassland at the Chester River Field Research Station (CRFRS) in Queen Anne's County, Maryland (39.23°N, 76.00°W). The grassland was planted in 1999 in an experimental design with eight warm-season and two cool-season grasses creating areas of short, medium, and tall vegetation. Twelve fields, with six paired replicates, ranging in size from 8 to 14 ha were planted with a combination of three grass species to establish a mosaic of different stature heights across the grassland. Grasses planted included big bluestem (Andropogon gerardii), switchgrass (Panicum virgatum), coastal panicum (Panicum amarum), eastern gamagrass (Tripsacum dactyloides), Indian grass (Sorghastrum nutans), little bluestem (Schizachyrium scoparium), sideoats grama (Bouteloua curtipendula), and deer-tongue (Dicanthelium clandestinum). Twenty-four annual and perennial forbs were also included in the planting mixtures. This planting

Vol. 86, No. 1

design created a gradient of microhabitats throughout the grassland that is representative of a range of other CRP warm-season grasslands in the region (USDA 2011, 2014). The management regime included prescribed burning on a 3-yr rotation from 2000 to 2010 and then a 2-yr rotation beginning in 2011. Herbicides have been used to control noxious weeds as needed. Parts of this grassland have now become dominated by two aggressive tall warm-season grasses: big bluestem and switchgrass. More than 260 species of plants have been documented in the grassland since restoration began (Gill et al. 2006). For a comprehensive description of the experimental planting regime and bird colonization of these restored grasslands, see Gill et al. (2006). Intensive row crop agriculture (e.g., corn, soybeans) and mixed deciduous woodlots dominate the surrounding landscape.

Bird handling and radio-tracking. Juvenile Grasshopper Sparrows were captured and banded through a combination of nest searching and passive mist-netting. Nest searching was conducted daily from May to August 2011–2012. Nests were located using systematic searches, behavioral cues, and rope dragging (Koford 1999). We monitored each nest every 3–4 d until the nest failed or nestlings fledged. Nestlings were banded with a USGS band at approximately 6-d-old (2-3 d prior to fledging). Passive mist-netting was conducted daily during the breeding season to recapture previously banded known-age nestlings and attach radio transmitters (Gill et al. 2006, Anthony et al. 2013).

Each juvenile sparrow was classified as either dependent (<32-d-old) or independent (≥ 32 d-old) based on Vickery's (1996) report that independent juvenile Grasshopper Sparrows were observed in conspecific flocks 3 to 4 weeks after fledging in Florida. Thirty-two days after hatching in our study (day 1 was set at hatch date) was the median between 3 and 4 weeks of age post-fledging (day 1 equaled fledge date in the Florida study). For the dependent-age subset, one 6- to 8-d-old nestling from each nest (N = 18) was selected at random for tracking. Only one nestling was tracked per nest to ensure independence of marked individuals (Kershner et al. 2004, Berkeley et al. 2007, Hovick et al. 2011). For the independent-age subset, previously banded nestlings \geq 32-d-old were selected for tracking.

Transmitters (model LB-2X, Holohil Systems, Carp, Ontario, Canada, 0.31 g with an average battery life of 21 d, or model A2412, Advanced Telemetry Systems, Isanti, MN, 0.3 g with an average battery life of 18 d) were attached using a figure-8 leg harness (Rappole and Tipton 1991). Harness material was 0.5mm-diameter white thin beading cord elastic (Prym Consumer, Spartanburg, SC). Transmitters weighed <3% of the birds' body mass and harnesses were designed to allow for additional growth after attachment. A small drop of glue was placed on the bottom of transmitters to secure harnesses to the lower back feathers before placing nestlings back in nests (Suedkamp Wells et al. 2008).

