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EFFECTS OF FOREST MANAGEMENT ON DENSITIES AND NEST SURVIVAL OF BREEDING BIRDS IN UPLAND HARDWOOD ECOSYSTEMS

Michael Barnes
Pittsburg State University, mwbarnes@gus.pittstate.edu

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EFFECTS OF FOREST MANAGEMENT ON DENSITIES AND NEST SURVIVAL OF BREEDING BIRDS IN UPLAND HARDWOOD ECOSYSTEMS

A Thesis Submitted to the Graduate School
in Partial Fulfillment of the Requirements
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Master of Science

Michael Wade Barnes

Pittsburg State University

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EFFECTS OF FOREST MANAGEMENT ON DENSITIES AND NEST SURVIVAL OF BREEDING BIRDS IN UPLAND HARDWOOD ECOSYSTEMS

Michael Wade Barnes

APPROVED:

Thesis Advisor: ______________________________
Dr. Andrew George, Department of Biology

Committee Member: ______________________________
Dr. Neil Snow, Department of Biology

Committee Member: ______________________________
Dr. Ananda Jayawardhana, Department of Mathematics

Committee Member: ______________________________
Dr. Paul Porneluzi, Central Methodist University,
Department of Biology

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EFFECTS OF FOREST MANAGEMENT ON DENSITIES AND NEST SURVIVAL OF BREEDING BIRDS IN UPLAND HARDWOOD ECOSYSTEMS

An Abstract of the Thesis by
Michael Wade Barnes

Over the past 50 years, significant declines in 47% of Neotropical migrant bird species have been documented in North America. Declines are most likely due to the loss and fragmentation of breeding, wintering, and stopover habitat mainly caused by agriculture and urban development. This loss of critical habitat results in population sinks that need to be maintained by immigration from a population source found in continuously forested landscapes. However, in landscapes harvested for timber, forest management practices alter the landscape and as a result, affect breeding bird abundances and nest survival. The objective of our study was to determine the effects that forest management has on the densities and nest success of breeding birds. Territory density and nest survival data were compiled from nine landscape-scale experimental forest plots in the Ozark Highlands region of southeast Missouri. We fit linear mixed models of the relationships between territory densities and predictor variables that represented habitat structure, silvicultural treatment type, and time period. We also fit generalized linear models of the relationship between nest success and predictor variables that represented edge density, silvicultural treatment type, time period, nest stage, and day of season. For territory densities, we found support for models that included habitat structure, time period, and silvicultural treatment as predictors of seven focal species. Mature-forest species typically responded to habitat structure, whereas shrubland species responded to prescribed silvicultural treatment. For nest success, we found support for models that included edge density, time period, nest stage, and day of season for Acadian flycatcher and indigo bunting nest survival. Acadian flycatcher nest success decreased with increases in edge density. Our findings demonstrate that forest management affects abundances and nest success and that habitat structure variables and edge effects should be considered when managing breeding birds in upland hardwood ecosystems.

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AVIAN RESPONSE TO HABITAT STRUCTURE AND EXPERIMENTAL FOREST MANAGEMENT IN UPLAND HARDWOOD ECOSYSTEMS

Introduction

Forests provide many ecosystem services including wood production, carbon sequestration, and preservation of biodiversity (Duncker et al. 2012). Forest management is a tool that can be used to maintain ecosystem services for the benefit of people and the environment. Balancing the needs of people with the needs of the wildlife that rely on managed forests to survive influences forest management decisions (Kohm and Franklin 1997). Therefore, understanding how forest management practices affect wildlife populations is crucial to conservation efforts. Knowledge gained from forest management studies allows for the integration of wildlife conservation and forest management, thus allowing for more informed decisions (Miller et al. 2009).

The effects of forest management on breeding bird densities have been studied extensively (reviewed by Thompson et al. 1995, Sallabanks and Arnett 2005). Species-specific responses to forest management vary across regions and spatial scales (Millington et al. 2011, Kendrick et al. 2015, Nolet et al. 2018). Mature-forest species typically respond negatively to even-aged management, whereas shrubland species often respond positively to both even-aged and uneven-aged management practices (Morris et al. 2013, Perry and Thill 2013, Perry et al. 2018). However, recent studies have found that species that prefer mature forests use habitat created by even-aged management practices, suggesting that they have more diverse habitat requirements than traditionally recognized (Porneluzi et al. 2014, Demarais et al. 2017, Perry et al. 2018). The habitat requirements of forest bird species can be dynamic and change over an individual's lifetime (Anders et al. 1998, Alterman et al. 2005, Vitz and Rodewald 2006, Wallendorf et al. 2007). Therefore a combination of management practices is needed to provide habitat for species with diverse habitat requirements.

Habitat structure can be useful in predicting wildlife abundances, acting as a proximate and ultimate factor of habitat selection (Rotenberry and Wiens 1980, Bakermans and Rodewald, 2009, Di Stefano et al. 2011, Bakermans et al. 2012, Sitters et al. 2014). Habitat structure, including canopy cover, canopy height, vegetation volume (or visual obstruction), plant species composition and density, influences densities of breeding birds (Beedy 1981, James and Wamer 1982, Lynch and Whigham 1984, Swift et al. 1984, Mills et al. 1991, Bakermans et al. 2012). Habitat structure influences the availability of food, shelter, nesting, predation, and competition (Beese and Bryant 1999, Rodewald and Yahner 2000, Brawn et al. 2001). Many studies include canopy variables when describing the effects of habitat structure. Our study used remaining basal area that can be a suitable surrogate for canopy measurements (Mitchell and Popovich 1997, Jennings et al. 1999, Sonohat et al. 2004, Raptis et al. 2018). Using prescribed silvicultural treatments to manage bird densities does not account for residual structures such as coarse woody debris, spatial structure, and the high variability in the development of forest stands (Franklin et al. 2002). Several interrelated factors including climatic factors, topography, forest management practice and intensity, and land-use change, influence structural development of forests (Kane et al. 2015, Gatti et al. 2015, Clark et al. 2016, Holmes and Matlack 2017, Jucker et al. 2018). Conclusions on the effects of forest management on breeding birds can be difficult to make when using prescribed silvicultural treatments to predict densities due to the variability in this structural development. Directly measuring habitat factors will account for variability in the development of stands following harvest.

Uncertainty remains regarding how forest management affects breeding bird populations. Studies examining the effects of forest management on birds are inherently complex in design due to different silvicultural practices used within the same experimental framework and confounding effects such as landscape effects. These complexities are only amplified by the difficulty of conducting large-scale, long-term manipulative experiments in an ecological setting. Also, responses typically are species-specific and variable, making it difficult to make broad conclusions on breeding forest birds as a group (Thompson et al. 2000).

Studies examining the effects of forest management practices on the densities of breeding birds generally use prescribed silvicultural treatments as predictors of abundances, rather than the change in habitat structure resulting from treatments (Kendrick et al. 2015, Kellner et al. 2016, Margenau et al. 2018). However, several studies have concluded that the spatial scale should be considered at multiple levels to address relationships between breeding birds and the habitat that they occupy (Vergara and Armesto 2009, Richmond and Burke 2012, Shew et al. 2019). For example, wood thrush (*Hylocichla mustelina*) densities in the Prairie Hardwood Transition showed different responses to an index of wetness at varying spatial scales (Thogmartin and Knutson 2007). Wood thrush densities decreased at fine (800 ha) and coarse (80,000 ha) scales but increased at an intermediate scale (8,000 ha). Therefore, analyses on the densities of breeding birds should include multiple scales.

