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RESEARCH ARTICLE

Minimal bias in surveys of grassland birds from roadsides

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ABSTRACT

Edges, including roads, can have unintended deleterious impacts on wildlife. However, roads also present opportunities for replicable, and spatially and temporally consistent, wildlife monitoring. Assessing sources of variability associated with roadside-based surveys could improve the accuracy and extend the inferences of surveys, thus strengthening their applicability to management. We assessed roadside effects on abundance (λ) and detection probability (p) of high-priority grassland and shrubland songbirds in western Kentucky and Tennessee, USA. We delineated transects 300 m apart perpendicular to secondary roads and, along each transect, positioned point counts at 0 m, 300 m, and 600 m off the road. We surveyed 8 species: Northern Bobwhite (*Colinus virginianus*), Bell's Vireo (*Vireo bellii*), Prairie Warbler (*Setophaga discolor*), Field Sparrow (*Spizella pusilla*), Grasshopper Sparrow (*Ammodramus savannarum*), Henslow's Sparrow (*Ammodramus henslowii*), Dickcissel (*Spiza americana*), and Eastern Meadowlark (*Sturnella magna*). We used Royle N-Mixture models to estimate species-specific abundance and detection probability. For abundance, distance from the road affected only Henslow's Sparrow; mean Henslow's Sparrow abundance increased by 59% at points 600 m away from a road. For detection probability, distance from the road was not important for any species, suggesting that noise or activity associated with low-traffic roads did not affect bird singing behavior or observer hearing ability enough to affect survey results. Abundance was more strongly related to land-cover covariates than distance from the road. With the exception of Henslow's Sparrow, roadside surveys for 8 high-priority grassland bird species produced estimates of abundance and detection probabilities representative of the broader landscape. Roads can provide opportunities to accurately monitor occupancy, abundance, and density of grassland birds using surveys that account for land-cover variation and seasonal variation in detection probability.

Keywords: abundance, convenience sampling, detection probability, grassland birds, roadside effects

Sesgo mínimo en estudios de aves de pastizal realizados desde el borde de las rutas

RESUMEN

Los bordes, incluyendo las rutas, pueden tener impactos negativos imprevistos sobre la fauna silvestre. Sin embargo, las rutas también brindan oportunidades para el monitoreo replicable, espacial y temporalmente consistente, de la fauna silvestre. La evaluación de las fuentes de variabilidad asociadas a los estudios realizados en el borde de las rutas podría mejorar la exactitud y extender las inferencias de los estudios, por ende fortaleciendo su aplicabilidad para el manejo. Evaluamos los efectos del borde de la ruta en la abundancia (λ) y la probabilidad de detección (p) en aves canoras de alta prioridad de pastizales y arbustales en el oeste de Kentucky y Tennessee, EEUU. Emplazamos transectas separadas por 300 m de modo perpendicular a rutas secundarias, y en cada transecta establecimos puntos de conteo a 0, 300 y 600 m desde la ruta. Censamos ocho especies: *Colinus virginianus*, *Vireo bellii*, *Setophaga discolor*, *Spizella pusilla*, *Ammodramus savannarum*, *Ammodramus henslowii*, *Spiza americana* y *Sturnella magna*. Usamos modelos mixtos de Royle para estimar la abundancia específica y la probabilidad de detección de las especies. En términos de abundancia, la distancia desde la ruta afectó solo a *A. henslowii*; la abundancia media de *A. henslowii* aumentó en un 59% en los puntos alejados a 600 m de la ruta. Para la probabilidad de detección, la distancia desde la ruta no fue importante para ninguna especie, sugiriendo que el ruido o la actividad asociada con las rutas de bajo tráfico no perturbaron el comportamiento del canto o la habilidad observada de escucha de las aves lo suficiente como para afectar los resultados del estudio. La abundancia se relacionó más fuertemente con las covariables de la cobertura del suelo que con la distancia desde la ruta. Con la excepción de *A. henslowii*, los estudios a lo largo de la ruta para ocho especies de aves de alta prioridad de los pastizales brindaron estimaciones de abundancia y probabilidades de detección representativas del paisaje en su conjunto. Las rutas pueden brindar oportunidades para estudiar con exactitud la ocupación, la abundancia y la densidad de las aves de pastizal usando muestreos que tienen en cuenta la variación en la cobertura del suelo y la variación estacional en la probabilidad de detección.

Palabras clave: abundancia, aves de pastizal, efectos de borde de las rutas, muestreo de conveniencia, probabilidad de detección

INTRODUCTION

Fundamental to ecological research is the ability to monitor populations in space and through time (Brown 1984). Monitoring schemes established to understand how underlying ecological processes can influence abundance or detection probability can lead to incorrect inferences if the sampling framework is inappropriately designed (Bart et al. 1995, Anderson 2001). A potential confounding factor is the spatial arrangement of the sampling design. Often, monitoring schemes are suboptimal, with design dictated by convenience (Garton et al. 2005, Morrison et al. 2008). For example, researchers typically sample along existing landscape features such as game trails (Rabe et al. 2002, McGrann et al. 2014, Cusack et al. 2015), railroads (Dorsey et al. 2015, Wiącek et al. 2015a), industrial linear corridors (Anderson et al. 1977, Latham and Boutin 2015), and roads (Sauer et al. 1994, Forman et al. 2003). In particular, sudden or abrupt changes in landscape features that create edges can affect abundance or detection probability in ways unrelated to the underlying ecological process of interest (Donovan et al. 1997, Fletcher 2005).

Road and edge effects are typically considered deleterious to wildlife because they contribute to direct habitat loss and degradation, act as barriers to movement (Desrochers and Hannon 1997, Laurance et al. 2004, Wiącek et al. 2015b), and are avoided by some species (Forman and Alexander 1998, Fahrig and Rytwinski 2009, VanDerRee et al. 2015). Roads and anthropogenic features can also alter land cover in a way that attracts songbird nest predators (Heske et al. 2001, Walker and Marzluff 2015). A major difference between roads and other edges is the unique influence of anthropogenic disturbances along roads, particularly vehicle noise (Parris and Schneider 2009, Halfwerk et al. 2011) and direct mortality through vehicle collisions (Groot Bruinderink and Hazebroek 1996, Erickson et al. 2005).

Despite the potential problems of roadside surveys, they remain the most common form of convenience sampling for monitoring taxa including snakes and turtles (Enge and Wood 2002, Steen and Smith 2006), anurans (Weir and Mossman 2005, Weir et al. 2005), birds (Andersen et al. 1985, Peterjohn and Sauer 1999), ungulates (Collier et al. 2007), and lepidopterans (Munguira and Thomas 1992). For some species, such as white-tailed deer (*Odocoileus virginianus*), anurans, and many birds, the only trend data available are based on long-term roadside-based surveys. The North American Breeding Bird Survey (BBS) is perhaps the best-known convenience sampling design; since its establishment in 1966, BBS data have been used in hundreds of studies (Ziolkowski et al. 2010, Sauer and Link 2011, Sauer et al. 2012).