We tracked each radio-tagged bird twice a day using a hand-held receiver (model R410, Advanced Telemetry Systems, Isanti, MN) with a Yagi five-element directional antenna (Advanced Telemetry Systems). Tracking times ranged between 07:00 and 19:00 EDT and the same bird was not tracked at the same time of day on consecutive days. We used the homing method to attempt to visually locate marked birds (Mech 1983). We slowly approached the general area of marked birds to minimize disturbance and determine their location. If a bird did not flush, which is typical of recently fledged birds (DMS, pers. observ.), we detached the cable connecting the antenna and held the end of the cable a few feet above the vegetation until we located the bird. If a bird flushed and we did not see it, or we suspected a bird was running along the ground, we did not take vegetation measurements at that location. Once a bird was located, we used a hand-held global positioning system unit (GPS, Garmin GPS72) to determine its coordinates and marked the location with a flag. For birds that flushed, we assumed that they had not moved from their original location and placed the flag at the flush location. Analysis of daily movement patterns was restricted to morning tracking periods only (07:00–12:00).

Vegetation measurements. Habitat features were measured using $1-m^2$ quadrats at bird locations (bird plots) as well as at paired randomly selected locations (random plots). Vegetation of both bird and random plots was measured on the same day. Random plots were located from 1 to 75 m from bird plots in a random direction (0–360 degrees); random numbers for distances and directions were generated in Microsoft Excel (Version 2010) using a random number generator. We chose a maximum distance of 75 m to ensure that random plots were in the same general vegetation type as the paired bird plots. If unsuitable habitat (e.g., woodlot or hedgerow) was encountered at a random plot location, another random plot was chosen.

At each bird location and random point, we recorded the percent cover of bare ground, litter, warm season grasses, forbs, and total vegetation. We also recorded litter depth (measured in the northwest corner of the quadrat), height (cm) of tallest live plant, species richness (species/m²), and vertical density. Cover estimates were nonoverlapping and summed to 100%. Vertical density was quantified by recording the height, from the four cardinal directions, at which a Robel pole was 100% obscured when viewed from a distance of 4 m away at a height of 1 m above ground (Robel et al. 1970). Average vertical density per plot was calculated from the four measurements for each plot.

Statistical analyses. Because our goal was to describe the vegetation characteristics of sampling plots, we considered the plots as experimental units and vegetation variables as response variables. We converted the date of the survey into a continuous variable representing days after 1 June. To ensure that sampling plots did not overlap and to improve independence of the plots, we deleted bird plots <5 m apart (based on GPS coordinates) from the analysis in ArcMap 10 (ESRI 2011).

To model each vegetation variable, we used the lme function in the nlme package (Pinheiro et al. 2013) in R (R Development Core Team 2013), which fits linear mixed-effects models and allows for nested random effects. We created a variable containing a unique identification number for each bird (Bird ID) and included Bird ID as a random effect in all models to account for variation due to individual bird effects. We considered adding year as a random effect, but found no evidence that adding a year effect improved the models.

To compare vegetation variables between bird and random plots, we took the difference between the bird and random plots for each pair of vegetation measurements, used the differences as response variables, and included only an intercept term as an explanatory variable. If the intercept was significantly different from zero, we interpreted the vegetation variable to be different between the bird and random plots. Because the vegetation of each pair was measured on the same day, using the differences from the pairs as response variables directly controlled for the survey date and for differences among pairs due to changes in grassland vegetation during the growing season. We tested for differences in vegetation variables between plots where dependent (< 32-d-old) and independent $(\geq 32$ -d-old) birds were observed, treating bird age as a categorical variable (age class: dependent or independent). All models comparing vegetation variables between age classes included the survey date (days after 1 June) as a covariate to account for differences in vegetation during the growing season. In some cases, residuals of the models were non-normally distributed and/or the residual variances were not homogeneous, violating the assumptions of the models. In such cases, we included either a fixed weight or constant variance structure to improve the fit of the models (Zuur et al. 2009). For models comparing age classes, we tested for spatial autocorrelation by examining semi-variograms with the Variogram function. If there was evidence of spatial autocorrelation, we added either a Gaussian, exponential, or spherical correlation structure to the model. The choice of variance structures and correlation structures was based on choosing the model with the lowest AIC value (Zuur et al. 2009).

