

POSTFLEDGING SURVIVAL OF GRASSHOPPER SPARROWS IN GRASSLANDS MANAGED WITH FIRE AND GRAZING

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Abstract. More accurate estimates of survival after nestlings fledge are needed for population models to be parameterized and population dynamics to be understood during this vulnerable life stage. The period after fledging is the time when chicks learn to fly, forage, and hide from predators. We monitored postfledging survival, cause-specific mortality, and movements of Grasshopper Sparrows (*Ammodramus savannarum*) in grassland managed with fire and grazing. In 2009, we attached radio transmitters to 50 nestlings from 50 different broods and modeled their survival in response to climatic, biological, and ecological variables. There was no effect of treatment on survival. The factor most influencing postfledging survival was age; no other variable was significant. The majority of chicks (74%) died within 3 days of radio-transmitter attachment. We attributed most mortality to mesopredators (48%) and exposure (28%). Fledglings' movements increased rapidly for the first 4 days after they left the nest and were relatively stable for the remaining 10 days we tracked them. On average, fledglings took flight for the first time 4 days after fledging and flew ≥ 10 m 9 days after fledging. Our data show that the Grasshopper Sparrow's survival rates may be less than most models relying on nest-success estimates predict, and we emphasize the importance of incorporating estimates of survival during the postfledging period in demographic models.

Key words: *Ammodramus savannarum*, Grasshopper Sparrow, patch-burn grazing, postfledging survival, prescribed fire, tallgrass prairie

Supervivencia Posterior al Emplumamiento de *Ammodramus savannarum* en Pastizales Manejados con Fuego y Pastoreo

Resumen. Se necesitan estimados más precisos de la supervivencia luego de que los pichones dejan el nido para parametrizar los modelos poblacionales y para entender las dinámicas poblacionales durante esta etapa vulnerable de la vida. El período luego del emplumamiento es el momento en el cual los pichones aprenden a volar, a alimentarse y a esconderse de los depredadores. Monitoreamos la supervivencia posterior al emplumamiento, las causas específicas de mortalidad y los movimientos de *Ammodramus savannarum* en los pastizales manejados con fuego y pastoreo. En 2009, colocamos radiotransmisores a 50 pichones provenientes de 50 nidadas diferentes y modelamos sus supervivencias en respuesta a variables climáticas, biológicas y ecológicas. No hubo un efecto del tratamiento sobre la supervivencia. El factor que más influyó la supervivencia posterior al emplumamiento fue la edad; ninguna otra variable fue significativa. La mayoría de los pichones (74%) murió dentro de los 3 días luego de la colocación de los radiotransmisores. Atribuimos la mayoría de la mortalidad a los depredadores de porte mediano (48%) y a la exposición (28%). Los movimientos de los volantones aumentaron rápidamente durante los primeros 4 días luego de que dejaron el nido y fueron relativamente estables durante los restantes 10 días que los seguimos. En promedio, los volantones alzaron vuelo por primera vez 4 días después de emplumar y volaron ≥ 10 m nueve días después de emplumar. Nuestros datos muestran que las tasas de supervivencia de *A. savannarum* pueden ser menores que las predichas por la mayoría de los modelos que se basan en estimados del éxito del nido. Además, enfatizamos la importancia de incorporar en los modelos demográficos estimados de supervivencia durante el período posterior al emplumamiento.

INTRODUCTION

Grassland birds have declined more in recent decades than has any other group of North American birds (Peterjohn and Sauer 1993, Knopf 1994, Vickery et al. 1999, Sutter and Ritchison

2005). Historically, these declines have been driven by conversion of grasslands to row crops and degradation of remnant habitats (Vickery 1996, Vickery and Herkert 2001). More recently the situation has been exacerbated by withdrawal of lands from the Conservation Reserve Program and their use

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for biofuel production (Fargione et al. 2009). These trends underscore the importance of enhancing habitat on remnant prairies and restoring grasslands where possible (Fletcher and Koford 2002, 2006). Furthermore, to assess the quality of these habitats, it is essential that we understand survival demographics for all life stages (Knutson et al. 2006).

Habitat quality for birds is typically assessed with count data (Bock and Jones 2004). Yet abundance may not accurately reflect habitat quality (Van Horne 1983), particularly if a given area is functioning as a population sink or ecological trap (Bock and Jones 2004). For a more accurate measure of habitat quality, Garshelis (2000) and Johnson (2007) recommended recording demographic information such as nest survival, and many studies have addressed factors affecting this variable (Johnson 2007). Under some conditions, however, daily nest survival may not be correlated with population growth, and annual productivity and survival during various life stages may be more robust measures of habitat quality (Knutson et al. 2006).

The stage after nestlings fledge, the postfledging period, is essential for grassland birds because in general fledglings' mortality rates are extremely high (Anders 1998, Lang et al. 2002, Kershner et al. 2004, Berkeley et al. 2007). During this period, fledglings remain dependent on parental care while they learn to fly, feed on their own, and hide from predators (Kershner et al. 2004, Yackel Adams et al. 2006). Despite fledglings' vulnerability at this time and the potential importance of the postfledging stage in the decline of grassland birds, few studies have focused on this period (Berkeley et al. 2007), likely because of the logistical challenges of monitoring birds during a stage when they can be especially cryptic and difficult to locate (Vega Rivera et al. 1998, Suedkamp Wells et al. 2007).

We studied postfledging survival of the Grasshopper Sparrow (*Ammodramus savannarum*) in heavily stocked remnant tallgrass prairie managed with two spatially contrasting applications of prescribed burning. The first, known as patch-burn grazing, was proposed by Fuhlendorf and Engle (2001) as a grassland-management approach to increase habitat heterogeneity. Patch-burn grazing creates heterogeneity through the application of discrete fires followed by the focal grazing of large herbivores (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009). The second approach focused on more traditional management, representative of many private lands in the area, referred to as the graze-and-burn treatment. We focused on the Grasshopper Sparrow because it is a species of concern in the Eastern Tallgrass Ecoregion (Panjabi et al. 2005) and has experienced population declines of nearly 78% across the United States since the 1960s (Sauer et al. 2008). To our knowledge, this is the first time postfledging survival rates of the Grasshopper Sparrow have been reported. Our objectives were to (1) identify cause-specific mortality and timing of mortality as a function of fledglings' age, (2) quantify daily

movement after fledging, and (3) model daily survival rates as a function of ecological and biological factors.