Roadside bird surveys have at least 3 problems that could compromise their generality to larger spatial scales:

(1) altered habitat conditions affecting bird dispersion; (2) altered avian behavior affecting detectability; and (3) altered observer ability to detect birds. Roadside surveys could be a misrepresentation of a metric of interest (i.e. abundance, density, diversity) if a species is attracted to or avoids roads, if roadside surveys do not representatively sample land-cover types that occur off-road, or if land-cover changes along a roadside survey route differ from off-road land-cover changes (Keller and Scallan 1999, Harris and Haskell 2007, McCarthy et al. 2012). Road noise can affect the singing rate, frequency, and amplitude for certain species, contributing to reduced pairing and nesting success (Brumm and Todt 2004, Parris and Schneider 2009, Griffith et al. 2010, Halfwerk et al. 2011). Additionally, background noise caused by roads might impede observer ability to hear singing birds, although this effect is variable and dependent on the frequency and amplitude of the background noise (Pacifiçi et al. 2008).

Our goal was to assess roadside effects in estimates of abundance (λ) and detection probability (p) of high-priority grassland and shrubland bird species in the Central Hardwoods Bird Conservation Region of western Kentucky and Tennessee, USA, using a roadside vs. off-road survey design. We used N-mixture models to evaluate the underlying ecological process of interest (abundance [λ]), while simultaneously accounting for sampling variation associated with detection probability (p) and including categorical or continuous covariate effects, including land cover, on abundance. We hypothesized that the abundance of 8 bird species would be lower along roads. We also hypothesized that detection probability would be lower on roadside counts.

METHODS

Study Area

We conducted surveys in 3 sites in western Kentucky (KY) and Tennessee (TN): Peabody Wildlife Management Area (Peabody), KY; Fort Campbell Military Reservation (Fort Campbell), TN-KY; and private lands in Livingston County (Livingston County), KY. We chose these sites based on accessibility to off-road areas and presence of secondary roads, and because they were representative of the Central Hardwoods Bird Conservation Region, the target landscape of interest for inference (Lituma 2014). Roads within sites were randomly selected from a collection of roads that were directly adjacent to grassland or shrubland cover extending for at least 600 m. Peabody is an 18,854-ha reclaimed surface mine located in Ohio, Muhlenberg, and Hopkins counties, KY, managed by the Kentucky Department of Fish and Wildlife Resources. Herbaceous cover established during reclamation was dominated by sericia lespedeza (*Lespedeza cuneata*), but

also included big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*). We focused surveys on a 3,321-ha unit comprised predominantly of mixed deciduous forest, open herbaceous areas, nonnative cool-season grasses such as tall fescue (*Schedonorus arundinaceus*), native warm-season grasses, and shrubs. Fort Campbell is a 41,842-ha U.S. Department of Defense Army installation straddling the Tennessee–Kentucky border. The topography is flat to gently rolling, with open oak woodlands, planted pines, leased agricultural fields, and managed grasslands. We conducted surveys in native grasslands, cool-season grass patches, and mixed grass–forb areas that ranged in size from 73 ha to 570 ha. Private lands in Livingston County were restored to native warm-season grasses and were part of a Northern Bobwhite (*Colinus virginianus*) focus area developed by the Kentucky Department of Fish and Wildlife Resources (Morgan and Robinson 2008). The total focal area was 12,860 ha. We surveyed a subset of 3 fields ranging in size from 25 ha to 450 ha (~4% of the focal area).

We did not record a measure of traffic for use in analyses. However, Average Annual Daily Traffic (AADT) is a metric used by transportation departments that is calculated as the total annual volume of traffic based on a 24-hr 2-directional count on a given road for a given location divided by 365 days. For secondary roads near Fort Campbell in 2010, AADT ranged from 84 to 7,400 cars per day (TDOT 2012). Traffic volumes on the actual roads surveyed in Fort Campbell were unavailable but, based on direct observation during surveys, were likely at the low end of the range measured for nearby secondary roads. AADT for Peabody in 2010 ranged from 229 to 2,032 cars per day (KYTC 2011), and AADT for Livingston County in 2010 ranged from 248 to 2,280 cars per day (KYTC 2011). Roads in Fort Campbell were paved or gravel, roads in Peabody were gravel, and roads in Livingston County were paved.

Surveys

We conducted roadside vs. off-road surveys in Peabody ($n = 12$ transects) and Fort Campbell ($n = 39$ transects) in 2010, and in Peabody ($n = 31$ transects) and Livingston County ($n = 8$ transects) in 2011. Surveys in Fort Campbell were not conducted in 2011 because of access restrictions, so we increased sampling in Peabody and added Livingston County in 2011. We used National Agricultural Statistics Service (NASS) grassland, pasture, and hay cover types in ArcGIS 10.0 (ESRI, Redlands, California, USA) to identify potential survey fields. Fields were large enough to fit >2 transects and were at least 700 m long to allow for a 100-m buffer from forest edges. We randomly placed the first transect along the adjacent secondary road. To reduce the

potential for detection of the same individuals and spatial autocorrelation (Fletcher and Koford 2002, Alldredge et al. 2006), we systematically positioned all other survey transects 300 m from the first transect, and extended points ($n = 3$) on each transect perpendicularly for 600 m away from the road (i.e. 0 m = on the road, 300 m, and 600 m). At each point we conducted a 5-min 100-m fixed-radius point count, recording all individuals seen and heard (Hutto et al. 1986, Matsuoka et al. 2014); we truncated observations for analyses at 100 m to avoid double-counting on subsequent counts, and because species detection probabilities are dramatically reduced beyond 100 m (Lituma 2014). We surveyed each transect 3 times at ~2-week intervals to determine seasonal variation in detection and abundance. The first visit occurred between May 19 and June 3, the second visit between June 1 and June 25, and the third visit between June 25 and July 11. We surveyed a total of 153 points on 51 off-road transects in 2010, and 117 points on 39 off-road transects in 2011. We surveyed 8 grassland and shrubland bird species that were of conservation concern in the Central Hardwoods Bird Conservation Region: Northern Bobwhite, Bell's Vireo (*Vireo bellii*), Prairie Warbler (*Setophaga discolor*), Field Sparrow (*Spizella pusilla*), Grasshopper Sparrow (*Ammodramus savannarum*), Henslow's Sparrow (*Ammodramus henslowii*), Dickcissel (*Spiza americana*), and Eastern Meadowlark (*Sturnella magna*).