RESULTS

We attached radio-transmitters to 18 dependent and 10 independent Grasshopper Sparrows during the breeding seasons of 2011-2012. Young came from 24 different territories with different parents. Two independent siblings were tracked in 2011, and two siblings were tracked (one dependent and one independent) in 2012. Six dependent birds were excluded from the vegetation analysis (four died and two lost transmitters). Of birds that fledged, 15 of 18 (83.3%, two deaths and one unknown fate) dependent birds survived the duration of the tracking period as did all independent birds. The mean number of days tracked per bird was 15 (range = 4 - 22) for dependent birds and 13 (range = 3 - 27) for independent birds, for a total of 267 tracking days. Nine birds were tracked for <10 d either because of transmitter

failure or birds slipping out of their harnesses. Age ranges were 9-31 d post-hatching (mean = 18 d) for dependent birds and 32-74 d post-hatching (mean = 48 d) for independent birds. Average nestling mass of dependent birds was 12.7 g at the time of transmitter attachment and 13.6 g on the day of fledging. Average mass of independent birds was 15.6 g and mean age at the time of transmitter attachment was 42 d.

Our analysis was restricted to 22 juvenile Grasshopper Sparrows; we tracked 12 dependent birds to 255 vegetation plots and 10 independent birds to 135 vegetation plots. The mean number of vegetation plots per bird was 21 (range = 6-36) for dependent birds and 14 (range = 4-34) for independent birds. The mean distance from bird plots to paired random vegetation plots was 37 m. Overall, 780 vegetation plots (390 bird plots and 390 random plots) were included in our analysis (Table 1). Microhabitats where dependent birds were found had significantly more bare ground, litter, and plant species richness than paired random plots. Random plots had significantly greater warm-season grass cover, total vegetation cover, and vertical density than dependentbird plots (Table 1). Plots where independent birds were located had significantly more bare ground than random plots. Random plots had significantly greater warm-season grass cover, total vegetation cover, and vertical density than independent-bird plots (Table 1).

Four of the nine vegetation variables modeled differed with age class. Dependent birds selected plots averaging 16% less bare ground (t = 4.5, P < 0.001), 11% more warm-season grass cover (t = 2.7, P < 0.015), 17% more total vegetation cover (t = 10.1, P < 0.001), and 7% more forb cover (t = 2.3, P < 0.03) than independent birds. No other vegetation variables differed between plots used by dependent and independent juveniles.

Daily movement distances of recently fledged dependent Grasshopper Sparrows increased with age (Fig. 1A); average daily distance from nests was 88.8 m (range = 3.4-1042 m, N = 164). The average distance travelled from the previous day's location by dependent birds was 46.3 m (range = 6.1-401.5 m, N = 160), and was relatively consistent with an overall increase in distance moved from the previous day's location as the birds aged (Fig. 1B). The average distance moved from the previous day's location

by independent birds was 146.1 m (range = 5.2–966 m, N = 89) and varied daily (Fig. 1C). Averaged across birds, daily movement was greater for independent juveniles than dependent juveniles (Mann-Whitney U = 121, $N_1 = 24$, $N_2 = 27$, P < 0.0001). Mean time interval between bird locations on successive mornings was 24.0 h (range = 19.1–28.7 h).

DISCUSSION

During the first 2.5 to 3.5 weeks after fledging, dependent juvenile Grasshopper Sparrows in our study remained within natal home ranges. In contrast, independent birds moved greater distances and traversed neighboring territories on a daily basis. Territorial males in our population are tolerant of nonrelated juvenile Grasshopper Sparrows foraging throughout their territory (DMS, pers. observ.). Independent juvenile Grasshopper Sparrows were more likely to be located at sites with more bare ground, less warm season grass cover, and less total vegetation cover than were dependent sparrows. Few investigators have examined how habitat use and movement patterns change across the early life stages of recently fledged grassland birds (Davis and Fisher 2009, Fisher and Davis 2011). Our results add to this relatively sparse literature by identifying an important transition in habitat preferences for recently fledged juvenile Grasshopper Sparrows as they become independent. We assumed that juveniles made their own choices concerning habitat use, but acknowledge that parents may influence habitat use of dependent juveniles to some extent. More study is needed to determine how parent birds may influence these choices.