METHODS

STUDY SITES

Our study focused on eight pastures ranging in size from 22.5 to 37 ha in Ringgold County, Iowa. Pastures were under the jurisdiction of the Iowa Department of Natural Resources, the Nature Conservancy, or were privately owned. Five of the pastures were managed with patch-burn grazing, the other three pastures with a graze-and-burn treatment. Beginning in 2007, one third of each patch-burn pasture (hereafter, a patch) was burned annually, whereas the graze-and-burn pastures were not burned in the first 2 years of the study but were burned in their entirety in 2009 to prevent the encroachment of woody vegetation. We assigned pastures randomly to one of the two treatments, and baseline measurements showed that abundances of the vegetation's functional groups under the two treatments were similar. All pastures were grazed at 1.1–1.5 animal units per month per 0.4 ha (1 acre) and had only an exterior fence to contain cattle. Pastures were grazed from 1 May until 1 October and had no application of herbicide or fertilizer prior to the initiation of the study.

Dominant native plants included the grass rough dropseed (*Sporobolus clandestinus*), sedges (*Carex* spp.), and Baldwin's ironweed (*Veronica baldwinii*; McGranahan 2008). Tall fescue (*Lolium arundinaceum*), a forage species introduced from Europe, was present on all pastures and was the dominant grass species on most (McGranahan 2008). Other common exotic species included black medick (*Medicago lupulina*) and Kentucky bluegrass (*Poa pratensis*). During the study period, precipitation averaged 15.3 cm per month (May–August) with the greatest amounts falling in June and August.

NEST SEARCHING

In 2009, we searched for nests from 15 May to 25 July from 06:00 to 12:00 (CST) on days with no precipitation. We located nests by rope dragging (Higgins et al. 1969), incidentally flushing adults, and observations of parental behavior (Kershner et al. 2004). To ensure complete coverage, we flagged one end of each rope drag as we made systematic passes through pastures and did return drags along the flagged line. Upon flushing a bird, both draggers searched the vicinity. If they did not find the nest, they marked the location as a probable nest site and searched again within 3 days by walking and using flushing sticks (Winter et al. 2003). In addition to the two draggers, on most occasions a third observer acted as a spotter and followed behind the rope.

We recorded the Universal Transverse Mercator (UTM) coordinates of each nest with a Trimble GeoXT global positioning system. We candled eggs to determine their age (Lokemoen and Koford 1996) and subsequently monitored

nests every 3 days, more frequently near the time of hatching and fledging. During each visit, we recorded the date, time, number and stage of eggs/nestlings, and the number and age of Brown-headed Cowbird (*Molothrus ater*) eggs/nestlings (Ralph et al. 1993).

RADIO ATTACHMENT AND TRACKING

We attached radio transmitters to nestlings near the time of fledging, typically on day 8 (Vickery 1996), to reduce the possibility of inducing fledging prematurely (Berkeley et al. 2007). On the day of attachment, we measured each nestling's culmen length, wing chord, mass, and tarsus length. We attached transmitters with glue and a figure-8 leg harness (Rappole and Tipton 1991, Suedkamp Wells et al. 2007) to one randomly selected nestling per nest to ensure independence of marked individuals (Kershner et al. 2004, Cohen and Lindell 2004, Berkeley et al. 2007). We placed transmitters just above the rump of each selected nestling with the whip tail pointing toward the tail of the chick and the transmitter resting on the synsacrum (Rappole and Tipton 1991). We used series A2412 transmitters (Advanced Telemetry Systems, Isanti, MN) weighing ~0.26 g, <3% of the mass of a Grasshopper Sparrow fledgling (>10.5 g, Vickery 1996; >12 g, Hovick 2010). Battery life was expected to be 30 days. At the time of attachment, we placed a U.S. Geological Survey band on the right leg and a unique combination of plastic, UV-resistant Darvic bands (Avinet, Dryden, NY) on the left leg to assist in accurate identification of resighted fledglings. We returned nestlings to the nest after handling, which took <5 min, and covered them with a bird bag until they were calm. All protocols were approved by the Iowa State University Institutional Animal Care and Use Committee (Protocol 4-09-6720-Q).

After each bird fledged, we tracked it daily until we obtained evidence of its death, leaving the area, or the transmitter battery expired (Anders 1997, Kershner et al. 2004, Berkeley et al. 2007). We categorized a bird as dead if there was no signal and the bird was unable to leave the area under its own power (i.e., <10 days of age). If parents were chipping in the area of a lost signal, we searched for a fledgling with leg bands (e.g., the fledgling with the transmitter). Under no circumstances did we relocate a fledgling with a lost signal (assumed dead) that was actually still alive. If we heard no signal at the time of relocation, we walked the pasture's entire perimeter and searched adjacent fields by driving roadways and listening for a signal. Under ideal conditions signals could be heard at a distance of ~300 m, which was greater than any movement recorded during the study. We selected relocation times randomly from one of three intervals (06:00–11:00, 11:00–16:00, and 16:00–21:00). Selection of an interval was never the same on consecutive days. We used extreme caution when relocating fledglings, and if a given bird did not flush but was seen alive (eyes open but bird not moving), we noted its location and measured the vegetation features the next day.

This approach was intended to reduce the stress imposed on young fledglings by limiting the time we spent in the area. When a fledgling did flush, we recorded its age and the approximate distance flown.