Initiated in 1989 by the Missouri Department of Conservation, the Missouri Ozark Forest Ecosystem Project (MOFEP) is a long-term, large-scale experiment that is testing, in part, the effects of even-aged and uneven-aged forest management on breeding bird densities in upland hardwood forests (Knapp et al. 2014). In general, previous MOFEP studies have examined the effects of forest management at the landscape scale but did not account for stand-level characteristics such as habitat structure (Clawson et al. 2000, Gram et al. 2003, Morris et al. 2013). However, one stand-level analysis has been conducted (Kendrick et al. 2015). However, our analysis included an additional round of harvest compared to Kendrick et. al. Within the MOFEP framework, bird densities and habitat structure variables are measured before and after prescribed silvicultural treatments have been applied to a portion of forest stands. Overall, MOFEP studies have found declines in mature-forest species and increases in shrubland species following harvest with greater responses on even-aged sites then uneven-aged sites. Effects were also found in the no-harvest sites adding complexity to the interpretation of results.

The objective of our study was to compare the effects of habitat structure and prescribed silvicultural treatment on breeding bird densities. Understanding the relationship between on-the-ground habitat structure (basal area, stem density, and heterogeneity) and breeding bird densities may lead to a mechanistic understanding of how bird densities change over time in response to forest management. Therefore, we examined the effects of habitat structure (basal area, structural heterogeneity, and stem density) following harvest on breeding bird densities using 14 years of stand-level data. We predicted that habitat structure would be a better predictor of breeding bird densities than prescribed silvicultural treatments. Habitat structure is the underlying mechanism of forest management and can account for the variability in stand development that landscape-level factors cannot.

Study Area

The MOFEP study area is located in Carter, Reynolds, and Shannon Counties, in the Ozark Highlands region of southeast Missouri. The region is approximately 84% forested comprising oak (*Quercus* spp.)-hickory (*Carya* spp.) and oak-pine (*Quercus-Pinus* spp.) forests, oak savannas, bluestem (*Andropogon-Schizachyrium* spp.) prairies, and glades (Brookshire and Shifley 1997). At the beginning of the project, most overstory trees were 50-70 years old. However, all sites contained trees older than 100 years (Shifley and Brookshire, 2000). Over the past 300 years, the region has been exposed to many natural and anthropogenic disturbances, such as fire, logging, and agriculture. Before MOFEP, the land was managed primarily for timber (Guyette and Larsen 2000).

Methods

Experimental Design

The MOFEP study area was divided into 9 sites that averaged 400 ha (Fig. 1.1). Sites were assigned 1 of 3 management treatments: even-aged management, uneven-aged management, or no-harvest. Each site includes 36–74 stands ranging from 0.16 to 62 ha. Stands were classified by ecological land type, slope, and aspect (Fig. 1; Brookshire and Shifley, 1997). Harvested sites had a re-entry period of 15 years on a 100-year rotation with approximately 10–15% of the total forested area removed during each harvest. All stands were assigned the silvicultural treatment they received during the first harvest in 1996: clearcut, single-tree selection, group-selection, intermediate harvest (thinning and timber stand improvement (TSI)), or no-harvest. Clearcut sites were accompanied by forest thinning to promote the growth of residual trees. In uneven-aged site treatments, single-tree and group-selection cuts were applied to 41–69% of each site. Approximately 10% of both even-aged and uneven-aged sites were designated as "old growth" stands and would not be cut for the duration of the 100-year study See Brookshire and Shifley, (1997) for additional details on experimental design.

Bird Densities

Densities of breeding birds were estimated using the spot-mapping technique (Svensson et al. 1970) before the initial harvest (1991–1995), after the initial harvest (1997–2003; 2008–2011), and after the second harvest (2012–2014). From mid-May through the end of June, we surveyed for birds at each site for 3-4 hours, 5 mornings per week. For surveys, sites were divided into 7 subplots. All 7 subplots were surveyed before 2001, and a subset of 4 subplots was surveyed from 2001 to 2014. Each subplot was sampled 8–10 times at 2–3-day intervals. Trained observers were rotated to reduce observer bias. All observations of singing males were recorded on a topographic map of each subplot and territories were designated when at least 3 clustered observations were observed on 3 separate dates. Territories were also identified by counter-singing males and the presence of nests.

Once territories were identified, the densities of each species were calculated by dividing the number of territories by the area of the stand that was sampled. Following the methods of Kendrick et al. (2015), partial stands that were split by plot boundaries and stands < 2.89 ha were removed based on the minimum average territory size reported for ovenbirds (*Seiurus aurocapilla*). Ovenbirds have the largest territories of the focal species (Porneluzi and Faaborg 1999).

Vegetation Surveys

Within the MOFEP study area were 648 permanent vegetation plots randomly located with the requirement that each stand received at least 1 plot. Vegetation plots measured 0.2 ha in size and included 4 subplots measuring 0.02 ha. Within each 0.2 ha plot, trees measuring ≥ 11.4 cm diameter at breast height (DBH) were recorded. Within each 0.02 ha subplot, trees measuring between 3.8 cm to 11.4 cm were recorded.

Stem density was calculated by dividing the total number of stems by plot area (0.2 ha). Stem density per stand was calculated by averaging tree density across stands. Basal area (BA; ft^2/ac) and structural heterogeneity were both calculated from DBH measurements. Structural heterogeneity was calculated as the standard deviation of DBH to show variation in tree sizes within a stand.

Statistical Analysis

Eleven focal species were included in the analysis based on abundances and detectability. Seven of the 11 species were classified as mature-forest species: Acadian flycatcher (*Empidonax virescens*), black-and-white warbler (*Mniotilta varia*), eastern wood-pewee (*Contopus virens*), Kentucky warbler (*Geothlypis formosa*), ovenbird, worm-eating warbler (*Helmitheros vermivorum*), and wood thrush. The remaining 4 were classified as shrubland species: hooded warbler (*Setophaga citrina*), indigo bunting (*Passerina cyanea*), prairie warbler (*Setophaga discolor*), and yellow-breasted chat (*Icteria virens*).

We fit linear mixed models for each focal species on the relationship between territorial densities and habitat structure, time period, and treatment type. Data were separated into four time periods: pre-harvest (1992–1995), early post-harvest (1997–2002), late post-harvest (2008–2010), and post-second-harvest (2012–2013). Year and site were designated as nested random effects in all models to account for potential non-independence of data collected within the same sites and years. Thirty-three models were fit for each species representing different combinations of habitat structure, treatment type, and time period. All analyses were performed in R (R Core Team Version 3.5.1) using the package lme4 with the lmer function (Bates et al. 2015). Akaike's Information Criterion (AIC) was used to select the best-supported models for each species (Burnham and Anderson 2002). The model with the lowest AIC values and a delta AIC of < 2 was chosen as the best-supported model. Conditional R-squared (R^2_c) values were reported to show variance explained by fixed and random effects (Nakagawa and Schielzeth, 2013).

Results

A total of 11,303 territories across eleven focal species were included in our analyses. The total number of territories identified per year ranged from 2,395 in 1992 to 1,263 in 2010 (Table 1.1). By species, territories ranged from 70 for prairie warblers to 2947 for Acadian flycatchers. A total of 358,722 trees were measured and used to calculate basal area, stem density, and structural heterogeneity. Following initial harvest, basal area and stem density were highest in intermediate harvest stands, whereas heterogeneity was highest in clearcut stands. Before the second harvest, basal area and stem density remained highest in intermediate harvest stands, and heterogeneity was highest in uneven-aged stands. Overall, basal area and stem density of treated stands declined from 1992 to 2013 while heterogeneity increased (Table 1.1).