Studies of other grassland birds have shown how vegetation characteristics influence survivorship and movement patterns of juvenile birds, but few have focused on how these vegetation characteristics may differ between juvenile age classes. Microhabitat selection by dependent juvenile Botteri's Sparrows, for example, was similar to that of dependent juvenile Grasshopper Sparrows in our study, preferring areas with taller vegetation and less bare ground (Jones and Bock 2005). In contrast, independent juvenile Grasshopper Sparrows were found in areas with more bare ground and less vegetation cover, habitat features also characteristic of areas used by adult Grasshopper Sparrows during the

	Bird plots	lots	Random plots	plots	Mean difference			
Vegetation variable	Mean	SE	Mean	SE	between paired pious (bird plot – random plot) ^a	SE (Difference)	t	P
Dependent bird plots vs. paired random plots	n plots							
Bare ground (%)	11.5	1.0	7.6	1.0	3.8	1.3	2.9	0.004
Litter (%)	27.0	1.4	23.5	1.5	4.4	1.7	2.7	0.008
Forbs (%)	26.2	1.5	25.9	1.6	0.2	2.1	0.1	0.92
Warm-season grasses (%)	31.8	1.8	38.4	2.0	-6.6	2.2	3.0	0.003
Total vegetation cover	61.6	1.5	68.7	1.7	-8.4	2.6	3.2	0.001
Plant species richness (species/ m^2)	6.9	0.2	6.1	0.2	0.9	0.2	3.7	< 0.001
Litter depth (mm)	19.2	2.2	23.4	2.3	-1.5	2.5	0.6	0.56
Tallest plant (cm)	108.5	2.6	107.5	2.6	1.0	3.2	0.3	0.76
Vertical density ^b	32.5	1.2	37.2	1.5	-3.7	1.8	2.1	0.04
Independent bird plots vs. paired rando	E							
Bare ground (%)		2.5	9.5	1.4	17.5	2.7	6.4	0.000
Litter (%)	28.7	2.4	30.5	2.3	-0.9	4.6	0.2	0.84
Forbs (%)	18.5	1.4	18.5	1.7	0.6	1.4	0.4	0.66
Warm-season grasses (%)	17.3	2.0	34.3	2.6	-16.1	3.8	4.2	< 0.001
Total vegetation cover	43.8	2.1	60.0	2.3	-14.2	4.3	3.3	0.001
Plant species richness (species/ m^2)	6.9	0.2	6.6	0.2	0.3	0.3	1.1	0.26
Litter depth (mm)	19.3	3.0	31.9	4.4	-9.1	4.6	2.0	0.051
Tallest plant (cm)	98.8	3.7	115.3	3.9	-14.5	7.6	1.9	0.059
Vertical density ^b	30.7	2.3	41.3	2.7	-10.3	3.7	2.8	0.006