Land-cover Assessment

We visually estimated to the nearest 10% the percent cover of 8 land-cover types within a 100-m radius of the point center for all point count stations to match the area covered by the 100-m fixed-radius point counts. We included 7 different land-cover types in our analyses based on our knowledge about focal species habitat use: cool-season grass (CG; unmowed fields with $>70\%$ cool-season grass cover [typically tall fescue]), forest (FO; mature forested areas with a closed canopy [$>80\%$] and well-developed understory), grass mixture (GM; 30–70% mixture of native warm-season grass, cool-season grass, and herbaceous cover), native warm-season grass (NG; $>70\%$ native warm-season grasses), old field (OF; fields with woody encroachment undergoing the early stages of succession), shrubland (SC; abandoned fields dominated by saplings and shrubs), and woodland (WD; areas with widely spaced trees and limited canopy cover [50%]). To confirm the accuracy of our visual percent cover estimation, we compared our on-the-ground land-cover assessment with remotely sensed NASS cover types, which are commonly used to classify land cover in wildlife research, analyzed in ArcGIS 10.0. Our classifications were more detailed than those available through NASS; thus, for the purposes of comparison, we aggregated forest, old field, shrubland, and woodland cover types as Forest, and

we pooled cool-season grass, grass mixture, and native warm-season grass cover types as Grass.

Analyses

We used correlation coefficients to determine whether on-the-ground cover measurements were consistent with geospatial cover estimates. We considered correlation coefficients sufficient if $r > 0.5$. We used a multivariate analysis of variance (MANOVA) to compare percent land cover among the 3 distance-from-road (DFR) categories among all points ($n = 270$). We inspected Q-Q plots for normality of residuals and we tested for equality of variances via a Levene's test. If test results violated normality or equality of variance assumptions, then we used nonparametric Kruskal-Wallis analysis to test for differences among categories (Zar 1996). We considered means different at $\alpha < 0.05$, and used univariate comparisons among land-cover types. We used Fisher's LSD tests for post hoc comparisons among distance-from-road categories (IBM SPSS Statistics for Windows 21.0; IBM, Armonk, New York, USA).

We calculated species-specific abundance (λ) and detection probability (p) using N-mixture abundance models (Royle 2004) in package unmarked (Fiske and Chandler 2011) in program R (R Core Team 2014). N-mixture models utilize count data replicated in time and space, and assume either a Poisson, a zero-inflated Poisson (ZIP), or a negative binomial (NB) distributed population of individuals to estimate mean site abundance while accounting for detection probability. Detection probability is modeled as a binomial observation process of the counts (C_{ij}), accounting for both the latent abundance state (N_i) and individual detection probability (p_{ij}) at site i and during survey j ($C_{ij} \sim \text{Binomial}(N_i, p_{ij})$), so we did not include abundance as a covariate affecting detection probability because it would have been redundant in the modeling process (Royle 2004). Hierarchical models evaluate sample (detection probability) and process variability (abundance) simultaneously (Royle and Dorazio 2008), and are superior to ANOVA or regression models because covariates affecting detection probability and abundance can be simultaneously evaluated, and abundance estimates are adjusted for detection probability.

We grouped surveys based on year and distance from the road to assess the potential effect on detection of these factors. We did not evaluate distance from the road as a continuous variable because observations were collected in discrete distance categories. To assess within-year temporal effects on detection probability, we assigned each visit a continuous date value by considering the first day (May 17) that any point was visited in either year as day 1. We also determined the time since sunrise at which each point count began. Although observer effects can significantly

affect detection probabilities (Lituma 2014), we omitted observer effects because >90% of the point counts were conducted by 1 experienced observer, and the sample size of the secondary observer ($n = 27$) was not large enough for analyses. We did not include habitat effects on detection probabilities because we used a fixed-radius point count (100 m) in open areas with minimal opportunities for vegetation to obstruct sound. We included the effects of distance from the road and year on abundance. Additionally, we evaluated heterogeneity in land cover at points by including a covariate for percent cover of cool-season grass, forest, grass mixture, native warm-season grass, old field, shrubland, and woodland cover types because we hypothesized that they could affect abundance.

We developed a suite of species-specific a priori models based on our objectives and plausible covariates. We used Akaike's Information Criterion adjusted for small sample size (AIC_c) for model selection. We considered models with $\Delta AIC_c \leq 2$ to be the most influential in explaining the variability in the system (Burnham and Anderson 2002). To examine explicit distance-from-road effects, we always first modeled distance from a road singularly for detection probability and abundance. We included every potential combination of distance-from-road, year, date, and time-since-sunrise covariates in the model set for detection probability, and we modeled every potential combination of distance-from-road, year, and vegetation land-cover covariates in the model set influencing the parameter for abundance. We also included quadratic terms for land cover, date, and time-since-sunrise covariates, to evaluate potential nonlinear relationships. Then, we examined different abundance distributions by including negative binomial (NB) and zero-inflated Poisson (ZIP) parameters. Lastly, after we determined a final candidate model, if the top model did not include distance-from-road effects on either detection probability or abundance, we added the distance-from-road effect back into the top model for each parameter to be certain that distance from a road was still not influencing the parameters. We did not include any models with interaction terms because they did not make biological sense. We used the most parsimonious model(s) and the mean covariate values of land-cover types included in top models to generate abundance parameter estimates; we did not use model averaging. We assessed model goodness-of-fit ($\alpha < 0.05$) with 3 different tests (sums of squares, chi-square [χ^2], and Freeman-Tukey), and considered model fit adequate if 2 of the 3 tests were insignificant (Fiske and Chandler 2011). All results are presented as mean \pm SE, and we used mean covariate values to calculate parameter estimates. All beta estimates are presented using results from top models. Rather than presenting complete model sets for each species, we only present the most parsimonious models with the distance-

TABLE 1. Goodness-of-fit ($\alpha < 0.05$) results for top models for on- and off-road point counts conducted in 2010 and 2011 in Fort Campbell Military Reservation, Kentucky–Tennessee, Peabody Wildlife Management Area, Kentucky, and Livingston County, Kentucky, USA.

Species	Sums of squares	Chi-square (χ^2)	Freeman-Tukey
Northern Bobwhite	0.53	0.24	0.36
Bell's Vireo	0.88	0.80	0.73
Prairie Warbler	0.55	0.75	0.52
Field Sparrow	0.99	0.99	0.99
Grasshopper Sparrow	0.27	0.00	0.39
Henslow's Sparrow	0.58	0.08	0.68
Dickcissel	0.93	0.45	0.40
Eastern Meadowlark	0.52	0.41	0.80

from-road covariate, land-cover covariates of significance, and constant models.