We found support for models that included habitat structure, time period, and silvicultural treatment as predictors of densities of seven focal species (Table 2.1, 3.1). The best-supported models for four species included habitat structure variables solely, whereas the best-supported models for the remaining three included time period and treatment variables.

The best-supported model for the Acadian flycatcher included a quadratic relationship with basal area (Fig. 2.1a). The best-supported model predicted that densities would be lowest at low and high basal area with the highest densities at approximately 40 ft^2/ac basal area. The best-supported model for black-and-white and hooded warblers included a negative relationship with basal area (Fig. 2.1b), in which bird densities declined with increasing basal area. The best-supported model for the eastern wood-pewee included a positive relationship with basal area and a negative relationship with stem density and heterogeneity (Fig. 2.1d,e,f). In this case, bird densities increased with increasing basal area and declined with increasing stem density and heterogeneity.

The best-supported models for the indigo bunting, prairie warbler, and yellow-breasted chat included an interactive effect between time period and treatment type. The densities of indigo buntings in clearcut stands, were low in the pre-harvest period, spiked in the early post-harvest period, declined in the late post-harvest period, and increased following the second harvest in 2011 (Fig. 3.1). Trends were similar for the densities of indigo buntings in intermediate harvest and uneven-aged management stands. The remaining combinations of time period and treatment type (leave, no-harvest, and old growth) showed little effect on the densities of indigo buntings. The densities of prairie warblers in clearcut stands showed similar responses (Fig. 4.1), being low in the pre-harvest period, declining in the late post-harvest period, and increasing following the second harvest. However, the remaining treatment types showed little effect. The responses of yellow-breasted chats were similar to indigo buntings (Fig. 5.1). Their densities in clearcut stands increased from the pre-harvest period to the early post-harvest period, declined in the late post-harvest period, and increased following the second harvest. Responses in intermediate harvest and uneven-aged management stands were similar to indigo bunting responses.

Discussion

Habitat structure can help account for variability in responses found at the landscape-level and should be incorporated into further studies on forest management and its effect on breeding bird densities. In general, studies analyzing the effects of forest management practices on the densities of breeding birds have relied on prescribed silvicultural treatments as their explanatory variables. However, such studies did not explain the mechanisms by which changes in densities occurred. Our findings demonstrate that habitat structure can be a more reliable predictor of densities in breeding birds than silvicultural treatment across time. Therefore, managing for structural characteristics should be taken into consideration in conservation and restoration efforts.

Several studies have evaluated the relationship between habitat structure and breeding bird populations in managed forests focusing on canopy openness, canopy cover, and canopy closure as their predictor variables (Bakermans and Rodewald 2009, Bakermans et al. 2012, Newell and Rodewald 2012, Richmond and Burke 2012, Bouvet et al. 2016). Responses are typically species-specific and reveal the complex relationships between local- and landscape-level metrics and breeding bird populations that occupy managed landscapes. As a result, studies have suggested multiscale approaches to avian management in managed forests. Our findings are consistent with other studies examining the effects of habitat structure on breeding bird densities. Results of our study demonstrated that habitat structure plays an important role in predicting breeding bird densities. Responses were species-specific, and a multiscale approach might prove the best course of action to quantify the effects of forest management on breeding bird populations.

As predicted, species responded to habitat structure. All species with habitat structure as their best-supported model contained basal area as a primary determinant of density. However, responses varied among species. Differences in nesting behavior and life histories strategies could be a potential explanation for these variable relationships.

Acadian flycatcher densities were highest at intermediate basal areas. A relationship potentially explained by the fact that Acadian flycatchers nest and forage in midstory canopies of mature forests (Allen et al. 2017). Midstory canopies can be dominant in mature forests occupying more leaf area than other canopies (Parker and Russ 2004).

Black-and-white warbler densities were highest in stands with low basal area. Their abundances have been associated with understory and shrub densities within mature tracts of even-aged forest stands (Yahner 1986), and their nests are often built on the ground against shrubs and trees (Kricher 2014).

Eastern wood-pewee densities were highest at high basal area, low stem density, and low heterogeneity. Eastern wood-pewees use more open woodland with large diameter trees, clear understory, and high and open canopy cover for nesting (Reidy et al. 2014).

Densities of hooded warblers were highest in stands with low basal area. Hooded warblers are known as "gap specialists," wherein they use gaps within forest tracts as well as edge habitat. Small gaps created by intermediate harvests and uneven-aged management create the low basal area and dense shrub cover where hooded warblers nest (Chiver and Stutchbury 2011).

Prescribed silvicultural treatments were better predictors of the densities for three species. Responses were similar to previous MOFEP studies analyzing the effects of forest management on breeding bird densities (Morris et al. 2013, Kendrick et al. 2015).

The indigo bunting, prairie warbler, and yellow-breasted chat showed substantial increases in densities following clearcuts, as expected for shrubland species. This result is consistent with other studies, corroborating previous evidence that shrubland species generally peak within 2–5 years of harvest and begin to decline around 10 years post-harvest (Twedt and Somershoe 2009, Kendrick et al. 2015). Densities of shrubland species increased following the second harvest, but at a lower magnitude than the initial harvest. This relationship could be attributed to early post-harvest having more data (5 years) than post-second-harvest (2 years), but more data are needed to confirm this hypothesis. Indigo bunting densities in intermediate harvest and uneven-aged management stands resembled those of clearcut stands, but at a lower magnitude.

Indigo buntings use early-successional, edge, and mature forest habitat (Alterman et al. 2005). Small gaps in the canopy of mature forest allow for the understory development that creates potential nesting habitat for indigo buntings.

The results of our study revealed an interesting trend. With the exception of hooded warblers, all species with best-supported models including habitat structure are considered mature-forest species. As for shrubland species, all best-supported models included prescribed silvicultural treatment with the exception of hooded warblers. As a gap specialist, hooded warblers require openings with shrubland habitat surrounded in close proximity by mature forest. This trend may suggest that mature-forest species are more selective in the habitat that they choose as compared to shrubland species.

Overall, habitat structure models were better predictors of breeding bird densities than silvicultural treatment models for the majority of models that were supported. The results of this study show that it is important to incorporate habitat structure variables when analyzing breeding bird densities. Solely using silvicultural treatment across time to predict densities allows for variability that cannot be accounted for and does not address the underlying mechanisms that drive the densities of breeding birds. Therefore, a multiscale approach might prove beneficial to make up for any shortcomings from analyzing at a single scale.

Management Implications

To create habitat for the greatest number of species, managers could use forest management to alter habitat structure directly. Maintaining intermediate basal areas (approximately 40 ft^2/ac) could promote densities of Acadian flycatchers, black-and-white warblers, and hooded warblers by promoting large diameter trees with a well-developed understory to meet the habitat requirements of these species. For eastern wood-pewee, low levels of stem density and heterogeneity should be maintained by removing midstory and understory trees creating the open woodlands that eastern wood-pewees prefer. Within the current MOFEP framework, harvests occur on a 15-year rotation. From the results of our study, managers could reduce the rotation to 10 years or less to promote greater densities of indigo buntings, prairie warblers, and yellow-breasted chats.

Our findings suggest that manipulation of habitat structure may provide habitat for a variety of species. Species-specific responses described in our study should be considered when making appropriate management decisions. We demonstrate that knowledge of vegetation characteristics can be used to enhance classic silvicultural systems. Local-level, vegetation measures can be used in conjunction with landscape-level management to more accurately manage for breeding birds.

Table 1.1. Summary statistics of habitat structure variables and bird territories for prescribed silvicultural treatments (n = 21,450). $\bar{x}$ = mean of vegetative variable. SD = standard deviation.