VEGETATION MEASUREMENTS

We measured vegetation at the nest and in each cardinal direction at a distance of 5 m from the nest (nest site) to determine the effects of vegetation structure and composition on postfledging survival, a method adapted from Dieni and Jones (2003). To do so, we used a 0.5-m² quadrat and estimated canopy cover (%) of tall fescue, warm-season grasses, cool-season grasses (including tall fescue), forbs, legumes, bare ground, litter, and woody vegetation. We estimated tall fescue separately because it is an invasive species of management concern and has been associated with poor brood rearing by other grassland birds (Barnes et al. 1995). Subsequently, we classified these measurements by the midpoints of the following intervals: 0–5, 6–25, 26–50, 51–75, 76–95, and 96–100 (Daubenmire 1959). We recorded visual obstruction at a distance of 4 m and a height of 1 m above ground, noting the height at which the pole was 50% obscured by vegetation (Robel et al. 1970).

DETERMINING CAUSE-SPECIFIC MORTALITY

We determined cause-specific mortality for each fledgling by the methods of Suedkamp Wells et al. (2007). We reasoned that mesopredators such as raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), red foxes (*Vulpes vulpes*), or farm cats were the agent of mortality if we recovered a transmitter with teeth holes and found very little remains of the bird. We identified snakes as predators when signals led us to them and in one case when a fledgling appeared to have been regurgitated. We identified birds such as Loggerhead Shrikes (*Lanius ludovicianus*) or corvids as the predator when we found a transmitter hanging in a tree or a juveniles plucked with little meat left on its skeleton. We considered exposure the cause of mortality if we found a fledgling dead with no obvious wounds. In addition, when we found a fledgling dead with parcels of flesh missing, we classified the predator as unknown. We hypothesized that these events were the result of predation by small mammals, but it was unclear if small mammals killed the bird or were opportunistically scavenging its carcass after its death.

STATISTICAL ANALYSIS

To examine postfledging survival, we used the nest-survival model in program MARK (White and Burnham 1999) because it allows for the inclusion of parameters explaining survival of individuals with known fates and accounts for exposure days. Program MARK uses a maximum-likelihood framework with a logit function. We examined the first 2 weeks after fledging

because this interval has been identified as the period when fledglings are most vulnerable and because the small transmitters' limited pulse strength, relocating fledglings becomes difficult if they move great distances (Kershner et al. 2004, Suedkamp Wells et al. 2007). To standardize nest ages, we set 3 June as day 1 and numbered days sequentially through 15 August.

We used hierarchical modeling because this approach decreases the total number of models when many covariates are included (Dinsmore and Dinsmore 2007). At each step, we ranked models by Akaike's information criterion, adjusted for small sample sizes (AIC_c ; Burnham and Anderson 1998). We used only the model with the lowest AIC_c score from each step as the base model for adding variables in the next. After the final step of modeling, we followed the approach outlined by Burnham and Anderson (2002) for interpreting our set of models and considered all models within two AIC_c units of the best model to be competitive. Model building entailed four steps:

(1) We incorporated constant (null), linear (T), and quadratic (TT) time trends. Dinsmore and Dinsmore (2007) reported increased survival through the breeding season as a result of greater availability of other prey.

(2) We added climatic variables to the best model from the first step (National Climatic Data Center 2009). These included daily minimum and maximum temperatures as well as daily precipitation totals. Young fledglings are unable to thermoregulate for long periods (Yackel Adams et al. 2006). Therefore, we hypothesized that cool, wet nights should decrease daily survival rates, as should extreme heat.

(3) We included biological variables of interest such as clutch size, Brown-headed Cowbird parasitism, morphometrics, and fledging age to the best model from step 2. We used parasitism and clutch size as an indirect means of examining resource allocation to nestlings and investigating whether cowbirds or an increased number of nestlings decreased the probability of survival. For examining chick condition we used the culmen length, wing chord, tarsus length, and mass that were measured at the time we attached the transmitter. We also created a rank of body condition by dividing the mass of the chick with the transmitter attached by the greatest mass of any chick in the clutch (Yackel Adams et al. 2006). Body condition, whether by rank or mass alone, has been related to fledging survival (Krementz et al. 1989, Yackel Adams et al. 2006, Suedkamp Wells et al. 2007).

(4) Finally, we added the effect of treatment and vegetation variables from the nest site (5 m) to the best model from step 3. We averaged these measurements across the four quadrats and assumed them to be representative of habitat used by fledglings during the first few days after leaving the nest.

All descriptive statistics are reported as means and standard errors. This information was gathered from individual birds and averaged for birds of the same age. Averages are based on the number of active (living birds with transmitters) fledglings for a given age in days since fledging.

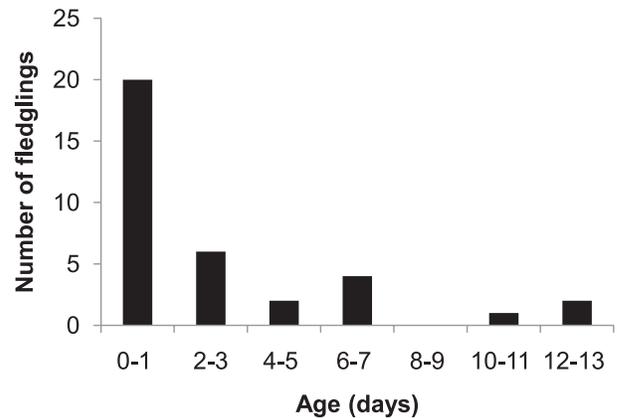


FIGURE 1. Grasshopper Sparrow mortality as a function of age in pastures treated with fire and grazing in Ringgold County, Iowa, 2009.

RESULTS

Between 28 May and 5 August, 2009, we attached 50 transmitters to pre-fledging Grasshopper Sparrows representing 50 broods. Chicks weighed 12.0 ± 0.3 g (range 8.5–14 g) at the time of attachment. We determined that 37 birds successfully fledged and 10 survived the first 2 weeks after fledging. In total, we tracked individuals for 217 days and found an average survival period of 6.8 ± 1.2 days (range 0–27 days).