Assumptions associated with N-mixture abundance models include: (1) that populations remain closed for the duration of the surveys; (2) that individuals are never falsely detected at a site when absent and may or may not be detected when they are present; (3) that detection of an individual at a site is independent of detection of individuals at other sites; and (4) that detection probabilities among individuals within a species are homogeneous (Royle 2004). We minimized the likelihood of immigration and emigration by surveying within a 2-month window during the peak breeding season. Our populations of interest were largely closed; the 8 focal species establish distinct breeding territories and defend them during the breeding season. Some movement of individuals probably did occur if nests failed, but we assumed that this had minimal effect on the results. We limited the number of species being surveyed to 8 readily recognizable species and used only 2 experienced observers to conduct surveys, thereby minimizing false detections. Our individual fixed-radius point count stations were separated by 300 m to minimize the possibility of movement among them during counts, and to ensure spatial independence. We minimized detection heterogeneity among individual birds by truncating observations to within 100 m.

RESULTS

Distance-from-Road Effects

Forest ($r = 0.57$) and Grass ($r = 0.58$) on-the-ground cover classifications were correlated with NASS classification types at the same point, so we included our more detailed on-the-ground cover types as covariates in the analyses and excluded NASS data. The 7 cover types included in our analyses comprised $\sim 83\%$ of the land cover at points (CG [cool-season grasses] = $\sim 5\%$, FO [forest] = $\sim 5\%$, GM [grass mixture] = $\sim 38\%$, NG [native warm-season grasses]

= $\sim 7\%$, OF [old field] = $\sim 4\%$, SC [shrubland] = $\sim 20\%$, WD [woodland] = $\sim 4\%$). Mean percent land cover of OF (MANOVA, $n = 270$, $F = 5.40$, $P < 0.01$) was greater at points 600 m away from the road and mean percent land cover of FO (MANOVA, $n = 270$, $F = 16.12$, $P < 0.05$) was greater at roadside points. No other land-cover comparisons differed among distance-from-road categories ($P > 0.05$).

All top models met goodness-of-fit assumptions (Table 1). The distance-from-road covariate was included in the top model explaining Henslow's Sparrow abundance only. Distance from a road was included in competing models ($\Delta AIC_c \leq 2$) for Northern Bobwhite, Prairie Warbler, and Dickcissel abundance, but was never in the top model related to detection probability for any species (Table 2). In all cases, we examined 95% confidence intervals of beta estimates to determine the significance of distance-from-road effects. The abundance of Northern Bobwhite and Henslow's Sparrow was 20% and 59% greater, respectively, at points located away from a road than along a road (Figure 1), although for both species the 95% confidence intervals of beta estimates overlapped zero for 2 distance-from-road categories (Table 3). Prairie Warbler abundance was similar at points along the road and 300 m from the road, but was 40% greater at points 600 m from the road (Figure 1), although the 95% confidence intervals of beta estimates overlapped zero for every distance category (Table 3). Dickcissel abundance was 15% greater at points 300 m from the road than at points along the road and 600 m from the road, although 95% confidence intervals of beta estimates overlapped zero for 2 distance-from-road categories.

Temporal Effects

The abundance of Bell's Vireo, Field Sparrow, Grasshopper Sparrow, and Eastern Meadowlark varied with a combination of year and land-cover covariates (Table 2). Abundances were much greater in 2010 than in 2011 for Grasshopper Sparrow (2010: $\lambda = 1.07 \pm 0.29$; 2011: $\lambda = 0.29 \pm 0.08$; $\beta = 1.31 \pm 0.28$) and Eastern Meadowlark (2010: $\lambda = 7.1 \pm 4.0$; 2011: $\lambda = 0.11 \pm 0.05$; $\beta = 4.14 \pm 0.65$). Abundances were greater in 2011 than in 2010 for Bell's Vireo (2010: $\lambda = 0.09 \pm 0.03$; 2011: $\lambda = 0.23 \pm 0.08$; $\beta = -0.92 \pm 0.22$) and Field Sparrow (2010: $\lambda = 2.58 \pm 0.30$; 2011: $\lambda = 3.34 \pm 0.36$; $\beta = -0.26 \pm 0.16$). Northern Bobwhite ($\lambda = 9.33 \pm 4.63$), Prairie Warbler ($\lambda = 0.78 \pm 0.19$), Henslow's Sparrow ($\lambda = 6.92 \pm 3.91$), and Dickcissel ($\lambda = 3.19 \pm 0.54$) abundance did not differ between years.

Time since sunrise was the most common covariate related to detection probability and was included in the top model for Northern Bobwhite, Bell's Vireo, Field Sparrow, Henslow's Sparrow, Dickcissel, and Eastern Meadowlark, although date and/or year were also included in some combination in the top model for all species (Table 2).

TABLE 2. Top candidate models of abundance (λ) and detection probability (p), with land-cover covariates, of high-priority grassland and shrubland species based on off-road point counts conducted in 2010 and 2011 in Fort Campbell Military Reservation, Kentucky–Tennessee, Peabody Wildlife Management Area, Kentucky, and Livingston County, Kentucky, USA. Models for which λ and p were held constant are also shown for comparison. Models are ranked by the difference from the top model in Akaike's Information Criterion adjusted for small sample size (ΔAIC_c). w_i = AIC_c weight. K = number of parameters.