Treatment	Year	Territories	Basal Area		Stem Density		Heterogeneity	
			$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Clearcut	1992	104	43.50	3.89	362.63	87.46	4.43	0.56
	1995	111	47.35	4.25	374.87	89.01	4.52	0.55
	1998	173	8.57	5.98	105.95	99.79	4.22	3.48
	2002	28	6.06	4.23	42.01	45.38	5.84	2.71
	2010	52	7.81	4.08	146.41	73.02	2.72	1.71
	2013	61	6.75	4.29	29.85	19.13	5.07	2.18
Intermediate harvest	1992	92	45.27	6.57	440.44	95.35	4.01	0.75
	1995	129	49.64	6.74	456.30	95.32	4.12	0.75
	1998	90	34.39	9.00	364.52	104.98	3.59	0.83
	2002	92	35.80	7.31	355.83	77.94	3.72	0.78
	2010	87	43.09	8.22	387.77	73.00	4.05	0.66
	2013	122	33.48	6.64	263.23	63.40	4.72	0.84
Leave	1992	607	40.99	7.91	398.08	104.78	4.04	0.80
	1995	663	45.02	8.58	404.26	104.65	4.16	0.75
	1998	466	42.56	7.42	384.20	98.30	4.18	0.82
	2002	345	43.15	5.98	361.12	88.38	4.39	0.78
	2010	345	46.49	7.11	362.66	86.72	4.57	0.79
	2013	525	38.73	13.92	348.42	97.44	3.98	1.07

Treatment	Year	Territories	Basal Area		Stem Density		Heterogeneity	
			$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
No-harvest	1992	776	46.06	6.62	427.00	94.55	3.89	0.86
	1995	857	49.78	6.74	433.31	93.58	4.03	0.85
	1998	585	46.94	6.21	402.06	98.38	4.17	0.85
	2002	334	46.10	6.43	377.54	94.01	4.34	0.84
	2010	380	48.17	7.34	367.45	85.74	4.68	0.86
	2013	486	48.30	7.97	356.13	80.77	4.79	0.88
Old growth	1992	349	42.91	7.16	383.78	73.43	4.13	0.70
	1995	404	46.22	7.54	387.78	74.15	4.24	0.71
	1998	294	43.62	7.74	368.26	84.60	4.34	0.67
	2002	38	43.03	6.72	341.90	74.15	4.46	0.38
	2010	57	46.43	6.32	333.21	62.04	4.97	0.55
	2013	49	47.06	7.46	373.36	54.83	4.65	0.74
Uneven-aged management	1992	467	44.61	6.66	416.41	77.31	3.88	0.67
	1995	432	47.82	6.95	421.44	80.43	4.03	0.64
	1998	419	32.50	8.38	304.86	89.16	3.73	0.54
	2002	385	33.27	8.54	298.37	94.72	3.93	0.62
	2010	342	39.40	9.18	322.55	86.09	4.26	0.58
	2013	457	32.87	9.48	256.72	89.44	4.57	0.78

Table 1.2. AIC results for breeding bird densities in the Missouri Ozark Forest Ecosystem Project. The model parameters are described in the text. Models include a combination of habitat structure (basal area, stem density, and heterogeneity), treatment type, and years since harvest. *K* = number of parameters in each model. w_i = weight of evidence for models. R^2_c = model validation metric explaining variance of fixed and random effects.

Species	**Model**	**k**	w_i	R^2_c
Acadian flycatcher	Basal area^2	6	0.96	0.14
Black-and-white warbler	Basal area	5	0.62	0.15
Eastern wood-pewee	Basal area + Stem density + Heterogeneity	7	0.97	0.18
Hooded warbler	Basal area	5	0.89	0.37
Indigo bunting	Period × Treatment	27	0.98	0.38
Prairie warbler	Period × Treatment	27	0.99	0.39
Yellow-breasted chat	Period × Treatment	27	0.99	0.37

Table 1.3. Estimated coefficients for best-supported models of 7 focal species. Significant effects are in bold.

Species	Parameter	Coefficient	Standard Error	Lower 95% CI	Upper 95% CI
Acadian flycatcher	Intercept	-0.01	0.05	-0.11	0.09
	Basal area	**0.01**	**0.002**	**0.006**	**0.014**
	Basal area^2	**-0.0002**	**0.00003**	**-0.0003**	**-0.0001**
Black-and-white warbler	**Intercept**	**0.13**	**0.02**	**0.09**	**0.17**
	Basal area	**-0.002**	**0.0003**	**-0.003**	**-0.0014**
Eastern wood-pewee	**Intercept**	**0.19**	**0.03**	**0.13**	**0.25**
	Basal area	**0.004**	**0.0005**	**0.003**	**0.005**
	Stem density	**-0.0004**	**0.00005**	**-0.0005**	**-0.0003**
	Heterogeneity	**-0.03**	**0.005**	**-0.04**	**-0.02**
Hooded warbler	**Intercept**	**0.07**	**0.02**	**0.03**	**0.11**
	Basal area	**-0.001**	**0.0002**	**-0.0014**	**-0.0006**
Indigo bunting	Intercept	0.02	0.03	-0.04	0.08
	Early post-harvest	**0.56**	**0.04**	**0.48**	**0.64**
	Late post-harvest	-0.01	0.05	-0.11	0.09
	Post second-harvest	**0.25**	**0.05**	**0.15**	**0.35**
	Intermediate harvest	-0.009	0.03	-0.07	0.05
	Leave	0.002	0.02	-0.04	0.04
	No-harvest	0.002	0.02	-0.04	0.04

Species	Parameter	Coefficient	Standard Error	Lower 95% CI	Upper 95% CI
	Old growth	0.003	0.03	-0.06	0.06
	Uneven-aged management	-0.001	0.03	-0.06	0.06
	Early post-harvest × Intermediate harvest	**-0.34**	**0.04**	**-0.42**	**-0.26**
	Early post-harvest × Leave	**-0.55**	**0.04**	**-0.63**	**-0.47**
	Early post-harvest × No-harvest	**-0.56**	**0.05**	**-0.66**	**-0.46**
	Early post-harvest × Old growth	**-0.56**	**0.04**	**-0.64**	**-0.48**
	Early post-harvest × Uneven-aged management	**-0.34**	**0.04**	**-0.42**	**-0.26**
	Late post-harvest × Intermediate harvest	0.01	0.05	-0.09	0.10
	Late post-harvest × Leave	0.01	0.05	-0.09	0.11
	Late post-harvest × No-harvest	-0.004	0.06	-0.12	0.11
	Late post-harvest × Old growth	-0.005	0.06	-0.12	0.11
	Late post-harvest × Uneven-aged management	0.02	0.05	-0.08	0.12
	Post second-harvest × Intermediate harvest	-0.06	0.05	-0.16	0.04
	Post second-harvest × Leave	**-0.23**	**0.04**	**-0.31**	**-0.15**
	Post second-harvest × No-harvest	**-0.25**	**0.06**	**-0.37**	**-0.13**
	Post second-harvest × Old growth	**-0.21**	**0.05**	**-0.31**	**-0.11**
	Post second-harvest × Uneven-aged management	**-0.12**	**0.05**	**-0.22**	**-0.02**
Prairie warbler	Intercept	0.0004	0.007	-0.01	0.01
	Early post-harvest	**0.25**	**0.01**	**0.23**	**0.27**
	Late post-harvest	-0.0004	0.01	-0.02	0.02
	Post second-harvest	**0.16**	**0.01**	**0.14**	**0.18**
	Intermediate harvest	-0.00004	0.008	-0.02	0.02
	Leave	0.002	0.007	-0.01	0.02
	No-harvest	0.003	0.007	-0.01	0.02