22

D. M. Small et al.

J. Field Ornithol.

	Bird plots	lots	Random plots	t plots	Mean difference between naired plots			
Vegetation variable	Mean	SE	Mean	SE	$(bird plot - random plot)^a$	SE (Difference)	t	P
All bird plots vs. paired random plots								
Bare ground (%)	17.1	1.2	8.3	0.8	8.0	1.8	4.4	0.000
Litter (%)	27.6	1.3	25.9	1.3	1.7	2.0	0.9	0.38
Forbs (%)	23.5	1.1	23.4	1.2	0.2	1.6	0.1	0.91
Warm-season grasses (%)	26.7	1.4	36.8	1.6	-10.3	2.2	4.7	< 0.001
Total vegetation cover	55.4	1.3	65.6	1.4	-10.7	2.4	4.4	< 0.001
Plant species richness (species/m ²)	7.0	0.1	6.2	0.1	0.7	0.2	3.9	< 0.001
Litter depth (mm)	19.2	1.8	26.4	2.2	-3.0	2.0	1.5	0.13
Tallest plant (cm)	105.1	2.2	110.0	2.2	-5.3	3.8	1.4	0.17
Vertical density ^b	31.9	1.1	38.6	1.4	-5.3	1.7	3.2	0.002
^a Value of the fixed effect difference between bird plots and random plots. A random effect of individual bird ID was included in all models ($N = 12$ for dependent birds, $N = 10$ for independent birds, and $N = 22$ for all birds). The sign of the mean difference indicates direction of the relationship (positive greater in bird plots; negative = greater in random plots). Dependent bird plots vs. random plots models: $N = 255$, df = 243. Independent plots vs. random plots models: $N = 255$, df = 243. Independent plots vs. random ^b Minimum height of Robel pole visibility in cm.	ween bird I ent birds, an in random ird plots vs. ty in cm.	slots and $N = 22$ d $N = 22$ plots). De random p	random plo for all birds pendent bir lots models:	ts. A ranc). The sig d plots vs. N= 390	dom effect of individual bird ID gn of the mean difference indicat . random plots models: $N = 255$), df = 368.) was included in all es direction of the rel 5, df = 243. Independ	models (A lationship (dent plots v	I = 12 for positive = 78. random

Table 1. (Continued)

Vol. 86, No. 1

Habitat Use by Juvenile Grasshopper Sparrows

23

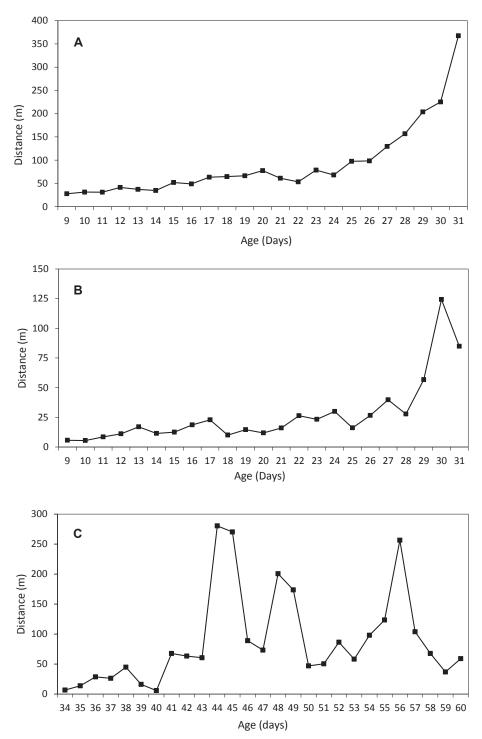


Fig. 1. Distances moved by juvenile Grasshopper Sparrows at the Chester River Field Research Station in Maryland in 2011–2012. (A) Mean daily distance from nests for dependent juveniles, and (B) mean daily distance moved from the previous day's location for dependent juveniles (N = 12). (C) Mean daily distance moved from the previous day's location for independent juveniles (N = 10).

breeding season (Vickery 1996). Although we did not quantify habitat used by adult Grasshopper Sparrows at our study site, other investigators have found that adults prefer grasslands and prairies with patchy bare ground (Vickery 1996) and generally avoid grasslands with shrub cover greater than 35% (Johnston and Odum 1956). In West Virginia, adult Grasshopper Sparrows selected sites with less litter, more bare ground, and sparser vegetation than unoccupied sites (Whitmore 1981).

Factors such as food availability and predator avoidance may influence habitat selection by juvenile Grasshopper Sparrows during the post-fledging period. Juvenile birds transitioning from dependence to independence must successfully forage on their own, possibly explaining their increased use of more open areas where foraging may be easier (Fisher and Davis 2011, Hovick et al. 2011). Independent juveniles must balance their exposure in more open habitats where foraging may be easier, with a potentially increased vulnerability to predators. Predation risk and the need to forage independently may thus exert counterbalancing selective pressures; both Grasshopper Sparrows and their predators (at least those that hunt visually) may have better foraging success in relatively open, less vegetated areas (Fisher and Davis 2011).