Species	Model ^a	ΔAIC_c	w_i	Model likelihood	K	Deviance
Northern Bobwhite	$\lambda(\text{FO} + \text{NG}) p(\text{Date}^2 + \text{TSS}^2)$ ^b	0.00	0.21	1.00	8	1831.35
	$\lambda(\text{FO} + \text{NG}) p(\text{Date}^2 + \text{TSS}^2)\text{ZIP}$	1.17	0.12	0.56	9	1830.52
	$\lambda(\text{FO} + \text{NG} + \text{DFR}) p(\text{Date}^2 + \text{TSS}^2)$	1.47	0.10	0.48	10	1828.82
	$\lambda(\text{FO} + \text{NG}) p(\text{Date}^2 + \text{TSS}^2)\text{NB}$	2.14	0.07	0.34	9	1831.49
	$\lambda(\text{Constant}) p(\text{DFR})$	63.73	0.00	0.00	4	1903.08
	$\lambda(\text{DFR}) p(\text{Constant})$	63.87	0.00	0.00	4	1903.22
	$\lambda(\text{Constant}) p(\text{Constant})$	64.71	0.00	0.00	2	1908.06
Bell's Vireo	$\lambda(\text{Year} + \text{GM}^2 + \text{SC}^2) p(\text{Date}^2 + \text{TSS})\text{ZIP}$ ^c	0.00	0.62	1.00	11	847.77
	$\lambda(\text{Year} + \text{GM}^2 + \text{SC}^2 + \text{DFR}) p(\text{Date}^2 + \text{TSS})\text{ZIP}$	2.60	0.17	0.27	13	846.37
	$\lambda(\text{Year} + \text{GM}^2 + \text{SC}^2) p(\text{Date}^2 + \text{TSS} + \text{DFR})\text{ZIP}$	2.68	0.16	0.26	13	846.45
	$\lambda(\text{Constant}) p(\text{Constant})$	117.67	0.00	0.00	2	983.44
	$\lambda(\text{Constant}) p(\text{DFR})$	121.30	0.00	0.00	4	982.20
Prairie Warbler	$\lambda(\text{DFR}) p(\text{Constant})$	121.52	0.00	0.00	4	982.42
	$\lambda(\text{GM} + \text{SC}^2) p(\text{Date})$ ^d	0.00	0.21	1.00	6	887.75
	$\lambda(\text{GM} + \text{SC}^2 + \text{DFR}) p(\text{Date})$	0.45	0.17	0.79	8	884.20
	$\lambda(\text{GM} + \text{SC}^2) p(\text{Date}^2)$	1.15	0.12	0.56	7	886.91
	$\lambda(\text{GM} + \text{SC}^2) p(\text{Date} + \text{TSS})$	1.17	0.12	0.55	7	886.93
	$\lambda(\text{GM}^2 + \text{SC}^2) p(\text{Date})$	2.01	0.08	0.36	7	887.77
	$\lambda(\text{Constant}) p(\text{Constant})$	134.44	0.00	0.00	2	1030.19
Field Sparrow	$\lambda(\text{DFR}) p(\text{Constant})$	135.72	0.00	0.00	4	1027.47
	$\lambda(\text{Constant}) p(\text{DFR})$	136.95	0.00	0.00	4	1028.70
	$\lambda(\text{Year} + \text{SC}) p(\text{Year} + \text{TSS})$ ^e	0.00	0.25	1.00	6	2093.49
	$\lambda(\text{SC}) p(\text{Year} + \text{TSS})$	0.46	0.20	0.80	5	2095.95
	$\lambda(\text{Year} + \text{SC}) p(\text{Year} + \text{TSS} + \text{DFR})$	1.38	0.12	0.50	8	2090.87
	$\lambda(\text{Year} + \text{SC} + \text{DFR}) p(\text{Year} + \text{TSS})$	2.20	0.08	0.33	8	2091.69
	$\lambda(\text{Constant}) p(\text{Constant})$	69.53	0.00	0.00	2	2170.74
Grasshopper Sparrow	$\lambda(\text{DFR}) p(\text{Constant})$	70.98	0.00	0.00	4	2168.30
	$\lambda(\text{Constant}) p(\text{DFR})$	71.17	0.00	0.00	4	2168.49
	$\lambda(\text{Year} + \text{GM}^2) p(\text{Year} + \text{Date}^2)\text{ZIP}$ ^f	0.00	0.37	1.00	9	1042.34
	$\lambda(\text{Year} + \text{GM}^2) p(\text{Year} + \text{Date}^2)\text{NB}$	0.36	0.31	0.84	9	1042.70
	$\lambda(\text{Year} + \text{GM}^2) p(\text{Year} + \text{Date}^2)$	0.91	0.23	0.63	8	1045.26
	$\lambda(\text{Year} + \text{GM}^2) p(\text{Year} + \text{Date}^2 + \text{DFR})\text{ZIP}$	1.41	0.15	0.49	11	1039.75
	$\lambda(\text{Year} + \text{GM}^2 + \text{DFR}) p(\text{Year} + \text{Date}^2)\text{ZIP}$	3.92	0.04	0.14	11	1042.26
Henslow's Sparrow	$\lambda(\text{Constant}) p(\text{Constant})$	94.79	0.00	0.00	2	1150.48
	$\lambda(\text{Constant}) p(\text{DFR})$	95.84	0.00	0.00	4	1147.64
	$\lambda(\text{DFR}) p(\text{Constant})$	98.51	0.00	0.00	4	1150.31
	$\lambda(\text{GM}^2 + \text{SC}^2 + \text{DFR}) p(\text{Year} + \text{TSS}^2)\text{NB}$ ^g	0.00	0.53	1.00	12	1360.42
	$\lambda(\text{GM}^2 + \text{SC}^2) p(\text{Year} + \text{TSS}^2)\text{NB}$	1.38	0.27	0.50	10	1365.80
	$\lambda(\text{GM}^2 + \text{SC}^2 + \text{DFR}) p(\text{Year} + \text{TSS}^2)\text{ZIP}$	2.72	0.14	0.26	12	1363.14
	$\lambda(\text{GM}^2 + \text{SC}^2) p(\text{Year} + \text{TSS}^2)\text{ZIP}$	4.33	0.06	0.12	10	1368.75
Dickcissel	$\lambda(\text{DFR}) p(\text{Constant})$	231.73	0.00	0.00	4	1608.15
	$\lambda(\text{Constant}) p(\text{DFR})$	235.15	0.00	0.00	4	1611.57
	$\lambda(\text{Constant}) p(\text{Constant})$	235.17	0.00	0.00	2	1615.59
	$\lambda(\text{GM}^2 + \text{SC}^2) p(\text{Date} + \text{TSS})\text{NB}$ ^h	0.00	0.17	1.00	9	2109.71
	$\lambda(\text{GM}^2 + \text{SC}^2) p(\text{TSS})\text{NB}$	0.02	0.17	0.99	8	2111.73
	$\lambda(\text{GM}^2 + \text{SC}^2 + \text{DFR}) p(\text{Date} + \text{TSS})\text{NB}$	0.02	0.17	0.99	11	2105.73
	$\lambda(\text{GM}^2 + \text{SC}^2) p(\text{Date} + \text{TSS} + \text{DFR})\text{NB}$	1.13	0.10	0.57	11	2106.84
Eastern Meadowlark	$\lambda(\text{GM}^2 + \text{SC}^2) p(\text{Date} + \text{TSS} + \text{Year})\text{NB}$	1.17	0.10	0.56	9	2110.88
	$\lambda(\text{GM}^2 + \text{SC}^2) p(\text{Date}^2 + \text{TSS})\text{NB}$	1.31	0.09	0.52	10	2109.02
	$\lambda(\text{GM} + \text{SC}^2) p(\text{TSS})\text{NB}$	1.48	0.08	0.48	7	2115.19
	$\lambda(\text{DFR}) p(\text{Constant})$	199.73	0.00	0.00	4	2318.59
	$\lambda(\text{Constant}) p(\text{DFR})$	204.13	0.00	0.00	4	2322.99
	$\lambda(\text{Constant}) p(\text{Constant})$	204.31	0.00	0.00	2	2327.06
	$\lambda(\text{Year} + \text{GM}^2 + \text{SC}^2) p(\text{Year} + \text{TSS})\text{NB}$ ⁱ	0.00	0.50	1.00	10	903.78
Eastern Meadowlark	$\lambda(\text{Year} + \text{GM}^2 + \text{SC}^2) p(\text{Year} + \text{TSS}^2)\text{NB}$	0.03	0.50	0.98	11	901.81
	$\lambda(\text{Year} + \text{GM}^2 + \text{SC}^2 + \text{DFR}) p(\text{Year} + \text{TSS})\text{NB}$	4.14	0.00	0.13	12	903.92
	$\lambda(\text{Year} + \text{GM}^2 + \text{SC}^2) p(\text{Year} + \text{TSS} + \text{DFR})\text{NB}$	4.25	0.00	0.12	12	904.03

TABLE 2. Continued.