Species	Parameter	Coefficient	Standard Error	Lower 95% CI	Upper 95% CI
	Old growth	-0.0005	0.008	-0.02	0.02
	Uneven-aged management	-0.0005	0.007	-0.01	0.01
	Early post-harvest × Intermediate harvest	**-0.26**	**0.01**	**-0.28**	**-0.24**
	Early post-harvest × Leave	**-0.26**	**0.01**	**-0.28**	**-0.24**
	Early post-harvest × No-harvest	**-0.26**	**0.01**	**-0.28**	**-0.24**
	Early post-harvest × Old growth	**-0.26**	**0.01**	**-0.28**	**-0.24**
	Early post-harvest × Uneven-aged management	**-0.25**	**0.01**	**-0.27**	**-0.23**
	Late post-harvest × Intermediate harvest	0.00004	0.02	-0.04	0.04
	Late post-harvest × Leave	-0.002	0.01	-0.02	0.02
	Late post-harvest × No-harvest	-0.003	0.01	-0.02	0.02
	Late post-harvest × Old growth	0.0005	0.02	-0.04	0.04
	Late post-harvest × Uneven-aged management	0.00005	0.01	-0.02	0.02
	Post second-harvest × Intermediate harvest	**-0.15**	**0.02**	**-0.19**	**-0.11**
	Post second-harvest × Leave	**-0.15**	**0.01**	**-0.17**	**-0.13**
	Post second-harvest × No-harvest	**-0.16**	**0.01**	**-0.18**	**-0.14**
	Post second-harvest × Old growth	**-0.16**	**0.01**	**-0.18**	**-0.14**
	Post second-harvest × Uneven-aged management	**-0.16**	**0.01**	**-0.18**	**-0.14**
Yellow-breasted chat	Intercept	0.0001	0.01	-0.02	0.02
	Early post-harvest	**0.37**	**0.02**	**0.33**	**0.41**
	Late post-harvest	-0.0001	0.02	-0.04	0.04
	Post second-harvest	**0.18**	**0.02**	**0.14**	**0.22**
	Intermediate harvest	-0.0002	0.01	-0.02	0.02
	Leave	0.002	0.01	-0.02	0.02
	No-harvest	0.01	0.01	-0.01	0.03

Species	Parameter	Coefficient	Standard Error	Lower 95% CI	Upper 95% CI
	Old growth	-0.0001	0.01	-0.02	0.02
	Uneven-aged management	0.003	0.01	-0.02	0.02
	Early post-harvest × Intermediate harvest	**-0.35**	**0.02**	**-0.39**	**-0.31**
	Early post-harvest × Leave	**-0.36**	**0.02**	**-0.40**	**-0.32**
	Early post-harvest × No-harvest	**-0.36**	**0.02**	**-0.40**	**-0.32**
	Early post-harvest × Old growth	**-0.35**	**0.02**	**-0.39**	**-0.31**
	Early post-harvest × Uneven-aged management	**-0.32**	**0.02**	**-0.36**	**-0.28**
	Late post-harvest × Intermediate harvest	0.0002	0.02	-0.04	0.04
	Late post-harvest × Leave	-0.002	0.02	-0.04	0.04
	Late post-harvest × No-harvest	-0.01	0.02	-0.05	0.03
	Late post-harvest × Old growth	0.0001	0.03	-0.06	0.06
	Late post-harvest × Uneven-aged management	-0.003	0.02	-0.04	0.04
	Post second-harvest × Intermediate harvest	**-0.12**	**0.02**	**-0.16**	**-0.08**
	Post second-harvest × Leave	**-0.17**	**0.02**	**-0.21**	**-0.13**
	Post second-harvest × No-harvest	**-0.18**	**0.02**	**-0.22**	**-0.14**
	Post second-harvest × Old growth	**-0.17**	**0.02**	**-0.21**	**-0.13**
	Post second-harvest × Uneven-aged management	**-0.14**	**0.02**	**-0.18**	**-0.10**

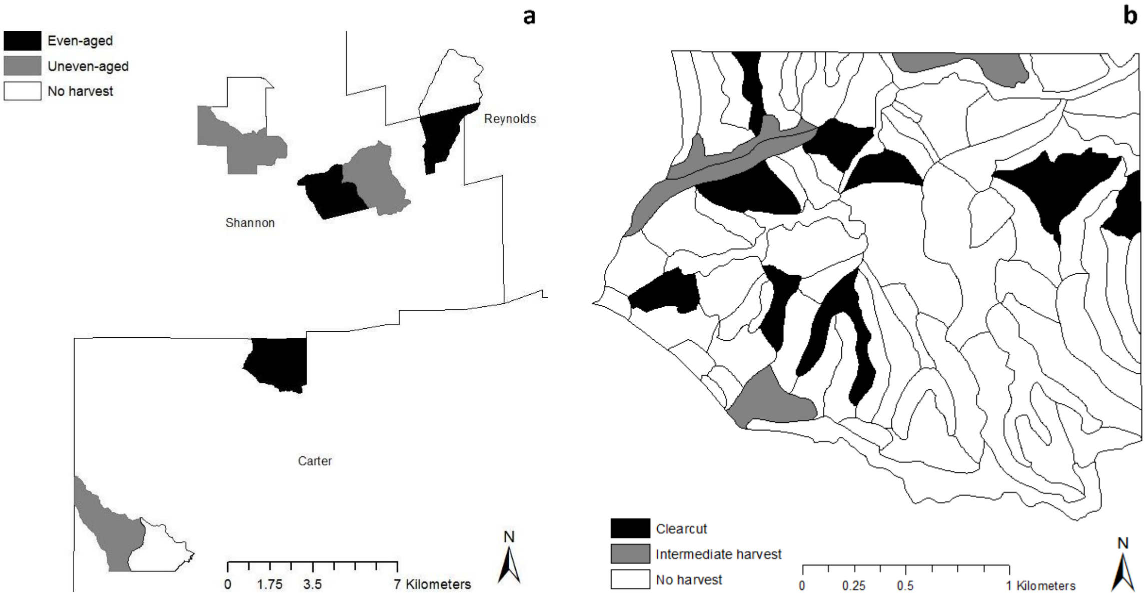

Figure 1.1. Map of the Missouri Ozark Forest Ecosystem Project in southeast Missouri (a), and an even-aged management site showing stand-level silvicultural treatment types (b).

