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FACTORS AFFECTING NEST SURVIVAL OF HENSLOW'S SPARROWS (*AMMODRAMUS HENSLOWII*) IN SOUTHERN INDIANA

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ABSTRACT.—Populations of Henslow's Sparrows have declined dramatically in recent decades, coinciding with widespread loss of native grassland habitat. Prescribed burning is a primary tool for maintaining grassland patches, but its effects on nest survival of Henslow's Sparrows remains largely unknown, especially in conjunction with other factors. We monitored 135 nests of Henslow's Sparrows at Big Oaks National Wildlife Refuge in southern Indiana from 1998–2001 in an effort to understand factors influencing nest survival, including prescribed burning of habitat. We used a mixed-effects implementation of the logistic exposure model to predict daily nest survival in an information theoretic framework. We found that daily survival declined near the onset of hatching and increased with the height of standing dead vegetation, although this relationship was weak. We found only nominal support to suggest that time since burn influenced nest survival. Overall, nest age was the most important factor in estimating daily nest survival rates. Our daily survival estimate from our marginal model (0.937) was similar to that derived from the Mayfield method (0.944) suggesting that our results are comparable to previous studies using the Mayfield approach. Our results indicate that frequent burning to limit woody encroachment into grassland habitats might benefit Henslow's Sparrow, but that a variety of factors ultimately influence daily nest survival. However, we note that burning too frequently can also limit occupancy by Henslow's Sparrows. We suggest that additional research is needed to determine the population-level consequences of habitat alteration and if other extrinsic factors influence demographics of Henslow's Sparrows. *Received 17 September 2014. Accepted 29 July 2015.*

Key words: *Ammodramus henslowii*, fire, grassland habitat, Henslow's Sparrow, logistic exposure, nest survival, shared frailty.

Like many grassland nesting birds, Henslow's Sparrow (*Ammodramus henslowii*) has experienced sharp declines in North America, decreasing in abundance by 8.7% per year between 1966–2004 (Sauer et al. 2005). The recent population decline of Henslow's Sparrows is principally associated with loss of grassland habitat from development, succession of abandoned agricultural lands to shrubland and forest, and habitat degradation resulting from increased frequency of hayfield mowing (Pruitt 1996, Burhans 2002). Combined with a small global population, this population decline has elevated the level of conservation concern for this species (Cooper 2012) – the Henslow's Sparrow is now a Partners in Flight (PIF) watch list species (Rich et al. 2004), a U.S. Fish and Wildlife Service focal species (Cooper 2012), and is listed as endangered, threatened, or of special concern in states throughout much of its breeding range (Pruitt 1996, Cooper 2012).

The breeding range of the Henslow's Sparrow originally coincided with the historical distribution of tallgrass prairie (Cooper 2012). With conversion of most tallgrass prairie to row crop agriculture, Henslow's Sparrows now breed in a variety of grasslands including hayfields, pastures, wet meadows, upland portions of coastal salt marshes, old fields, and reclaimed surface mine lands (Pruitt 1996, Bajema et al. 2001, Burhans 2002, Herkert et al. 2002). Nesting habitat for Henslow's Sparrows is generally characterized by tall, dense, grass-dominated vegetation, a large amount of standing, dead vegetation, little woody vegetation, and relatively large patches of suitable grassland habitat (Robins 1971; Zimmerman 1988; Herkert 1994a, b; Winter 1999; Winter and Faaborg 1999; Winter et al. 2000). Because such habitats are now often associated with small isolated patches, the potential for edge effects can be critical to understanding nest survival patterns (Winter et al. 2006). However, the influence of habitat structure on nesting success is often subsumed by issues related to the timing of nesting (Grant et al. 2005) or can be obfuscated by bias introduced as part of field observation procedures (Götmark 1992).

In undisturbed settings, vegetative succession may lead to the gradual conversion of grassland

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habitat to shrub and forests (e.g., woody encroachment). In these areas, prescribed burning is a common management action taken to limit the succession of woody vegetation and maintain grassland habitats. Despite this, the abundance of Henslow's Sparrows often decreases with increased burn frequency (Herkert and Glass 1999, Zimmerman 1992, Reinking et al. 2000, Herkert 2003), and are often absent from grassland patches in the year immediately following a prescribed burn (Powell 2006, 2008). However, Henslow's Sparrows are often found nesting in grass patches >1 year after prescribed burns (Reinking and Hendricks 1993, Reinking et al. 2000, Churchwell 2005), and often at relatively high densities (Powell 2008). This dynamic has led some to recommend against annual prescribed fires for maintaining nesting habitat for Henslow's Sparrows (Reinking 2005, Powell 2008). However, this issue is confounded in areas where high frequency prescribed burning is required to control woody encroachment into grassland habitats (Briggs et al. 2005). Thus, in some situations it can be difficult to use prescribed fire to limit woody encroachment without concomitantly limiting nesting habitat quality for Henslow's Sparrows.