Species	Model ^a	ΔAIC_c	w_i	Model likelihood	K	Deviance
	$\lambda(\text{Constant})$ $p(\text{Constant})$	296.30	0.00	0.00	2	1216.08
	$\lambda(\text{Constant})$ $p(\text{DFR})$	299.26	0.00	0.00	4	1215.04
	$\lambda(\text{DFR})$ $p(\text{Constant})$	299.96	0.00	0.00	4	1215.74

^a DFR = distance from road, FO = forest, GM = grass mixture, NB = negative binomial, NG = native warm-season grass, SC = shrubland, TSS = time since sunrise, and ZIP = zero-inflated Poisson.

^b $AIC_c = 1847.35$.

^c $AIC_c = 868.75$.

^d $AIC_c = 899.75$.

^e $AIC_c = 2105.49$.

^f $AIC_c = 1060.34$.

^g $AIC_c = 1384.42$.

^h $AIC_c = 2127.71$.

ⁱ $AIC_c = 923.78$.

Detection probability was negatively related to time since sunrise for every species except Bell's Vireo (Figure 2). Detection probabilities for Bell's Vireo ($\beta = -0.56 \pm 0.15$) and Prairie Warbler ($\beta = -0.68 \pm 0.09$) were negatively related to date, declining as the season progressed. The opposite was true of detection probabilities for Grasshopper Sparrow ($\beta = 0.15 \pm 0.08$), Henslow's Sparrow ($\beta = 0.18 \pm 0.05$), and Dickcissel ($\beta = 0.08 \pm 0.04$), which were lowest early in the season and increased as the season progressed.

Detection probabilities were greater in 2010 ($p = 0.06 \pm 0.03$) than in 2011 ($p = 0.02 \pm 0.01$) for Henslow's Sparrow ($\beta = 1.36 \pm 0.19$), although detection probabilities were very low in both years. Detection probabilities were lower in 2010 than in 2011 for Field Sparrow (2010: $p = 0.38 \pm 0.04$; 2011: $p = 0.51 \pm 0.05$; $\beta = -0.52 \pm 0.27$), Grasshopper Sparrow (2010: $p = 0.29 \pm 0.06$; 2011: $p =$

0.49 ± 0.07 ; $\beta = -0.84 \pm 0.39$), and Eastern Meadowlark (2010: $p = 0.05 \pm 0.03$; 2011: $p = 0.39 \pm 0.13$; $\beta = -2.56 \pm 0.74$), although the confidence intervals of beta estimates overlapped zero for Field Sparrow.

Land-cover Effects

There were 4 land-cover covariates included in competitive species abundance models: FO (forest; $\bar{x} = 0.04 \pm 0.01$, $n = 270$), GM (grass mixture; $\bar{x} = 0.40 \pm 0.02$, $n = 270$), NG (native warm-season grasses; $\bar{x} = 0.06 \pm 0.01$, $n = 270$), and SC (shrubland; $\bar{x} = 0.20 \pm 0.01$, $n = 270$). The abundance of Bell's Vireo ($\beta_{SC} = 5.04 \pm 1.14$; $\beta_{SC} = -5.37 \pm 1.54$ [two beta values indicate a quadratic relationship]), Prairie Warbler ($\beta_{SC} = 3.50 \pm 0.86$; $\beta_{SC} = -2.76 \pm 1.01$), and Field Sparrow ($\beta_{SC} = 0.78 \pm 0.16$) was positively related to percent SC cover, while the opposite was true for Henslow's Sparrow ($\beta_{SC} = -0.67 \pm 0.40$), Dickcissel ($\beta_{SC} = -2.59 \pm 0.73$; $\beta_{SC} = 2.70 \pm 1.01$), and Eastern Meadowlark ($\beta_{SC} = -4.90 \pm 1.46$; $\beta_{SC} = 4.05 \pm 2.25$). The abundance of Grasshopper Sparrow ($\beta_{GM} = 4.06 \pm 1.04$; $\beta_{GM} = -2.31 \pm 0.98$), Henslow's Sparrow ($\beta_{GM} = 4.53 \pm 0.97$; $\beta_{GM} = -3.02 \pm 0.94$), Dickcissel ($\beta_{GM} = 2.46 \pm 0.71$; $\beta_{GM} = -1.09 \pm 0.70$), and Eastern Meadowlark ($\beta_{GM} = 4.13 \pm 1.21$; $\beta_{GM} = -2.40 \pm 1.12$) was positively related to GM cover, but the opposite was true for Prairie Warbler ($\beta_{GM} = -1.29 \pm 0.33$). Northern Bobwhite abundance was positively related to percent NG ($\beta_{NG} = 0.59 \pm 0.26$), but negatively related to percent FO ($\beta_{FO} = -1.03 \pm 0.50$).

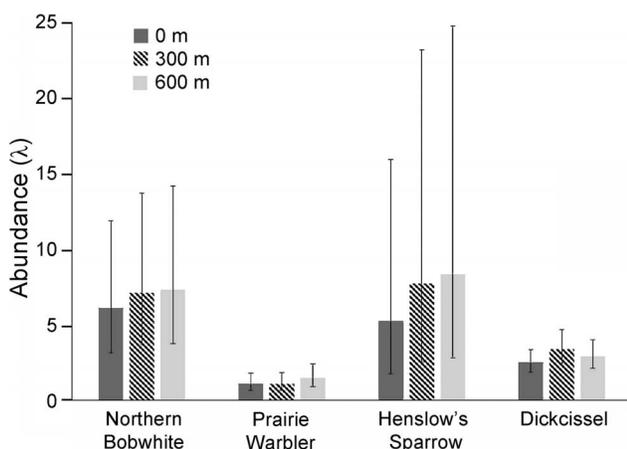


FIGURE 1. Species abundance (λ) values with 95% confidence intervals from models for on- and off-road point counts conducted in 2010 and 2011 in Fort Campbell Military Reservation, Kentucky–Tennessee, Peabody Wildlife Management Area, Kentucky, and Livingston County, Kentucky, USA.

DISCUSSION

Road ecology is a burgeoning field of research, and the various negative impacts of roads on wildlife, in particular birds, are well documented and expected to increase as global road systems expand (Forman et al. 2003, VanDer-Ree et al. 2015). Additionally, roads are being developed in remote areas in association with new energy infrastruc-

TABLE 3. Beta (β) values, standard errors (SE), and lower (LCL) and upper (UCL) 95% confidence limits from models for on- and off-road point counts conducted in 2010 and 2011 in Fort Campbell Military Reservation, Kentucky–Tennessee, Peabody Wildlife Management Area, Kentucky, and Livingston County, Kentucky, USA.