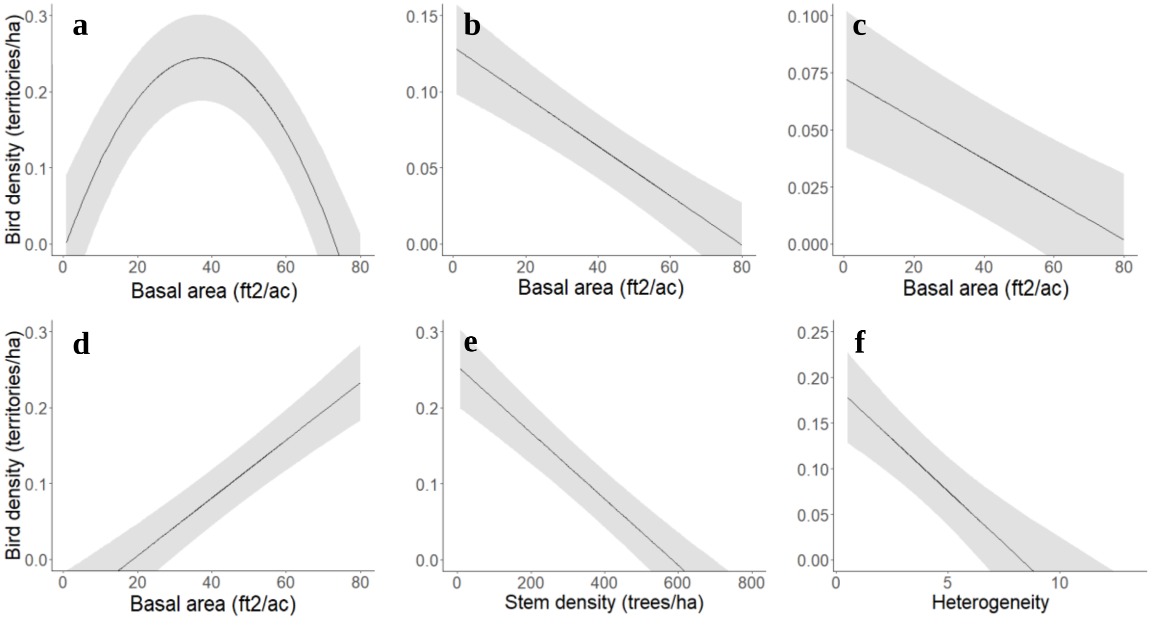

Figure 1.2. Predictions from the best-supported models of the relationship between (a) Acadian flycatcher, (b) black-and-white warbler, and (c) hooded warbler densities and basal area; and relationships between eastern wood-pewee densities and (d) basal area, (e) stem density, and (f) heterogeneity from experimental forest plots in southeast Missouri. Shaded areas represent 95% confidence intervals. Factor of interest varied while other variables were held at their mean.

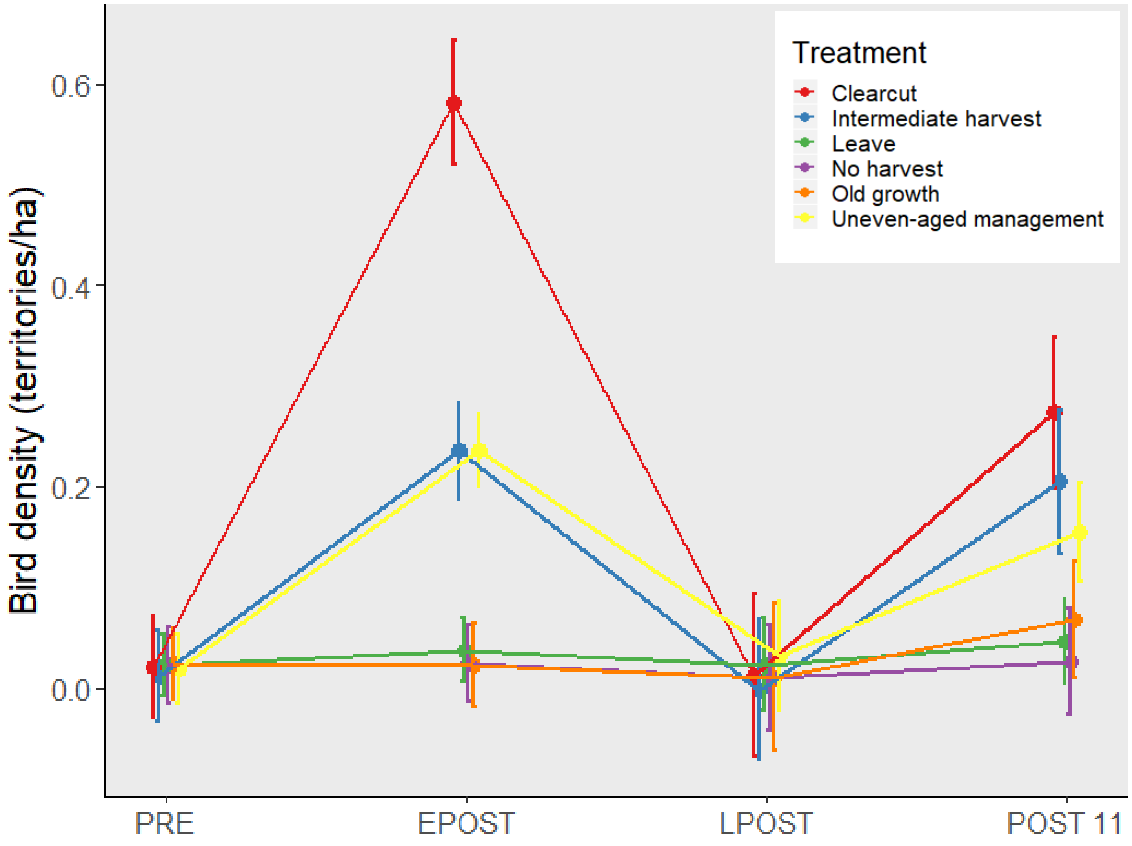

Figure 1.3. Predictions from the best-supported models of the relationship between indigo bunting densities and treatment type across time from experimental forest plots in southeast Missouri. Bars represent 95% confidence intervals. PRE = Pre-harvest. EPOST = Early post-harvest. LPOST = Late post-harvest. POST11 = Post second-harvest.

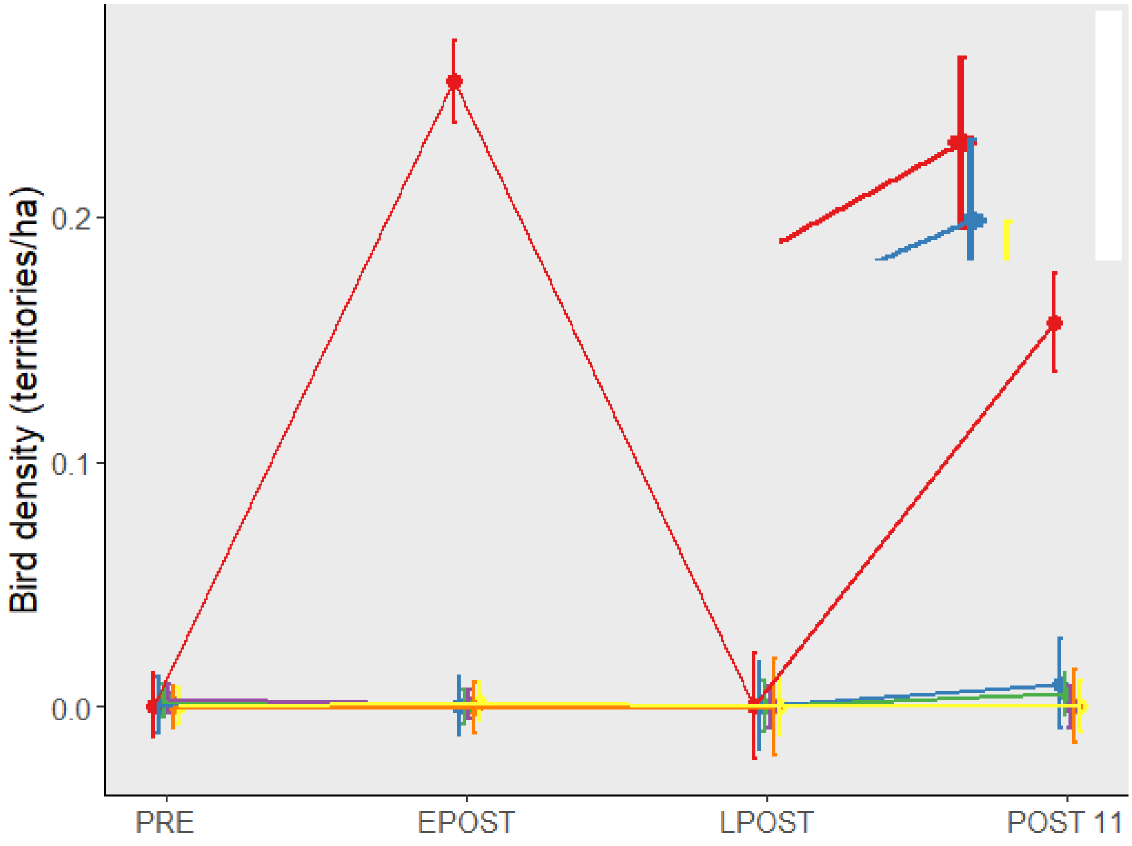

Figure 1.4. Predictions from the best-supported models of the relationship between prairie warbler densities and treatment type across time from experimental forest plots in southeast Missouri. Bars represent 95% confidence intervals. PRE = Pre-harvest. EPOST = Early post-harvest. LPOST = Late post-harvest. POST11 = Post second-harvest.