In this study, we sought to determine the factors that influence daily nest survival of Henslow's Sparrows in an area where prescribed burning is required to maintain open grassland patches. Specifically, we were interested in evaluating the relative influence of factors related to 1) nest timing, 2) nest-level habitat, 3) landscape structure, and 4) burning frequency. We predicted a priori that nest success could be positively influenced by larger grassland patches, areas dominated by tall standing dead grass with thick litter and lower densities of woody stems, longer distances from roads, and increased time since last prescribed fire.

METHODS

Study Area.—We conducted our study in the central portion of the breeding distribution of Henslow's Sparrows (Pruitt 1996, Cooper 2012) at Big Oaks National Wildlife Refuge (BONWR) in Jefferson, Jennings, and Ripley counties in southeastern Indiana (208 km^2; 85° 25′, 38° 57′). BONWR contains a total grassland area of 2,480 ha ($\bar{x}$ = 35.0; range = 0.5–312 ha) and is composed of generally poorly drained acidic, clay soils. Long-term surveys indicate that the area contains ~500 breeding pairs of Henslow's Sparrows (Cooper 2012). Vegetation was dominated by several species of broomsedge (*Andropogon* spp.) and steeplebush (*Spiraea tomentosa*) and, to a lesser extent, by spike-rush (*Eleocharis tenuis*), boneset (*Eupatorium perfoliatum*), round-leave boneset (*Eu. rotundifolium*), beard-tongue (*Penstemon digitalis*), narrow-leaved mountain mint (*Pycnantheum tenuifolium*), and early goldenrod (*Solidago juncea*). Grasslands were interspersed among forest and shrub cover, comprised of red maple (*Acer rubrum*), persimmon (*Diospyros virginania*), sweet gum (*Liquidambar styracifllua*), winged sumac (*Rhus coppalina*), black locust (*Robinia pseudoacacia*), and oak (*Quercus*). Shallow craters resulting from the detonation of artillery rounds combined with poorly drained soils created ephemeral, temporary, and seasonal wetlands throughout the refuge. The climate at BONWR is characterized as continental, with warm ($\bar{x}_{\text{temp}}$ = 24°C), humid summers (Jun–Aug) and cold winters (Dec–Feb; $\bar{x}_{\text{temp}}$ = 1.4°C) and annual precipitation ($\bar{x}_{\text{precip}}$ = 122 cm) ranging from a low of 92 cm to a high of 138 cm during the study as characterized by its local weather station (PJW, unpubl. data).

Natural fires occur once every 35 years and are generally of low severity (Saab et al. 2005). BONWR is the former site of Jefferson Proving Ground, a closed U.S. military ordnance testing facility where ~25 million rounds of artillery were discharged from 1941–1994. To meet their artillery-testing objectives, the U.S. Army maintained a network of >90 grassland patches using prescribed fire, disking, mowing, and persistent herbicides. After Jefferson Proving Ground closed in 1995, ordnance testing ceased, as did the capacity to use mechanized management tools (i.e., disking and mowing) in most areas because of presence of remnant unexploded ordnance. Since BONWR was established in 2000, U.S. Fish and Wildlife Service staff has prevented woody encroachment into grasslands patches with prescribed fire or aerially applied herbicides. BONWR staff burned an average of 3,440 ha/year from 2001–2010; burn units were composed of grasslands, savannah, shrubland, and forest. Grasslands here are typically burned every 3–5 years. Nevertheless, grassland area decreased by nearly a third during 1995–2005 from woody encroachment. The refuge also surrounds Jefferson Range, an Indiana Air National Guard air-to-ground practice range of 418 ha that contains large grassland habitat maintained by fire. Wildfires with increased severity have occurred three times within the past 15 years when range fires from Jefferson Range entered the refuge.

Data Collection.—In 1998, we established four, ~20-ha plots with an additional 20-ha plot added in 1999, for a total of five plots. Because the vast majority of grassland habitat on the refuge was closed to entry because of unexploded ammunitions, plots were located ad hoc among remaining available grassland habitat. These five plots represented all available grassland habitat ≥20 ha that was not closed to entry. We used standard spot-mapping protocols to estimate the density of territories (No. territories/ha) in plots. We spot-mapped plots 6–10 times and used the criteria of at least 2 registrations that were ≥10 days apart to determine the presence of a "territory"; we also used information such as counter-singing males to denote separate registrations and the presence of an active nest to denote the presence of a territory (Bibby et. al. 1992).

We searched for nests on these plots from the end of April until early September from 1998–2001. We found nests by systematically walking plots while paying close attention to behavioral cues such as vocalizations, flushing, erratic flight, or the carrying of food, fecal sacs or nesting material. Once found, nests were visited approximately every 3 days to count eggs or young and to determine stage and fate. We estimated nest predation by evidence of loss of eggs or young, presence of egg fragments, disturbed nests and other signs of predators. We marked nests with small (<1cm) blue or green colored flagging tape discretely tied to nearby vegetation; we did not leave blind trails to nests and care was taken to minimize disturbance to vegetation around nests. An empty nest was considered successful if on or near the fledge day, we observed adults chipping or carrying food or fledglings were observed close to the nest.