Species	0 m	SE	LCL	UCL	300 m	SE	LCL	UCL	600 m	SE	LCL	UCL
Northern Bobwhite	−0.18	0.11	−0.40	0.04	−0.03	0.10	−0.23	0.17	1.99	0.34	1.32	2.66
Prairie Warbler	−0.31	0.19	−0.69	0.06	−0.31	0.19	−0.69	0.06	0.31	0.29	−0.25	0.87
Henslow's Sparrow	−0.46	0.20	−0.86	−0.07	−0.08	0.19	−0.45	0.29	1.52	0.59	0.36	2.67
Dickcissel	−0.16	0.15	−0.45	0.13	0.15	0.14	−0.13	0.43	0.61	0.21	0.20	1.02

tures created for extraction, which can negatively affect bird abundance (Bayne et al. 2008, Kalyn Bogard and Davis 2014, Ludlow et al. 2015). However, there is the potential to use roads advantageously as a means to monitor wildlife. Contrary to some previous research (Reijnen and Foppen 1994, Hanowski and Niemi 1995, Griffith et al. 2010), we detected significant differences in abundance among distance-from-road categories only for Henslow's Sparrow. Additionally, the magnitude of the roadside effect for competing models for Northern Bobwhite, Prairie Warbler, and Dickcissel abundance was weak and small. Similarly, there was no evidence of a significant roadside bias on detection probability for any species. Detection probability was more affected by temporal variables than by the presence of a road.

For Henslow's Sparrow, abundance increased by 59% at points 600 m away from the road compared with points along the road or 300 m away from the road, although detection probability was very low (Figure 2), and Henslow's Sparrows were relatively rare at survey points. These conditions (low abundance and low detection probability) led to large, overlapping confidence intervals among distances, thus serving as a precaution against drawing any conclusion about Henslow's Sparrow roadside avoidance. Henslow's Sparrows are nomadic and have low site fidelity, which could explain the high degree of variation observed in our estimates (Dornak 2010).

Roadsides do not necessarily affect abundance, as evidenced by the 7 other species included in our analyses. Roadside and associated edge effects vary based on the species involved and the region or land-cover type (Rotenberry and Knick 1995, Reijnen et al. 1996, Keller and Scallan 1999, Forman et al. 2002, Ludlow et al. 2015). The relative abundance of 2 grassland bird species, Horned Lark (*Eremophila alpestris*) and Western Meadowlark (*Sturnella neglecta*), was not lower along roads in an open shrub-steppe landscape (Rotenberry and Knick 1995). In the eastern United States in a grassland-dominated matrix, apparent roadside survey effects were minimally negative for Eastern Meadowlark (*Sturnella magna*), Bobolink (*Dolichonyx oryzivorus*), and Red-winged Blackbird (*Agelaius phoeniceus*) relative abundances (Clark and Karr 1979, Forman et al. 2002). Similarly, the traffic volume of adjacent roads in conjunction with the size of fields and

amount of urbanization did not affect Eastern Meadowlark distribution (Forman et al. 2002).

The most influential variable related to abundance in our surveys was land cover. Species abundance was affected by changes in land cover among on- and off-road points, though land cover itself generally did not differ among distance-from-road categories. Had land cover differed among distance-from-road categories, then abundance could have been affected. Although Northern Bobwhite abundance was negatively related to percent forest cover, which differed among distance-from-road categories, this difference was not great enough to elicit a distance-from-road response in Northern Bobwhite abundance. Roadside surveys that incorporate these point-specific covariates will improve the accuracy of abundance parameter estimates. Similarly, spatial distribution models using on-road and off-road data can be comparable, and models that include land cover and detectability will improve the ability to account for variation in species occurrence or abundance (McCarthy et al. 2012). Roadside effects on abundance or detection probability not associated with land cover are often attributed to traffic disturbances related to noise inherent to the presence of roads (Reijnen et al. 1996, McClure et al. 2013).

Contrary to our a priori hypotheses, species-specific detection probabilities did not differ among on-road and off-road points. Unfortunately, we did not quantify noise associated with roadside surveys, though we expected that traffic noise inherent to roads could reduce species-specific detection probabilities (Hutto et al. 1995). Based on qualitative observations, road traffic was minimal; fewer than 10 vehicles drove past during the completion of a survey transect (30 min). Acoustic frequency for some species can shift in response to traffic noise levels, although low-traffic, rural roads may have a minimal effect on acoustic frequency shifts and detection probabilities (Parris and Schneider 2009, Griffith et al. 2010). Additionally, some species will adjust the rate at which they sing to compensate for noisy environments (Slabbekoorn and Peet 2003, Ríos-Chelén et al. 2015) or avoid noisy environments entirely (McClure et al. 2013). On BBS survey routes, 81% of species ($n = 37$) examined for song frequency differences had lower detection probabilities associated with greater road traffic volumes, which were