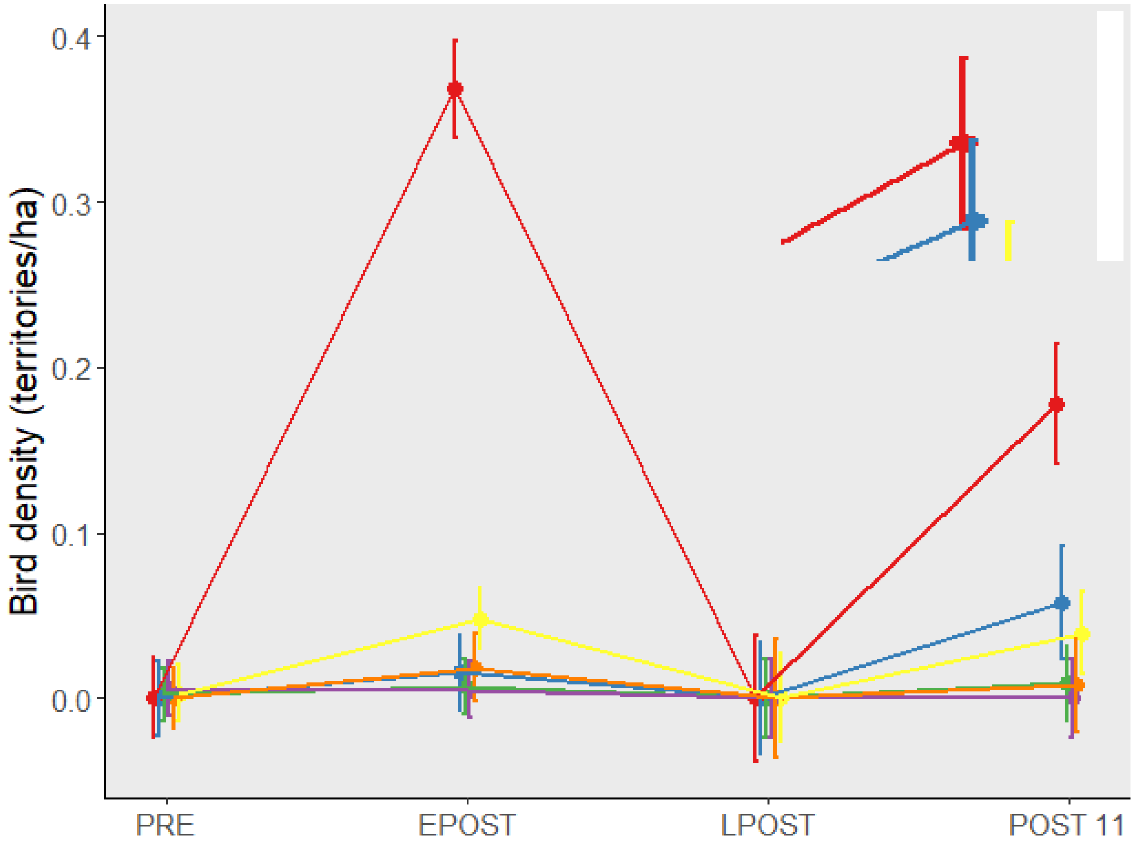

Figure 1.5. Predictions from the best-supported models of the relationship between yellow-breasted chat densities and treatment type across time from experimental forest plots in southeast Missouri. Bars represent 95% confidence intervals. PRE = Pre-harvest. EPOST = Early post-harvest. LPOST = Late post-harvest. POST11 = Post second-harvest.

Chapter II

EFFECTS OF EXPERIMENTAL FOREST MANAGEMENT AND EDGE ON NEST SUCCESS IN UPLAND HARDWOOD ECOSYSTEMS

Introduction

The North American Breeding Bird Survey (BBS) has documented significant population declines in 33% and 48% of woodland and shrubland bird species (respectively) in North America since the 1960s (Sauer et al., 2017). Population declines are mainly attributed to the loss and fragmentation of critical breeding and wintering habitat through agriculture and urban development (Sherry and Holmes 1995, Faaborg et al. 2010, Bregman et al. 2014). The loss and fragmentation of habitat results in population sinks, i.e. negative population growth rates (Donovan et al. 1995, Moore et al. 2010). Population sinks are landscapes, typically low in habitat quality, where population growth rates are negative. Conversely, population sources are landscapes, typically high in habitat quality, where population growth rates are positive. To mitigate population declines in birds, populations in fragmented landscapes need immigration from population sources found in continuously forested landscapes or large forest tracts (Manolis et al. 2002, Nol et al. 2005). However, breeding bird populations in continuously forested landscapes are affected by forest management. The effects of forest management on breeding bird populations are often species-specific and dependent on scale, making it difficult to generalize conclusions on forest birds.

Studies examining the effects of forest management on breeding birds typically measure abundances, i.e. territory densities (review by Thompson et al. 1995, Sallabanks and Arnett 2005, Perry and Thill 2013, Kendrick et al. 2015). However, measures of reproductive success are needed for understanding the underlying mechanisms that influence breeding bird populations in managed landscapes. Reproductive measures such as nest survival, i.e. how likely a nest is to survive a day or nesting cycle, are critical components for determining population growth rates and implementing effective management and conservation of declining species. Therefore, understanding how forest management affects nest survival is crucial in understanding how forest management affects breeding bird populations overall.

The results of studies analyzing the effects of forest management on nest survival have been mostly species-specific and vary depending on scale and forest management methods used. Uneven-aged management generally has little effect on nest survival (Dellinger et al. 2007, Leblanc et al. 2011, Richmond et al. 2012), whereas the effects of even-aged management on nest survival vary. Several studies have found little to no effect of even-aged management on nest survival (Duguay et al. 2001, Moorman et al. 2002), whereas others have found reduced rates of nest survival as a result of even-aged management (Flaspohler et al. 2001, Manolis et al. 2002). Some studies examining the effects of even-aged management on nest survival included edge variables (Duguay et al. 2001, Manolis et al. 2002, Hazler et al. 2006). However, they found little to no edge effects as a results of forest management. The creation of edge habitat may result in higher rates of nest predation (Chalfoun et al. 2002, Cox et al. 2012a, Cox et al. 2012b), which may result in ecological traps (Weldon and Haddad 2005). Ecological traps occur when animals use environmental cues to select habitat. However, due to human disturbance, environmental cues are no longer indicative of habitat quality which results in individuals choosing low quality habitat (Schlaepfer et al. 2002).