We evaluated four classes of explanatory variables: those associated with nest timing, nest-level habitat, landscape characteristics, and fire management. In each case, explanatory variables had been shown to influence nest survival in previous studies or were ones that we hypothesized may serve as proxies for unmeasured factors that have been shown to influence nest survival. In the timing class, we included initiation date (Init; date that first egg was laid), nest age (NestAge; days since initiation), and observation age (ObsAge; days since nest was first detected) as potential covariates. Initiation date and nest age were included because of the importance of date- or age-related covariates in models of nest survival in which survival is presumed to vary across time (Grant et al. 2005) and because Henslow's Sparrows in our study exhibited substantial variability in the timing of nesting-related events (Fig. 1). Observation age was included to test for potential observer effects on nest survival (Götmark 1992). We did not include the cumulative number of visits as a potential covariate, because it is highly correlated with observation age. Nest age, observation age, and cumulative visits are often confounded with mortality as time increases and additive exposure to risk grows (Grant et al. 2005).

To determine the role of nest-level habitat structure on nest survival, we measured a suite of eight commonly reported habitat variables. The variables we measured were common metrics of grassland bird nesting habitat and based on BBIRD protocols (Martin and Guepel 1993, Fisher and Davis 2010). Depth of the litter layer is important in determining presence of Henslow's Sparrows during the breeding season (Wiens 1969, Zimmerman 1988, Burhans 2002); therefore, we measured the height (cm) of standing dead vegetation and litter depth. We defined standing dead vegetation as any individual dead plant material standing vertical above the soil surface and litter as clumped dead vegetation lying on or near the soil surface, usually creating a thick mat. Because nest survival can be affected by composition of vegetative cover near the nest itself (e.g., Winter et al. 2000), we estimated the percentage cover of grass, shrubs, and nonvegetative cover in a 1-m^2 plot centered at the nest. In 1999–2001, we also counted the number of woody plant stems within a 5-m radius of each nest. However because these data were not collected the first year of the study, and because preliminary analyses indicated that this metric had little influence on nest success, it was not included in subsequent analyses. At each nest, we measured the straight-line distance (m) to the nearest forested edge to account for the potential impacts of edge effects on nest survival (O'Leary and Nyberg 2000, Winter et al. 2006). Tall and dense cover is commonly reported for nesting Henslow's Sparrows (Graber 1968, Wiens 1969, Burhans 2002, Dechant et al. 2003). We used Robel et al.'s (1970) method for measuring vertical vegetative density using visual obstruction readings at a 4-m distance from a pole at a 1-m height above the ground. A reading was taken in each cardinal direction centered from the nest, and these readings