We identified the fates of 45 birds. We could not determine the fate of three individuals because the transmitter failed or became detached, and the fate of two additional birds was researcher error. Predation was the leading cause of fledglings' mortality and was responsible for 49% (17/35) of all deaths. We attributed the majority of instances of predation to mesopredators (48%, 15/35). Other predators included snakes (6%, 2/35), and one death resulted from trampling by cattle. The second leading cause of mortality was exposure, which was responsible for 31% (11/35) and generally occurred within 3 days of fledging. The source of mortality was unknown in six cases, including four carcasses that had been chewed on by small mammals or insects but the actual cause of death could not be determined. The timing of death varied, but most deaths occurred during the first 3 days after the transmitter was attached (74%; Fig. 1). Six birds died between 4 and 8 days, and three birds died after 9 days.

Fledglings' daily movements from the nest increased for the first 4 days after fledging and then became relatively stable for the remainder of the 14-day interval (Fig. 2). Over the entire study, the maximum recorded distance a fledgling moved was 135 m, the shortest, <1 m. Average daily movement from the nest site was 37.5 ± 3.1 m. On average, fledglings first took flight 4 days after leaving the nest (range 1–7). Initial flights averaged 7 m, and fledglings averaged flights >10 m at 9 days (range 4–12).

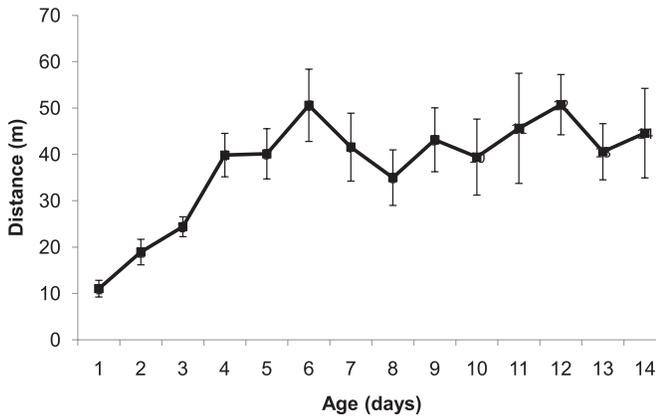


FIGURE 2. Average (\pm SE) daily movement from the nest bowl of postfledging Grasshopper Sparrows in time since fledging (days) in Ringgold County, Iowa, 2009.

TABLE 1. Candidate models that best explained postfledging survival of Grasshopper Sparrows in Ringgold County, Iowa, 28 May–19 August, 2009. Survival is modeled as a function of the following covariates: age of fledgling through the period of study (age \times effect), presence of Brown-headed Cowbird young the clutch (parasitize), forb abundance around the nest (forb), and height of vegetation surrounding the nest (Robel).

Model	Δ AIC _c ^a	K ^b	w _i ^c	Deviance
S(age_effect + parasitize + forb)	0.00 ^d	4	0.134	134.61
S(age effect + parasitize)	0.61	3	0.098	137.00
S(age_effect + parasitize + Robel)	0.83	4	0.088	133.67
S(age effect)	1.49	3	0.083	136.09

^aAkaike’s information criterion adjusted for small sample sizes.

^bNumber of parameters in model.

^cModel weight.

^dAIC_c of best model = 144.53.

We modeled postfledging survival for 32 fledglings. Thirteen birds died between the time of attachment and the first relocation, making it difficult to ascertain whether they died after fledging or were killed in the nest and removed. Therefore, we eliminated these birds from survival analyses. We also eliminated from analyses birds that fledged and whose fate was unknown because of transmitter detachment, battery failure, or observer error ($n = 5$). These analyses indicated that fledgling age had the greatest effect on daily survival rates. The age effect on survival was significant and positive in all four of the candidate models (i.e., as age increased the probability of surviving 1 day increased; $\beta_{\text{age_effect}} = 0.13$ on a logit

scale, SE = 0.07, 95% CI was 0.002, 0.26). Presence of the Brown-headed Cowbird was included in candidate models ($\beta_{\text{parasitism}} = 0.53$ on a logit scale, SE = 0.70, 95% CI was $-0.83, 1.88$), but estimates had low precision (Table 1). Forb abundance and vegetation height were also factors included in candidate models ($\beta_{\text{forbs}} = -0.04$ on a logit scale, SE = 0.02, 95% CI was $-0.084, 0.007$; $\beta_{\text{veg_height}} = -0.38$ on a logit scale, SE = 0.28, 95% CI was $-0.93, 0.17$) but had no significant effect on survival (Table 1). Cumulative survival rates decreased rapidly over the first 4 days after fledging, became relatively stable from age 5 to 11 days, and then increased for the remainder of the first 2 weeks (Fig. 3).

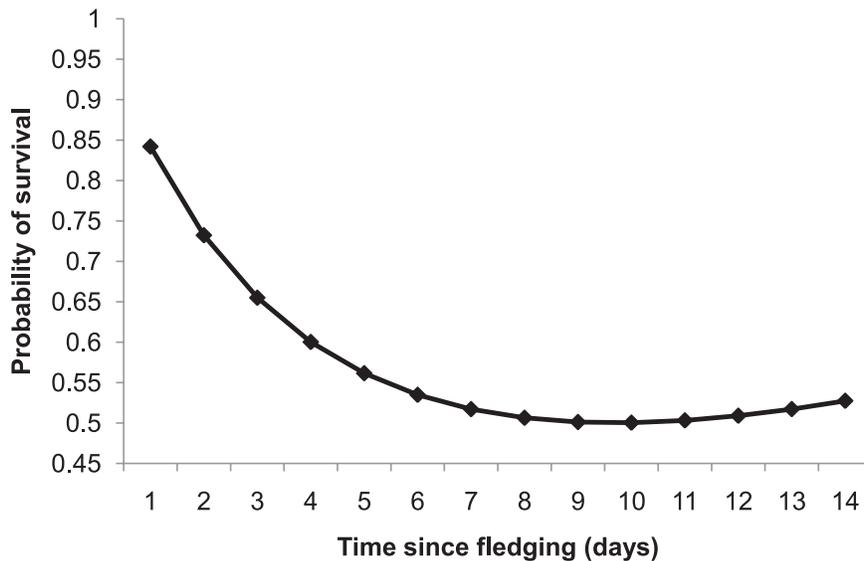


FIGURE 3. Cumulative probability of survival of fledgling Grasshopper Sparrows for the first 14 days after they left the nest for in Ringgold County, Iowa. Survival estimates were derived from the best candidate model (see Table 1).