Predation is generally the primary cause of mortality during the post-fledging period (Yackel Adams et al. 2006, Berkeley et al. 2007, Suedkamp Wells et al. 2007), particularly within the first week for fledgling Grasshopper Sparrows (Hovick et al. 2011). Because dependent birds are not foraging on their own, and are less able to escape predators because their flight feathers are not fully grown (Anders et al. 1997, Kershner et al. 2004, Suedkamp Wells et al. 2007, Hovick et al. 2011), they may benefit from remaining in areas of greater vegetation cover. However, Jackrel and Reinart (2009) found that snakes were more common in grassland areas with denser vegetation. Despite this, birds that are less mobile typically hide from predators (Pulliam and Mills 1977), so dependent birds may have an innate tendency to seek out dense vegetation to avoid detection.

To properly manage habitat for grassland birds, management strategies must account for the changing needs of individuals at different stages of development. Our results highlight the importance of diverse grassland ecosystems for juvenile grassland birds during the transition to independence when mortality rates are typically high (Anders et al. 1997, Kershner et al. 2004, Yackel Adams et al. 2006, Berkeley et al. 2007, Suedkamp Wells et al. 2007, Fisher and Davis 2011, Hovick et al. 2011). From a management perspective, simply establishing and managing habitat for adults may not provide the necessary resources for grassland birds, such as Grasshopper Sparrows, during other life stages. Our results suggest that grassland management strategies should focus on creating a diversity of plant structure throughout restored or managed grassland habitats, and on maintaining areas of open ground alongside areas of thicker vegetation to accommodate habitat needs of both juveniles and adults.

ACKNOWLEDGMENTS

We thank the 2011 and 2012 field crews, especially M. Rohde and M. Gimpel, for their help with radiotracking. H. Davis and G. Cole assisted with habitat management. Field work could not have been conducted without the generous support of H. Sears. D. Gill provided helpful comments on early drafts of this manuscript. We are grateful for the comments from the editor and three anonymous reviewers. This study was funded in part by the Maryland Ornithological Society.

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.
- ANTHONY, T., D. E. GILL, D. M. SMALL, J. PARKS, AND H. F. SEARS. 2013. Post-fledging dispersal of Grasshopper Sparrows (*Ammodramus savannarum*) on a restored grassland in Maryland. Wilson Journal of Ornithology 125: 307–313.
- BERKELEY, L. I., J. P. MCCARTY, AND L. L. WOLFEN-BARGER. 2007. Postfledging survival and movements in Dickcissels (*Spiza americana*): implications for habitat management and conservation. Auk 124: 396–409.
- BURGER, L. W., Jr., E. W. KURZEJESKI, T. V. DAILEY, AND M. R. RYAN. 1990. Structural characteristics of vegetation in CRP fields in northern Missouri and their suitability as bobwhite habitat. Transactions of the North American Wildlife and Natural Resources Conference 55: 74–83.
- DAVIS, S. K., AND R. J. FISHER. 2009. Post-fledging movements of Sprague's Pipit. Wilson Journal of Ornithology 121: 198–202.
- ESRI. 2011. ArcGIS Desktop: Release 10. ESRI, Redlands, CA.
- FISHER, R. J., AND S. K. DAVIS. 2011. Post-fledging dispersal, habitat use, and survival of Sprague's Pipits:

are planted grasslands good subsitutes for native? Biological Conservation 144: 263–271.