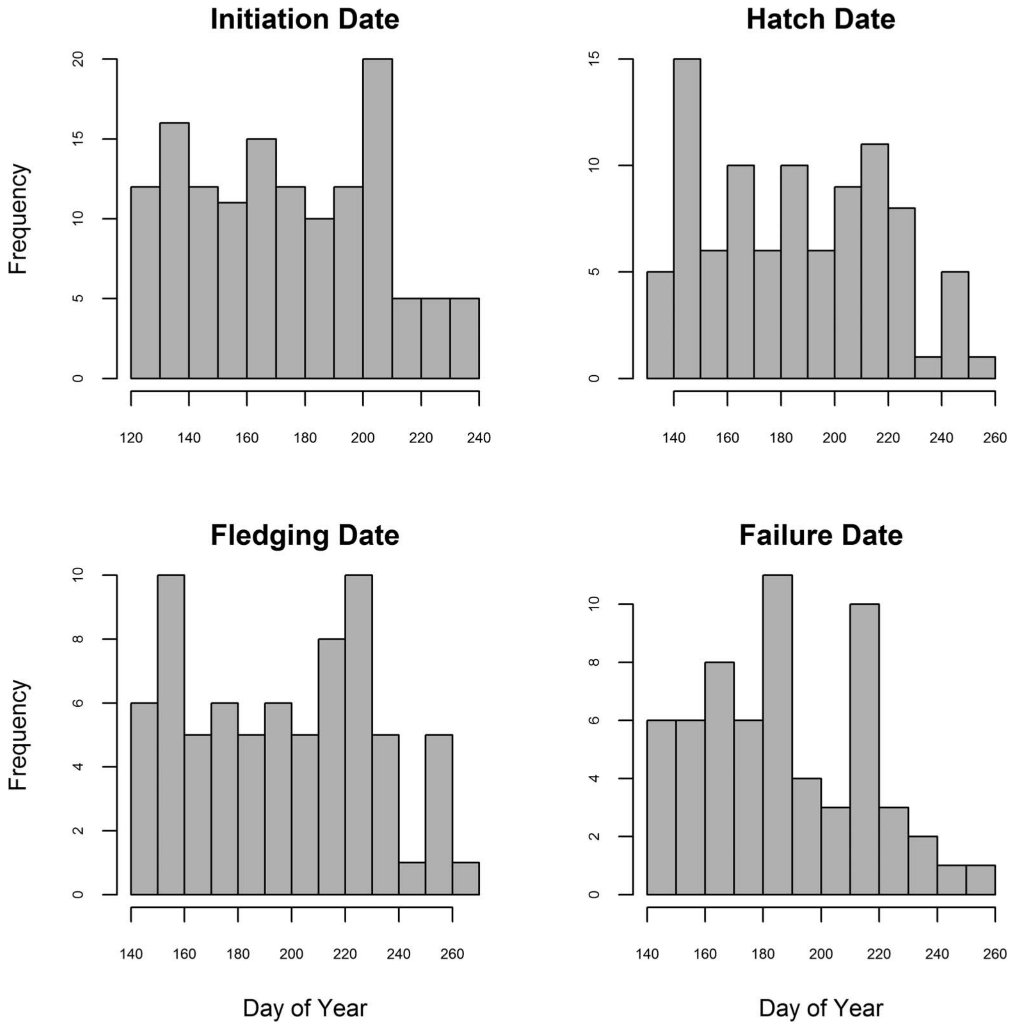

FIG. 1. Histograms of nesting timing events of Henslow's Sparrows at Big Oaks National Wildlife Refuge, southern Indiana, USA.

were then averaged. Lastly, we measured the nest height (cm) as the bottom of the nest to the ground.

Henslow's Sparrows may respond to landscape-scale habitat, including grassland patch size (Bollinger 1995, Winter and Faaborg 1999, McCoy 2000, O'Leary and Nyberg 2000, Burhans 2002, Thogmartin et al. 2006). Henslow's Sparrows tend to prefer larger grassland patches (Herkert 1994b), therefore we calculated the size (ha) of the patch in which each nest was located. We also calculated the total amount (ha) of grassland habitat and the number of grassland patches within 500-m of the plot as proxies for landscape-level habitat availability. We calculated the density of patch edges (total edge distance) within 500-m of the plot as a proxy for landscape-level edge effects. Lastly, we measured the distance from the centroid of the plot to the nearest road as a potential proxy for risk of nest predation (Jones and White 2012). We calculated landscape-scale covariates using ArcGIS 9.2 (ESRI 2006) and FRAGSTATS 3.3 (McGarigal et al. 2002).

With respect to fire management, we included the number of years since the plot was burned as a covariate (Table 1). All burns occurred in late winter to spring (Feb-Apr 15).

Statistical Analyses.—We used the logistic-exposure model (Shaffer 2004) to determine the effects of covariates on daily nest survival. The

TABLE 1. Estimated densities of Henslow's Sparrows' territories (with associated nest survival sample size) determined from spot-mapping techniques and prescribed fire timing for study plots at Big Oaks National Wildlife Refuge, 1998–2001. Year of spring prescribed fire during study, as well as the one most previous to this study, are identified.

Plot	1998	1999	2000	2001	$\bar{x}$	Year burned during study	Previous year burned
7	0.45 (1)	0.20 (4)	0.05 (1)	0.05 (2)	0.19 (8)	2001	1997
8	1.32 (7)	1.03 (10)	0.10 (2)	1.42 (26)	0.97 (45)	2000	1997
9	2.50 (6)	2.39 (29)	0.85 (14)	1.54 (15)	1.82 (64)	-	1984
10	0.00	0.00	0.07	0.00	0.02	1999	1995
11	-	0.15 (1)	0.05 (2)	0.61 (15)	0.27 (18)	2000	1993
$\bar{x}$	1.07 (14)	0.75 (44)	0.22 (19)	0.72 (58)	0.67	-	-

logistic-exposure model is essentially a logistic regression model with a modified logit link allowing the time between nest checks to vary. We employed a mixed-effects implementation of the logistic exposure model to allow the inclusion of random effects that we hypothesized would contribute additional variation to nest survival (Appendix 1). All models were implemented in the R programming language (R Core Team 2012). We included random intercept terms for Year and Plot in all models to account for non-independence; these logistic exposure models with block random effects are called shared frailty models (Therneau et al. 2003, Cam 2012). We employed the logistic exposure model in three successive stages of model refinement, using Bayesian Information Criteria (BIC) for covariate selection (Burnham and Anderson 2002). In the first stage, we modeled covariates individually, in the second stage we modeled the covariates within class (timing, nest-level, landscape, and fire management), and in the final stage we combined useful explanatory covariates from each class into a final set of tested models. Each stage was conditional upon the preceding stage. Each variable was standardized by subtracting the mean and dividing by the standard deviation (Newman and Browner 1991).

In the first stage, we investigated each covariate as linearly (x) or quadratically ($x + x^2$) related to nest survival. We also evaluated cubic terms (Grant et al. 2005) but found no support for this form and do not discuss it further. This stage was intended to find the best univariate form for the relationship between the explanatory variable and nest survival. Also included in the suite of models for each variable was a simple intercept. For each covariate, we retained the form with the lowest BIC provided it was ≥ 2 ΔBIC units of the null (intercept only) model; forms with ΔBIC <2 units from the null model were not considered to have substantial support and were discarded.

In the second stage of model development, we combined the covariate forms from the first stage in every possible additive combination within each of the three variable classes. These three suites of models were again ranked by BIC. For this stage, we chose the most parsimonious (lowest BIC) model within each of the three classes. We also used this process to determine the best form for years since burn.