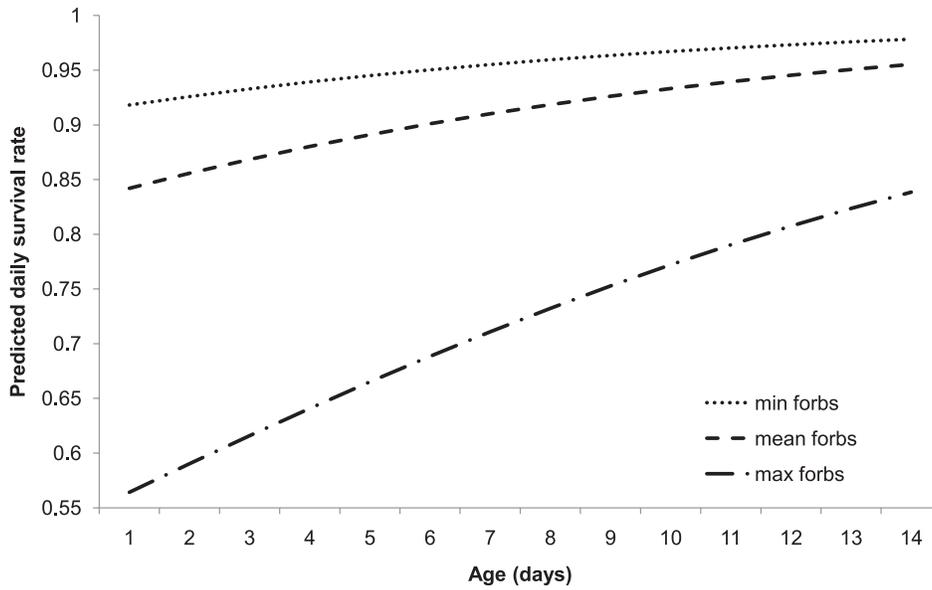


FIGURE 4. Predicted rates of daily survival of fledgling Grasshopper Sparrows as a function of abundance of forbs and fledgling age. Lines represent the minimum, mean, and maximum abundances of forbs recorded at sites where fledglings were relocated.

We created predictive models by using measurements of the vegetation canopy that influenced survival. We used the top two candidate models to predict survival rates as a function of these parameters. In the first model, survival rate was a function of fledgling age (1–14 days) and three levels of forb abundance (minimum, mean, and maximum) recorded at the nest site (Fig. 4). In the second model, survival rate was a

function of fledgling age and three levels of vegetation height (minimum, mean, and maximum) at the nest site (Fig. 5).

Survival analyses did not support the type of treatment as a parameter in candidate models predicting Grasshopper Sparrow survival. This was likely due to the lack of vegetation differences between the two treatments at nest sites of fledglings used in survival analyses (Fig. 6). We used mean

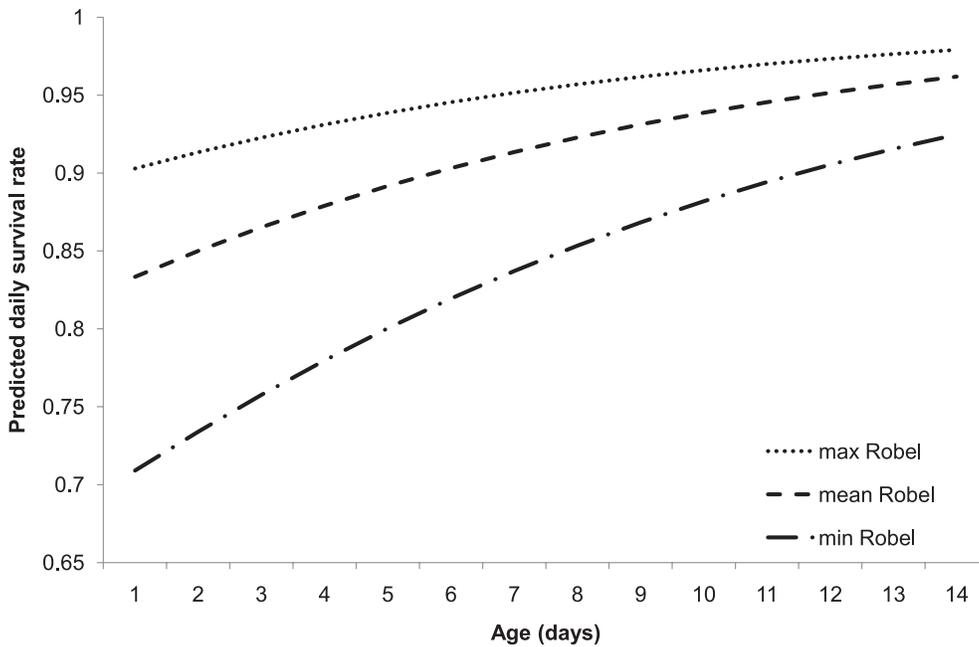


FIGURE 5. Predicted rates of daily survival of fledgling Grasshopper Sparrows as a function of vegetation height and fledgling age. Lines represent the minimum, mean, and maximum vegetation heights recorded at sites where fledglings were relocated.