- GILL, D. E., P. BLANK, J. PARKS, J. B. GUERARD, B. LOHR, E. SCHWARTZMAN, J. G. GRUBER, G. DODGE, C. A. REWA, AND H. F. SEARS. 2006. Plants and breeding bird response to a managed Conservation Reserve Program grassland in Maryland. Wildlife Society Bulletin 34: 944–956.
- HOVICK, J. H., 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. Condor 113: 429–437.
- aged with fire and grazing. Condor 113: 429–437. JACKREL, S., AND H. REINART. 2009. Habitat use by nesting grassland birds and their snake predators in tallgrass prairie. TCNJ Journal of Student Scholarships 11: 1–8.
- JOHNSTON, D. W., AND E. P. ODUM. 1956. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. Ecology 37: 50–62. JONES, Z. F., AND C. E. BOCK. 2005. The Botteri's Sparrow
- JONES, Z. F., AND C. E. BOCK. 2005. The Botteri's Sparrow and exotic Arizona grasslands: an ecological trap or habitat regained? Condor 107: 731–741.
- KERSHNER, E. L., J. W. WALK, AND R. F. WARNER. 2004. Postfledging movements and survival of juvenile Eastern Meadowlarks. Auk 121: 1146–1154.
- KOFORD, R. R. 1999. Density and fledging success of grassland birds in Conservation Reserve Program fields in North Dakota and west-central Minnesota. In: Ecology and conservation of grassland birds of the Western Hemisphere (P. D. Vickery and J. R Herkert, eds.), pp. 187–195. Studies in Avian Biology 19, Cooper Ornithological Society, Lawrence, KS.
- MECH, L. D. 1983. Handbook of animal radio-tracking. University of Minnesota Press, Minneapolis, MN.
- PINHEIRO, J., D. BATES, S. DEBROY, D. SARKAR, and THE R DEVELOPMENT CORE TEAM. 2013. nlme: linear and nonlinear mixed effects models. R package version 3.1–109.
- PULLIAM, H. R., AND G. S. MILLS. 1977. The use of space by wintering sparrows. Ecology 58: 1393–1399.
- 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.
- R DEVELOPMENT CORE TEAM. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

- 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– 298.
- SUEDKAMP WELLS, K. M. 2005. Resource selection, movement patterns, and survival of post-fledging grassland birds in Missouri. Ph.D. dissertation, University of Missouri, Columbia, MO.
- , M. R. RYAN, J. J. MILLSPAUGH, F. R. THOMPSON III, AND M. W. HUBBARD. 2007. Survival of postfledging grassland birds in Missouri. Condor 109: 781–794.
- J. J. MILLSPAUGH, M. R. RYAN, AND M.
 W. HUBBARD. 2008. Factors affecting home range size and movements of post-fledgling grassland birds. Wilson Journal of Ornithology 120: 120– 130.
- UNITED STATES DEPARTMENT OF AGRICULTURE [USDA]. 2011. Maryland CREP technical handbook. Natural Resources Conservation Service, Annapolis, MD.
- ——. 2014. Conservation Reserve Program, Monthly Summary, October. Farm Service Agency, Washington, D.C.
- VEGA RIVERA, J. H., J. H. RAPPOLE, W. J. MCSHEA, AND C. A. HASS. 1998. Wood Thrush postfledging movements and habitat use in northern Virginia. Condor 100: 69–78.
- VICKERY, P. D. 1996. Grasshopper Sparrow (Ammodramus savannarum). In: The Birds of North America 239 (F. B. Gill and A. Poole, eds.). Academy of Natural Sciences, Philadelphia, PA, and American Ornithologists' Union, Washington, D.C.
- WATTS, B. D. 1990. Cover use and predator-related mortality in Song and Savannah sparrows. Auk 107: 775–778.
- WHITMORE, R. C. 1981. Structural characteristics of Grasshopper Sparrow habitat. Journal of Wildlife Management 45: 811–814.
- YACKEL ADAMS, A. A., S. K. SKAGEN, AND J. A. SAVIDGE. 2006. Modelling post-fledging survival of Lark Buntings in response to ecological and biological factors. Ecology 87: 178–188.
- ZUUR, A. F., E. N. IENO, N. J. WALKER, A. A. SAVELIEV, AND G. M. SMITH. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, NY.