In the final stage, nest timing, nest-level, and landscape-level models were combined. We evaluated all possible additive combinations of the most parsimonious second stage models rather than the individual covariates within the models. For this stage, we also included a management-related covariate, years since burn, yielding a global model that included four different factors affecting nest survival (timing + nest-level + landscape + management). We ranked models within this final suite using BIC and conducted model weighting and averaging following Lukacs et al. (2010). Because most previous studies reported daily survival/mortality of nests with the Mayfield method (Mayfield 1961, 1975), we did so as well, estimating overall nest success by extrapolating and combining period (i.e., laying, incubating, and nestling) daily survival estimates.

RESULTS

Estimated densities of Henslow's Sparrows' territories on the plots varied from a high of 1.07 territories/ha in 1998 to a low of 0.22 territory/ha in 2000 (Table 1.). We found 135 nests of Henslow's Sparrows over the 4 years of our study. The earliest first date of initiation we observed was 30 April (Day of Year = 120). Median date of first initiation

TABLE 2. Model selection results for 15 candidate models of daily nest survival of Henslow's Sparrows at Big Oaks National Wildlife Refuge, 1998–2001. Model names refer to groups of covariates rather than individual terms (Burn = Years Since Burn; Nest = Standing Dead Vegetation; Timing = Nest Age + Nest Age^2). Model weight (ω_i) is relative to the entire model suite.

Model	BIC	K	ΔBIC	ω_i
Timing + Nest	321.0	4	0.0	0.6682
Timing + Nest + Burn	322.4	5	1.4	0.3318
Nest + Burn	352.7	3	31.7	0.0000
Nest	351.9	2	30.9	0.0000
Timing	381.5.8	3	60.5	0.0000
Timing + Burn	383.9	4	62.9	0.0000
Burn	403.2	2	82.2	0.0000

was 21 June (Day of Year = 172), median date of hatch was 11 days later (4 Jul, Day of Year = 185), followed 13 days later by the median date of fledging (17 Jul, Day of Year = 198) (Fig. 1). The latest nesting activity was a nest fledging on 18 September (Day of Year = 261). Date of nest failure was fairly consistent among years, occurring on average in the first 2 weeks of July ($\bar{x} = 187$ [6 Jul], 95% CI = 180, 194 [29 Jun–13 Jul]). For those nests where we were able to determine clutch size ($n = 67$), median clutch size was four eggs ($\bar{x} = 4.06$ eggs, range = 3–5 eggs). We were able to quantify accurately the number of successful fledglings for 50 nests, which had a mean number of young successfully fledged of 3.78 (95% CI = 3.54, 4.03).

A total of 74 nests were successful, for an apparent nest success rate (number of nests fledging/total number of monitored nests) of 54.8%. Conversely, the Mayfield method yielded a nest success estimate of 23.7%. The median predicted daily survival, across all observed nests, from the marginal form (fixed-effects only) of the final averaged model was 0.924, whereas the median daily survival from the global model including hierarchical random effects for Year and Plot was 0.853. Conversely, the estimated daily survival rate from the Mayfield method was 0.944. Predation was the largest source of nest failure ($n = 57$). We recorded only one instance of a nest of Henslow's Sparrows parasitized by a Brown-headed Cowbird (*Molothrus ater*), and that nest was not included in the analysis since there were no surviving host young when the nest was found. Preliminary analyses including the interaction of nest age and observation age as a covariate affecting daily nest survival had essentially no statistical support, suggesting little bias associated with detecting nests across the nesting cycle. Likewise, models including either term individually also had essentially no support.

The first stage of model development for nest timing covariates resulted in the inclusion of a quadratic term for nest age, with no support for any other timing covariate. In the first stage of model development for the nest-level habitat covariates, linear terms for the amount of standing dead vegetation, shrub cover, litter depth, grass cover, grass depth, bare ground, and vegetation density were all retained from the nest-level suite of covariates. No landscape-level metrics were retained during the first stage of model development, as all forms of each covariate yielded BIC values greater than the null model. The variable 'Years since burn' was supported only as a linear term. The most supported second-stage model for nest-level habitat covariates included only a linear term for the amount of standing dead vegetation, with all additive combinations of other variables yielding $\Delta BIC > 2$.

Once these forms of the second-stage models were established, we calculated a total of 6 candidate models in the final stage of model development (Table 2). The best single model, based on minimization of BIC, included terms for nest age and the height of standing dead vegetation (Table 2). Only the top two models garnered any support (Table 2). The final averaged model was most influenced by a curvilinear relationship with nest age (Fig. 2). Nest survival increased as standing dead vegetation increased, although this relationship was weak (Fig. 2). Nest survival decreased as years since burn increased (Fig. 2), although this relationship was also weak. There was a distinct decline in daily survival rates during the middle of the nest cycle, corresponding with the onset of hatching (Fig. 2), with dead vegetation and years since burn showing minimal impacts on survival. Parameter estimates for both standing dead vegetation and years since burn overlapped zero (Table 3).