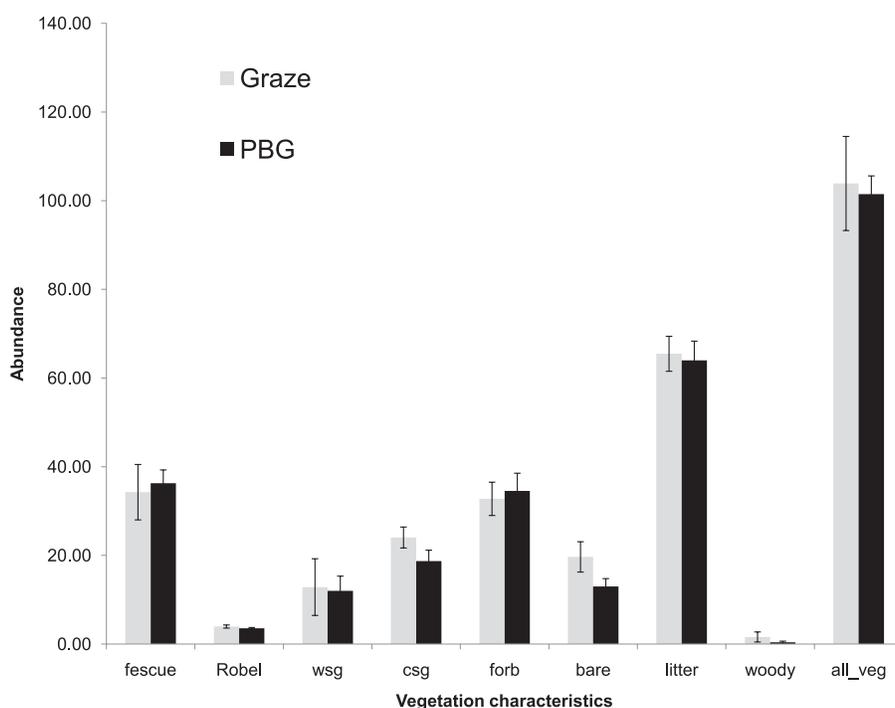


FIGURE 6. Mean of vegetation characteristics (\pm SE) measured at the sites of nests of Grasshopper Sparrow fledglings used in survival analyses. Bars represent patch-burn grazing (black) and graze-and-burn (gray) treatments in Ringgold County, Iowa, 2009.

estimates from our best model to estimate survival under the two treatments and found the probability of a 1-day-old fledgling surviving for 1 day in a patch-burn grazed pasture was 0.85 ($SE \pm 0.05$), that in a graze-and-burn pasture 0.82 ($SE \pm 0.07$).

DISCUSSION

Our findings suggest that the Grasshopper Sparrow, like other grassland-obligate birds, experience high rates of mortality during the postfledging period. Our survival estimate using mean parameters for the best model was $\sim 21\%$, which is lower than reported in many previous studies of fledglings of grassland birds. By comparison, Suedkamp Wells et al. (2007) found the rate of survival of the Dickcissel (*Spiza americana*) in Missouri over 29 days was 54%, Yackel Adams et al. (2006) found that of the Lark Bunting (*Calamospiza melanocorys*) in Montana over 21 days was 37%, and Berkeley et al. (2007) found that of the Dickcissels in Nebraska over 4 weeks was 33%. Regional differences in predator communities, variability in landscape context, and different life histories of the species studied make the interpretation of survival rates across studies difficult. More work on postfledging Grasshopper Sparrows in multiple regions and over varying intervals would help in clarifying the drivers influencing survival.

Predation by mesopredators was the most common cause of mortality we identified. The high levels of habitat fragmentation in southern Iowa have likely increased the abundance

of mesopredators because these species reportedly favor edge habitat adjacent to agricultural fields and wooded areas (Dijak and Thompson 2000). In addition, a lack of apex predators has left the mesopredator population unregulated (Crooks and Soulé 1999, Prugh et al. 2009). Other studies of grassland birds have identified snakes as major predators (Benson et al. 2010, Renfrew and Ribic 2003), and, while we hypothesize that snakes are common nest predators (Hovick 2010), we only observed two cases of predation by snakes during the postfledging stage.

Because postfledging Grasshopper Sparrows are cryptic, we did not compare fate of birds with transmitters to those without transmitters. Nonetheless, we have no evidence that transmitters had a direct negative effect on survival. At no time did we witness transmitters inhibiting fledglings' movements. Other studies have not shown radio tracking to have adverse effects on postfledging survival (Rappole and Tipton 1991, Powell et al. 1998, Naef-Daenzer et al. 2001). Moreover, Suedkamp Wells (2003) found the glucocorticoid levels of radio-marked Dickcissels to be within the normal range after initial handling, indicating that transmitters did not cause a negative physical response. In addition, we followed protocols for transmitter weight ($<3\%$ of body weight) and used attachment techniques that have been supported by previous work on small passerines (Rappole and Tipton 1991, Berkeley et al. 2007). Therefore, we maintain that the survival rates we observed are representative of postfledging Grasshopper Sparrows in grassland treated with fire and grazing.

Age was the most significant variable explaining Grasshopper Sparrow survival after fledging. Suedkamp Wells et al. (2007) found age to be associated with survival in the Dickcissel, the cumulative probability of survival declining rapidly over the first 3 days after fledging before stabilizing. Similarly, in eastern Nebraska Berkeley et al. (2007) found that 38 of 60 Dickcissels died in the first 8 days after fledging, and in Illinois Kershner et al. (2004) found that Eastern Meadowlarks (*Sturnella magna*) experienced 71% mortality during the first week after fledging. Fledglings are most vulnerable immediately after leaving the nest because they are unable to make long flights, rely on their parents for food, and have high energy demands that can result in thermal stress (Anders et al. 1997, Cohen and Lindell 2004, Yackel Adams et al. 2006). As a fledgling's age increases developmental factors become less influential and the mortality rate decreases. Our data suggest that as fledglings reach 9 days of age, the mortality rate stabilizes, likely because of an increase in mobility that allows for escape from predators and access to more areas for foraging.