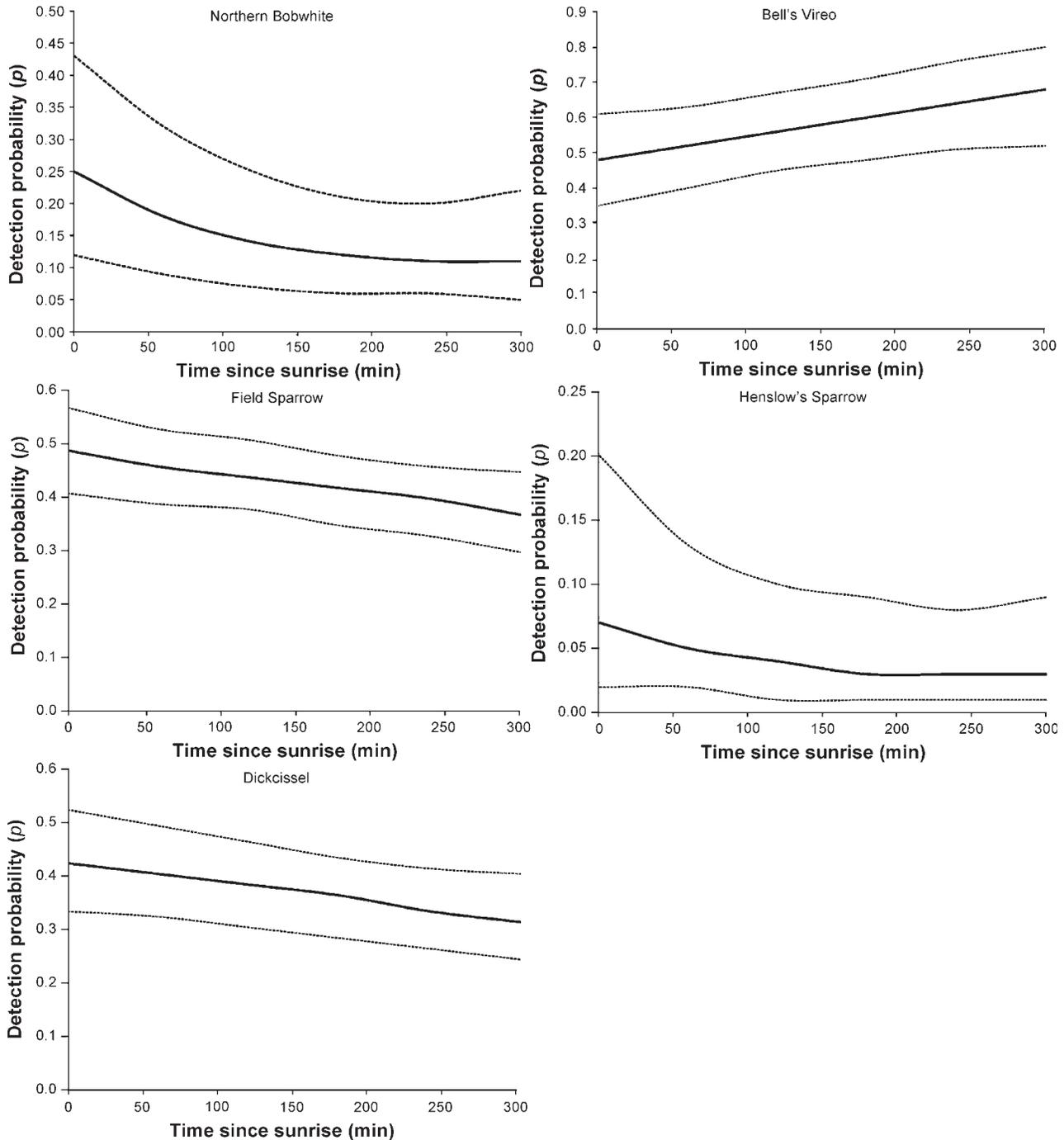


FIGURE 2. Time-since-sunrise effects with 95% confidence intervals on detection probability (p) from top models for on- and off-road point counts conducted in 2010 and 2011 in Fort Campbell Military Reservation, Kentucky–Tennessee, Peabody Wildlife Management Area, Kentucky, and Livingston County, Kentucky, USA.

assumed to be associated with roadside noise (Griffith et al. 2010).

Another factor potentially influencing detection probability is observer hearing ability along roads, especially on roads with high traffic volumes. Griffith et al. (2010) determined that observer-specific detection probabilities

consistently declined along roads, but the magnitude of the effect was small. Our intent to mimic BBS survey design by selecting rural, secondary roads for surveys did not capture the full range of roadside effects, especially effects related to greater traffic volumes. Undoubtedly there is a noise threshold at which observer hearing becomes impaired in a

roadside-based survey, thus effectively reducing detectability.

Most previous research has defined “off-road” points to be between 200 m and 400 m from the nearest road (Hanowski and Niemi 1995, Keller and Fuller 1995, Rotenberry and Knick 1995, Keller and Scallan 1999, McCarthy et al. 2012). Low traffic volume on secondary roads can be audible up to 100 m away, and noise from high traffic volumes can be audible up to 560 m from the road (Reijnen et al. 1996). Eurasian Skylark (*Alauda arvensis*) breeding density in an agricultural landscape was negatively affected by road noise from rural roads extending up to 100 m from low volume traffic ($\leq 5,000$ cars per day) and 490 m for high volume traffic ($\geq 50,000$ cars per day; Reijnen et al. 1996). Noise effects from roads may extend farther into the habitat in grasslands than in forested landscapes, because grasslands lack dense vegetation to attenuate background noise (Reijnen et al. 1996). Our farthest off-road point on each transect was 600 m from the nearest road. As a result, our experimental design was appropriate for assessing large-scale roadside effects. More localized effects (i.e. within 100 m) may have been missed by our survey design.

Differences in species-specific detection probabilities based on interspecific differences in breeding phenology can affect population parameter estimates (Wilson and Bart 1985); only Prairie Warbler and Grasshopper Sparrow detection probabilities were not significantly affected by time since sunrise, and only Field Sparrow, Henslow’s Sparrow, and Eastern Meadowlark detection probabilities were not significantly affected by date. In Denali National Park and Preserve, Alaska, USA, passerine detection probabilities were significantly affected by seasonal phenological shifts, and peak detection probabilities did not overlap among species (Schmidt et al. 2013). Clearly, population parameter adjustments based on detection probabilities need to include a within-season and within-day temporal component (Schmidt et al. 2013). We recommend either that surveys be explicitly designed for a species of interest and target its periods of peak detectability or that surveys continue to account for species-specific temporal shifts in detection probabilities for the duration of a survey by including year and day-of-year covariates.

We also documented annual differences in detection probability for 4 of our 8 target species, the most dramatic being for Eastern Meadowlark (detection probability in 2011 was 700% greater than in 2010) and Henslow’s Sparrow (200% greater detection probability in 2010 than in 2011). The magnitude of the difference between years for Field Sparrow and Grasshopper Sparrow was generally small (<65%). Though we did not directly evaluate causes of annual differences in detection probability, our observed results could reflect yearly fluctuations in the phenology of

singing behavior among individuals, or could be spurious effects as a result of small samples sizes and low detection incidences. Alternatively, annual differences in detection probabilities could be due to geographical variability among sites or annual population movements and nomadism (Dornak et al. 2013). The detection process is a function of bird singing behavior, observer ability, and local environmental conditions for sound transmission (Riddle et al. 2010). Because the same observer conducted >90% of the counts and environmental conditions were generally the same between years, the annual differences in detection probabilities were likely linked to changes in bird singing behavior as a result of geographical variation in breeding phenology.

Our results suggest that roadside surveys for grassland birds are not necessarily biased. Our surveys along low-traffic-volume secondary roads appeared to be largely unaffected by the presence of the road or the associated traffic noise (with the exception of Henslow’s Sparrow surveys). Hierarchical models in which sample and process variability are modeled simultaneously (Royle and Dorazio 2008) should also include careful consideration of spatially explicit covariates that could affect abundance along a roadside survey. It is also necessary to account for temporal and observational variables when modeling detection probability (Sauer et al. 1994, Schmidt et al. 2013). If land-cover and temporal effects are accounted for, then occupancy, abundance, or density estimates generated from roadside surveys should be representative of areas beyond roads. For the species in the grasslands where we worked, a roadside-based survey design can be used to effectively monitor abundance.

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Ethics statement: This study was purely observational. Because we did not attempt to approach our study animals nor to modify their behavior in any way, we did not have an IACUC protocol.

Author contributions: C.M.L. conceived the idea, design, experiment (supervised research, formulated question or hypothesis), performed the experiments (collected data, conducted the research), and analyzed the data; and C.M.L. and D.A.B. wrote the paper (or substantially edited the paper), developed or designed methods, and contributed substantial materials, resources, or funding.

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