DISCUSSION

Despite the considerable management interest and research focus on Henslow's Sparrow, there are comparatively few studies of reproductive success, principally because of the difficulty in finding nests of this species and the comparative rarity of the species as a whole. Overall, we found

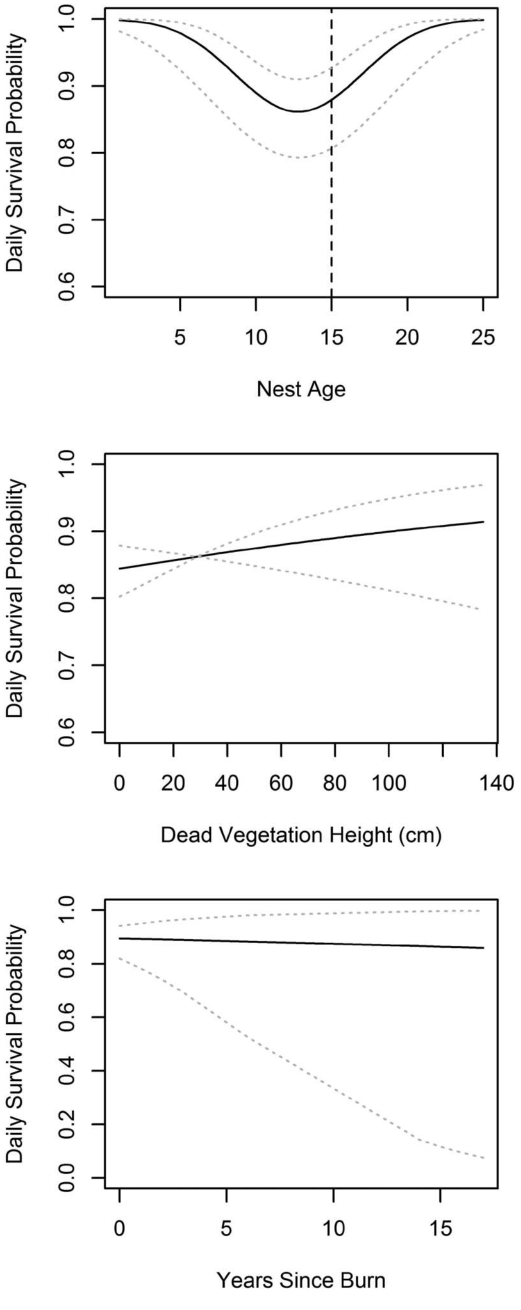

FIG. 2. Marginal response curves (solid line) and 95% confidence bands (dashed lines) relating daily nest survival to fixed effects. Confidence bands were based on confidence intervals of parameters estimates (Table 2). Vertical dotted line in top panel represent approximate average hatching date. The range of values on the x-axes reflect the observed range of values found at nest sites.

relatively weak support for habitat structure or management affecting Henslow's Sparrow nest survival. Henslow's Sparrow are generally described as disturbance intolerant, requiring abundant standing vegetation and generally absent from grasslands too frequently or intensely burned (Zimmerman 1988, Herkert 1994b, Herkert et al. 2002, Powell 2006). However, Fuhlendorf et al. (2006) found high densities of Henslow's Sparrows in landscapes where fire was an important component of management but none at sites without fire. Similarly, Pillsbury (2010) found Henslow's Sparrows to be more abundant in grasslands maintained only by burning as compared to fire and grazing management combinations. Estimated breeding densities of Henslow's Sparrows at BONWR usually peaked 1-year post burn and were lowest the same year of the burn (Table 1). We conducted our study in an area where prescribed fire was the primary means of controlling woody encroachment, suggesting that densities of Henslow's Sparrows in our study area might have been comparatively high. Observed breeding densities of Henslow's Sparrows at BONWR were among the highest observed for the species (Cooper 2012), despite the distinct possibility we may have failed to detect some number of territories and nesting attempts.

We found strong evidence for a decline in nest survival around hatching. This pattern has been observed previously for other grassland sparrow species and is thought to be the result of increased visual, auditory, and olfactory cues associated with hatching and increased foraging trips of parents that increase nest detection by predators (Grant et al. 2005). However, Winter (1999) and Giocomo (2005) did not detect differences in daily survival rates calculated with the Mayfield method between incubation or nestling stages for Henslow's Sparrows. The logistic exposure method should be more sensitive in detecting patterns of survival than the Mayfield estimator because of Mayfield's assumption of constant survival within stages, especially since the increase in mortality observed occurred around a stage transition.

It is often suggested that prolonged monitoring of bird nests can increase their risk of predation through cueing by predators on researcher behavior (Götmark 1992). Visits to nests disturb the vegetation and leave scents for predators to follow (Westmoreland and Best 1985, Esler and Grand 1993, Whelan et al. 1994). Given that nest predation was the single largest source of nest failure

TABLE 3. Parameter estimates (95% confidence interval) from final averaged model as per Lukacs et al. (2010). Variable weights (ω) are calculated as the sum of the model weights from all models including a particular covariate.