Features of vegetation at nest sites, such as forb abundance and vegetation height (Robel et al. 1970), were included in competitive models and had negative but nonsignificant effects on daily survival rates. Grasshopper Sparrows forage preferentially on bare ground and avoid tall and dense vegetation (Whitmore 1981, Patterson and Best 1996, Vickery 1996), which could explain the negative relationships we observed. Additionally, Jackrel and Reinart (2009) found that snakes and nests depredated by snakes at the Konza Prairie Biological Station were more common in areas of vegetation significantly denser than at successful nest sites or random locations. Parasitism by Brown-headed Cowbirds was also included in competitive models and had a positive association with survival, though confidence intervals did overlap zero. It is unclear why there may have been a positive association between parasitism and postfledging survival, but we speculate that it is an indirect consequence of reduced clutch size and a concurrent reduction in the fledglings' provisioning demands.

Assessing habitat quality through survival rates of nests and fledglings provides greater insight than other commonly used measures (i.e., density, territory mapping) (Van Horne 1983). Nest success alone may lead to inflated estimates of overall survival (Knutson et al. 2006). For example, in the pastures we studied, survival of Grasshopper Sparrow nests ranged from 13 to 23% (Hovick 2010). The addition of post-fledging survival to nest-survival rates yields an overall probability of survival of 2% in graze-and-burn pastures and 7% in patch-burn grazed pastures. The use of both life stages clarifies how poor Grasshopper Sparrow production was on these sites and more accurately represents this species' overall decline.

These data support the cautions of Knutson et al. (2006) that daily nest survival may not be correlated with population growth and that other measures taken at different life stages are necessary. Monitoring survival after fledging will serve to increase the accuracy of demographic models and also help us

to better understand key processes affecting grassland birds during this critical period.

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LITERATURE CITED

- ANDERS, A. D., D. C. DEARBORN, J. FAABORG, AND F. R. THOMPSON. 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. Post-fledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. *Auk* 115:349–358.
- BARNES, T. G., L. A. MADISON, J. D. SOLE, AND M. J. LACKI. 1995. An assessment of habitat quality for Northern Bobwhite in fescue-dominated fields. *Wildlife Society Bulletin* 23:231–237.
- BENSON, T. J., J. D. BROWN, AND J. C. BEDNARZ. 2010. Identifying predators clarifies predictors of nest success in a temperate passerine. *Journal of Animal Ecology* 79:225–234.
- BERKELEY, L. I., J. P. MCCARTY, AND L. L. WOLFENBERG. 2007. Post-fledging survival and movement in Dickcissels (*Spiza americana*): implications for habitat management and conservation. *Auk* 124:396–409.
- BOCK, C. E., AND Z. F. JONES. 2004. Avian habitat evaluation: should counting birds count? *Frontiers in Ecology and the Environment* 2:403–410.
- BURNHAM, K. P., AND D. R. ANDERSON. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multi-model inferences: a practical information theoretic approach, 2nd ed. Springer-Verlag, New York.
- COHEN, E. B., AND C. A. LINDELL. 2004. Survival, habitat use, and movements of fledging White-throated Robins (*Turdus assimilis*) in a Costa Rican agricultural landscape. *Auk* 121:404–413.
- CROOKS, K. R., AND M. E. SOULÉ. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400:563–566.
- DAUBENMIRE, R. F. 1959. A canopy coverage method of vegetation analysis. *Northwest Science* 33:43–64.
- DIENI, J. S., AND S. L. JONES. 2003. Grassland songbird nest site selection patterns in northcentral Montana. *Wilson Bulletin* 115:388–396.
- DIJAK, W. D. AND F. R. THOMPSON III. 2000. Landscape and edge effects on the distribution of mammalian predators in Missouri. *Journal of Wildlife Management* 64:209–216.
- DINSMORE, S. J., AND J. J. DINSMORE. 2007. Modeling avian nest survival in program MARK. *Studies in Avian Biology* 34:73–83.
- FARGIONE, J. E., T. R. COOPER, D. J. FLASHPOHLER, J. HILL, C. LEHMAN, T. MCCOY, S. MCLEOD, E. J. NELSON, K. S. OBERHASUER, AND D. TILMAN. 2009. Bioenergy and wildlife: threats and opportunities for grassland conservation. *BioScience* 59:767–777.