Parameter	β	ω
Intercept	2.2407 (1.4417, 2.9877)	-
Nest Age	1.2156 (0.6841, 1.7471)	1
Nest Age^2	1.1691 (0.6650, 1.6732)	1
Standing Dead Vegetation	0.1517 (−0.1411, 0.4444)	1
Years Since Burn	−0.0239 (−0.2624, 0.2146)	0.3318

for Henslow's Sparrows in this study and others, it is possible that we might have inadvertently affected nest survival with our study (Winter 1999, Giocomo 2005). We did exercise great care in finding, marking, and visiting each nest and took care in not leaving blind trails to nests. Additionally, some nests were found during the late nestling stage because of frequency of parental feeding; these nests required fewer visits to follow through fledging and thus would have a reduced risk of predators cueing on research activity. Our median age of nests at discovery was day 12 (Fig. 3). To avoid predation, older fledglings late in the nest cycle often fledge prematurely when predators attack the nest (Grant et al. 2005). These factors, coupled with lack of support for linear or quadratic effects of observation age or the interaction between observation age and nest age, showed no evidence that our field protocols had influence on nest survival. Some models that test observer influence assume the effect occurs after a nest visit but lasts less or equal to visitation intervals, but if observation risk accumulates beyond this interval it could be confounded and additive with other risks of mortality and difficult to detect with small samples (Rotella et al. 2000).

Giocomo et al. (2008) reported an apparent nest success of 58% (*n* = 113), similar to our findings of 54.8%. Apparent nest success estimates are biased because of differential detection of nests associated with exposure (Mayfield 1961, 1975). More recent efforts using Mayfield estimation suggested nesting success averages ~27% and ranges between 6.5–39.5% (6.5%, *n* = 16, Burhans 2002; 19%, *n* = 49, Moss 2001; 24%, *n* = 39, Hinnebusch 2008; 27%, *n* = 113, Giocomo et al. 2008; 29%, *n* = 22, Reinking et al. 2000; 39.5%, *n* = 59, Winter 1999; 23.7%, *n* = 135, this study). However, Mayfield estimates are biased if survival is not constant within nest stages, and estimates from logistic exposure models offer more information on survival patterns (Klett and Johnson 1982, Grant et al. 2005). Still, our daily nest survival estimates (0.930-logistic exposure; 0.944-Mayfield) were similar to those reported in other studies (0.95, Winter and Faaborg 1999; 0.88–1.00, Winter et al. 2000; 0.95, Hill 2012). That our daily survival estimate generated using the Mayfield approach is similar to what we found with the logistic exposure method suggests that our results are comparable to previous studies. Similarly, our mean observed clutch size (4.1 eggs) was similar to that reported in other studies (3.8 eggs, *n* = 56, Winter 1999; 3.9, *n* = 12, Peck and James 1987 [cited in Herkert et al. 2002]; 4.3, *n* = 56, Moss 2001). Taken together, it would appear that the nesting dynamics of Henslow's Sparrows on BONWR do not differ dramatically from those in other regions. This is potentially important because southern Indiana, where our study area was located, is not considered part of the tallgrass prairie biome in which Henslow's Sparrows historically occurred but was previously characterized by extensive hardwood forests. Thus, the nesting habitat provided to Henslow's Sparrows at BONWR, and in many grassland habitats, is strictly a function of active habitat management practices such as prescribed burning.

Grasslands providing Henslow's Sparrows with breeding habitat are generally tall, dense grass with a well-developed litter layer and a relatively high coverage of standing dead vegetation (Pruitt 1996). Therefore, it is typically mentioned that Henslow's Sparrows avoid recently burned grasslands (Powell 2006). Henslow's Sparrows nested successfully at BONWR during the same year following a spring prescribed fire but at lower densities (Table 1), and nests were not initiated until later in the breeding season (i.e., Jul–Aug; JRR, unpubl. data). Recent studies, however, have suggested locations with abundant Conservation Reserve Program lands have led to increasing populations of Henslow's Sparrows using less preferred habitat, including recently burned, grazed, and mowed sites (Herkert 2007a). This plasticity in nest-site selection at BONWR would seem to indicate that Henslow's Sparrows are sometimes capable of successfully nesting in recently burned habitats.

Although our model selection approach yielded some weight to the effect of years since burn, it was relatively clear that this was a largely uninforma-

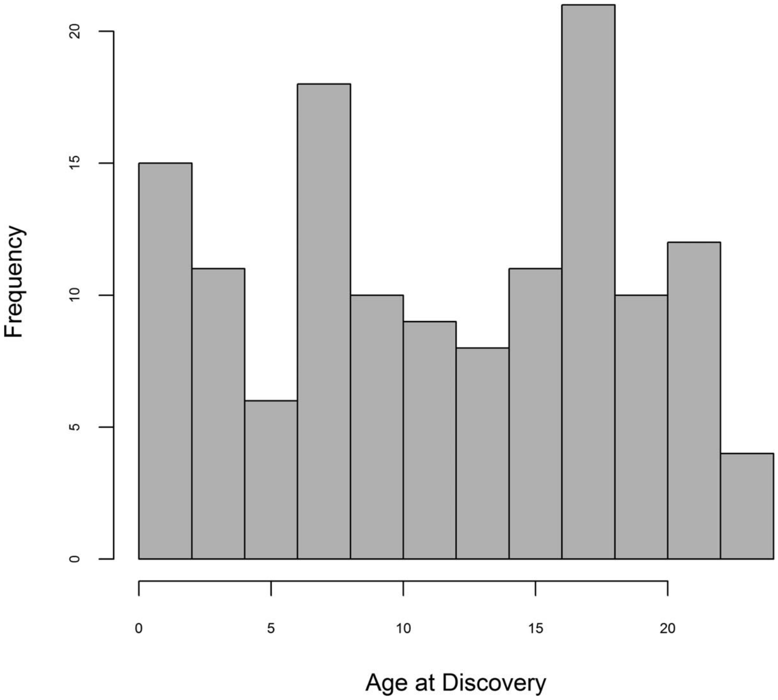

FIG. 3. Histogram of age of nests of Henslow's Sparrows at first discovery (in days) at Big Oaks National Wildlife Refuge, southern Indiana, USA. Nests found during building were assigned age 0.

tive parameter (Arnold 2010). The confidence interval of the parameter estimate for years since burn substantially overlapped zero (Table 3), and the magnitude of change in nest survival induced by this covariate was minimal across the range of values in our study (Fig. 2). However, this result does not imply that burning is not important to Henslow's Sparrows' nesting success. Burning is required to maintain suitable nesting habitat for Henslow's Sparrows at BONWR, thus the presence of burning on our study area is a prerequisite for nesting by Henslow's Sparrows. That we observed Henslow's Sparrows nesting in patches very recently burned (Table 1) suggests rapid structural changes to grassland patches following prescribed burns. Increased invertebrate density and improved vegetative structure from improved grass growth in areas with acidic soils might drive this relationship (Vogl 1974, Raison 1979). Because grassland patches in our study area also would likely revert to increased shrub or successional habitat in the absence of active management, that nest survival for a grassland obligate species such as Henslow's Sparrows declined monotonically with time since burn is not surprising. Previous studies suggesting that Henslow's Sparrows do not nest in recently burned areas occurred primarily in regions with lower precipitation and richer soils and native tallgrass prairie where successional dynamics might not result in rapid conversion of grassland habitats to successional habitat in the absence of fire as they would at BONWR (e.g., Powell 2006, 2008). The acidic wet grasslands at BONWR also concomitantly increase in productivity because of nutrient dynamics following a fire (Vogl 1974, Raison 1979). However, we note that we did not explicitly evaluate successional dynamics in our study system, and thus cannot definitively conclude that such relationships existed at BONWR. The high levels of plasticity in the timing of nesting events (Fig. 1) would also suggest that Henslow's Sparrows on BONWR can respond to small levels of variation in habitat conditions. However, even our parameter estimate for standing dead vegetation, the only structural habitat covariate retained in our final model, overlapped zero, suggesting that even variation in habitat structure had little influence on nest survival.

Woody encroachment is generally believed to negatively influence the occurrence of Henslow's

Sparrows (O'Leary and Nyberg 2000). Our results support this perspective, as areas dominated ($>50\%$ cover) by shrubs were effectively devoid of Henslow's Sparrow (JRR, unpubl. data). During the years after this study, woody encroachment decreased the available grassland habitat to 30% of its former amount (JRR, unpubl. data), resulting in less breeding habitat for this species of special conservation concern. This decrease in landscape-level habitat could have serious consequences for regional populations if active management practices cannot maintain extant grassland habitats. Our results indicate that maintaining grassland habitats through active management might provide benefits to local populations of Henslow's Sparrows by providing effective nesting habitat. We suggest that future research should focus on quantifying the effects of such management practices and populations to regional conservation targets.

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APPENDIX 1: Example R code for developing mixed-effects logistic exposure models. Modified from code developed by Ben Bolker (McMaster University).

```
# Define logistic exposure family
logisexpos <- function(exposure = 1)
  {
       linkfun <- function(mu) qlogis(mu^(1/exposure))
       linkinv <- function(eta) plogis(eta)^exposure
       mu.eta <- function(eta) exposure *
          plogis(eta)^(exposure-1) *
          .Call(stats:::C_logit_mu_eta, eta, PACKAGE = "stats")
       valideta <- function(eta) TRUE
       link <- paste("logexp(",
          deparse(substitute(exposure)), ")",sep="")
       structure(list(linkfun = linkfun, linkinv = linkinv,
          mu.eta = mu.eta, valideta = valideta, name = link),
       class = "link-glm")
  }
# Load updated package
require(lme4)

# Build mixed-effects model
# “Exposure” is measured as the number of days since the
# previous visit. “survival” is binary (0/1) for live/dead
glmer(survival~FixedEffect1 + FixedEffect2 + FixedEffect3 +
     (1|RandomEffect1) + (1|RandomEffect2), data=data,
     family=binomial(logisexpos(exposure=data$Exposure)))
```