- FLETCHER, R. J., AND R. R. KOFORD. 2002. Habitat and landscape associations of breeding birds in restored and native grasslands. *Journal of Wildlife Management* 66:1011–1022.
- FLETCHER, R. J., AND R. R. KOFORD. 2006. Critical demographic parameters for declining songbirds breeding in restored grasslands. *Journal of Wildlife Management* 70:145–157.
- FUHLENDORF, S. D., AND D. M. ENGLE. 2001. Restoring heterogeneity to rangelands: ecosystem management based on evolutionary grazing patterns. *BioScience* 51:625–632.
- FUHLENDORF, S. D., D. M. ENGLE, J. KERBY, AND R. HAMILTON. 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conservation Biology* 23:588–598.
- GARSHELIS, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance, p. 111–164. *In* L. Boitani and T. K. Fuller [EDS.], *Research techniques in animal ecology: controversies and consequences*. Columbia University Press, New York.
- HIGGINS, K. F., L. M. KIRSCH, AND J. I BALL JR. 1969. A cable-chain device for locating duck nests. *Journal of Wildlife Management* 33:1009–1011.
- HOVICK, T. J. 2010. Survival of Grasshopper Sparrows (*Ammodramus savannarum*) during two important life stages in grassland managed with fire and grazing. M.Sc. Thesis, Iowa State University, Ames, IA.
- JACKREL, S., AND H. REINART. 2009. Habitat use by nesting grassland birds and their snake predators in tallgrass prairie. *TCNJ Journal of Student Scholarship* 11:1–8.
- JOHNSON, M. D. 2007. Measuring habitat quality: a review. *Condor* 109:489–504.
- KERSHNER, E. L., J. W. WALK, AND R. E. WARNER. 2004. Postfledging movements and survival of juvenile Eastern Meadowlarks. *Auk* 121:1146–1154.
- KNOFF, F. L. 1994. Avian assemblage on altered grasslands. *Studies in Avian Biology* 15:247–257.
- KNUTSON, M. G., L. A. POWELL, R. K. HINES, M. A. FRIBERG, AND G. J. NIEMI. 2006. An assessment of bird habitat quality using population growth rates. *Condor* 108:301–314.
- KREMENTZ, D. G., J. D. NICHOLS, AND J. E. HINES. 1989. Postfledging survival of European Starlings. *Ecology* 70:646–655.
- LANG, J. D., L. A. POWELL, D. G. KREMENTZ, AND M. J. CONROY. 2002. Wood Thrush movements and habitat use: effects of forest management for Red-cockaded Woodpeckers. *Auk* 119: 109–124.
- LOKEMOEN, J. T., AND R. R. KOFORD. 1996. Using candlers to determine the incubation stage of passerine eggs. *Journal of Field Ecology* 67:660–668.
- MCGRANAHAN, D.A. 2008. Degradation and restoration in remnant tallgrass prairie: grazing history, soil carbon, and invasive species affect community composition and response to the fire-grazing interaction. M.Sc. Thesis, Iowa State University, Ames, IA.
- NAEF-DENZER, B., F. WIDMER, AND M. NUBER. 2001. Differential post-fledging survival of Great and Coal Tits in relation to their condition and fledging date. *Journal of Animal Ecology* 70:730–738.
- NATIONAL CLIMATIC DATA CENTER [ONLINE]. 2009. Annual climatological summary statistics. Local climatological data for Lamon, IA. <<http://cdo.ncdc.noaa.gov/dly/DLY?stnid:20006622>> (17 December 2009).
- PANJABI, A. O., E. H. DUNN, P. J. BLANCHER, W. C. HUNTER, B. ALTMAN, J. BART, C. J. BEARDMORE, H. BERLANGA, G. S. BUTCHER, S. K. DAVIS, D. W. DEMAREST, R. DETTMERS, W. EASTON, H. GOMEZ DE SILVA GARZA, E. E. IÑIGO-ELIAS, D. N. PASHLEY, C. J. RALPH, T. D. RICH, K. V. ROSENBERG, C. M. RUSTAY, J. M. RUTH, J. S. WENDT, AND T. C. WILL. 2005. The Partners in Flight handbook on species assessment. Version 2005. Partners in Flight Technical Series 3. <<http://www.rmbo.org/pubs/downloads/Handbook2005.pdf>>.
- PATTERSON, M. P., AND L. B. BEST. 1996. Bird abundance and nesting success in Iowa CRP fields: the importance of vegetation structure and composition. *American Midland Naturalist* 135:153–167.
- PETERJOHN, B. G., AND J.R. SAUER. 1993. North American Breeding Bird Survey annual summary: 1990–1991. *Bird Populations* 1:52–67.
- POWELL, L. A., D. G. KREMENTZ, J. D. LANG, AND M. J. CONVOY. 1998. Effects of radio transmitters on migrating Wood Thrushes. *Journal of Field Ornithology* 69:306–315.
- PRUGH, L. R., C. J. STONER, C. W. EPPS, W. T. BEAN, W. J. RIPPLE, A. S. LALIBERTE, AND J. S. BRASHARES. 2009. The rise of the mesopredator. *BioScience* 59:779–791.
- RALPH, C. J., G. R. GEUPEL, P. PYLE, T. E. MARTIN, AND D. F. DESANTE. 1993. Handbook of field methods for monitoring landbirds. PSW-GTR-144. USDA, Forest Service, Pacific Southwest Research Station, Albany, CA.
- 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.
- RENFREW, R. B., AND C. A. RIBIC. 2003. Grassland passerine nest predators near pasture edges identified on videotape. *Auk* 120:371–383.
- 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.
- SAUER, J. R., J. E. HINES, AND J. FALLON. 2008. The North American Breeding Bird Survey, Results and Analysis 1966–2007. Version 5.15.2008. USGS Patuxent Wildlife Research Center, Laurel, MD.
- SUEDKAMP WELLS, K. M., B. E. WASHBURN, J. J. MILLSPAUGH, M. R. RYAN, AND M. W. HUBBARD. 2003. Effects of radio-transmitters on fecal glucocorticoid levels in captive Dickcissels. *Condor* 105: 805–810.
- SUEDKAMP WELLS, K. M., M. R. RYAN, J. J. MILLSPAUGH, F. R. THOMPSON III, AND M. W. HUBBARD. 2007. Survival of postfledging grassland birds in Missouri. *Condor* 109:781–794.
- SUTTER, B., AND G. RITCHISON. 2005. Effects of grazing on vegetation structure, prey availability, and reproductive success of Grasshopper Sparrows. *Journal of Field Ornithology* 76:345–351.
- VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893–901.
- 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. *Condor* 100:69–78.
- VICKERY, P. D. 1996. Grasshopper Sparrow (*Ammodramus savannarum*), no. 239. *In* A. Poole and F. Gill [EDS.], *The Birds of North America*. Academy of Natural Sciences, Philadelphia.
- VICKERY, P. D., P. L. TUBARO, J. M. CARDOSA DA SILVA, B.G. PETERSON, J. R. HERKERT, AND R. B. CAVALCANTI. 1999. Conservation of grassland birds in the Western Hemisphere. *Studies in Avian Biology* 19:2–26.
- VICKERY, P. D., AND J. R. HERKERT. 2001. Recent advances in grassland bird research: where do we go from here? *Auk* 118:11–15.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (suppl.):120–138.
- WHITMORE, R.C. 1981. Structural characteristics of Grasshopper Sparrow habitat. *Journal of Wildlife Management* 45:811–814.
- WINTER, M., S. E. HAWKS, J. A. SHAFFER, AND D. H. JOHNSON. 2003. Guidelines for finding nests of passerine birds in tallgrass prairie. *Prairie Naturalist* 35:197–211.
- YACKEL ADAMS, A. A., S. K. SKAGEN, AND R. D. ADAMS. 2006. Movements and survival of Lark Bunting fledglings. *Condor* 103:643–647.