The objective of our study was to determine the effects of forest management and edge on the nest survival of breeding bird species in the Missouri Ozarks. Revealing how forest management and edge influence reproductive success may lead to a better understanding of effects on demographic variables that contribute to persistence of bird populations. Nest survival and other demographic variables contribute to the persistence of bird populations. Understanding how demographic variables respond to disturbances like forest management is crucial to managing populations and preventing declines.

We used Acadian flycatchers (*Empidonax virescens*) and indigo buntings (*Passerina cyanea*) in our analysis. Acadian flycatchers were chosen because they are abundant, vocally conspicuous, and their nests are relatively easy to locate and monitor. Acadian flycatchers demonstrate high habitat-specificity at local and landscape scales, and have been identified as a Neotropical migrant species of management concern in the Midwest, reflecting perceived threats on their breeding and overwintering grounds (Thompson et al. 1993, Allen et al. 2017). Indigo buntings were chosen because they are abundant, and because their nests are relatively easy to locate and monitor. We predicted that Acadian flycatcher nest survival would decrease following harvest as a response to loss of their preferred habitat and decrease with increases in edge density as a response to increased predator activity (Chalfoun et al. 2002, Allen et al. 2017). We predicted that indigo bunting nest survival would likewise decrease following harvest and decrease with increases in edge density. Although indigo buntings are shrubland species and typically respond positively to even-aged management, higher concentrations of edge may lead to an ecological trap by increasing predation rates in otherwise suitable habitat (Donovan and Thompson 2001, Weldon and Haddad 2005).

STUDY AREA

Our study sites are part of the Missouri Ozark Forest Ecosystem Project (MOFEP). Initiated in 1989 by the Missouri Department of Conservation, MOFEP is a 100-year, long-term, large-scale experiment that is testing (in part) the effects of even-aged and uneven-aged forest management on breeding bird populations in upland hardwood forests (Knapp et al. 2014). Study sites were chosen as representative of the Missouri Ozarks and upland hardwood ecosystems in the central US. The MOFEP study area is located in Carter, Reynolds, and Shannon Counties, in the Ozark Highlands region of southeast Missouri. The region is approximately 84% forested comprising oak (*Quercus* spp.)-hickory (*Carya* spp.) and oak-pine (*Quercus-Pinus* spp.) forests, oak savannas, bluestem (*Andropogon-Schizachyrium* spp.) prairies, and glades (Brookshire and Shifley 1997). At the initiation of MOFEP in 1989, most overstory trees were 50–70 years old with all sites containing some trees older than 100 years (Brookshire and Dey, 2000). Over the past 300 years, the region was exposed to many natural and anthropogenic disturbances, such as fire, logging, and agriculture. Before MOFEP, the land was managed primarily for timber (Guyette and Larsen 2000).

METHODS

Experimental Design

The MOFEP study area was divided into 9 sites that are arranged as a randomized block design with 3 blocks of 3 sites (Fig. 1.1). Sites averaged 400 ha in size and were assigned 1 of 3 management treatments: even-aged management, uneven-aged management, or no-harvest. Each site was divided into 36–74 stands, ranging from 0.16–62 ha, based on ecological land type and topography (Fig. 1; Brookshire and Shifley, 1997). Even-aged management sites followed a 100-year rotation with a 15-year reentry period starting in 1996. During initial harvest in 1996, 24 clearcuts were established ranging from 0.76–16.79 ha in size. Harvested sites had approximately 10–15% of the forested area removed. Group-selection and single-tree cuts were applied across 41-69% of each uneven-aged management site. Each uneven-aged site had 84–97 group-selection cuts and were interspersed uniformly across the site. Group-selection cuts remove all trees within a small diameter. For our study, group-selection cuts averaged 30 meters in diameter. All stands were designated the silvicultural treatment they received during the initial harvest. Approximately 10% of both even-aged and uneven-aged sites were designated as “old growth” stands that would not be cut for the duration of the 100-year study. See Brookshire and Shifley, (1997) for additional details on experimental design.

Data Collection

Nests were located and monitored from mid-May through the end of June in 1991–1999, except for 1996 when harvesting occurred. Nests were located by searching appropriate habitat and observing adult behaviors, and marked each nest location with flagging tape placed 5–10 meters from the nest (Ralph et al. 1993). Nests were monitored every 3–5 days until nest fate could be determined noting predation and parasitism events (Martin and Geupel, 1993). Nests were considered successful if at least one nestling fledged. Brood parasitism by brown-headed cowbirds (*Molothrus ater*) reduces reproductive success in passerines (Robinson et al. 1995). Therefore, all parasitized nests were considered failed. Nests were considered depredated if signs such as a destroyed nest, broken egg shells near nest, feathers, etc. were found. Once nests were found, nest stage (laying, incubation, or nestling) was recorded for each subsequent nest check.

We used ArcGIS 10.6 to calculate edge density (m/ha) using a 100-meter buffers around each nest location. For each nest, edge density was calculated by dividing the edge lenth (in meters) created by even-aged and uneven-aged management by the area of the 100-meter nest buffers. For even-aged management, edge density was calculated from clearcut stands whereas edge density for uneven-aged management was calculated from group-selection cuts. Although we did not differentiate between edge created by uneven- and even-aged management, models included silvicultural treatment and management variables that accounted for differences between the two management types.

Statistical Analysis

Data were separated into two time periods: pre-harvest (1991–1995) and post-harvest (1997–1999). We used the logistic-exposure method (Shaffer 2004) to estimate nest survival as a function of a priori hypotheses concerning prescribed silvicultural treatment, time period, and edge density. Generalized linear models were fit using the RMark package (Dinsmore and Dinsmore 2007, Laake and Rexstad 2008) within program R (R

Core Team Version 3.5.1). The logistic-exposure method uses the interval between nest checks as the sampling unit. Effective sample size for each species included the number of days that nests were known to have survived and the number of intervals that ended in a failed nest (Rotella et al. 2004). Nest stage and day of season are known to affect nest survival and were thus included in all models; day of season was represented as a quadratic term (Cox et al. 2012b, Morris et al. 2013). Day of season is adjusted from Julian date where day 0 represents the day the first nest was found for each species. For example, our first Acadian flycatcher nest was found on May 22nd, or the 142nd Julian date and the first indigo bunting nest was found on May 23rd, or the 143rd Julian date. Akaike's Information Criterion for small sample size (AICc) was used to select the best-supported models for each species (Burnham and Anderson 2002). Models with the lowest AICc values and a delta AICc of ≤ 2 were selected as the best-supported model. We did not consider models that added only uninformative parameters to best-supported models (Arnold, 2010).

For each species, we fit 6 candidate models that included a null model (nest stage, day of season, and day of season2); edge density alone; management models with a combination of time period, prescribed silvicultural treatment, and their interactions; and a global model with time period, prescribed silvicultural treatment, and edge density. Treatment was only included in models as an interaction with time period (BACI design).

We estimated daily nest survival for Acadian flycatcher and indigo bunting nests using predictions for the best-supported model for each species. We calculated period nest survival for Acadian flycatchers based on a 30-day nesting cycle (2 lay days, 14 incubation days, and 14 nestling days). Period nest survival for indigo buntings was calculated using a 25-day nesting cycle (3 lay days, 11 incubation days, and 11 nestling days). To calculate period survival, daily survival rates were raised to the power of the nest cycle length for each of the two species. When constructing predictive plots, we varied the covariate of interest across its range of values while holding the other covariates at their means.

Results

During harvest, 599 group-selection cuts created 56.4 km of edge, and 24 clearcuts created 26.7 km of edge for a total of 83.1 km of edge across the MOFEP sites. Following harvest, 106 nests of both species included edge within 100 meters. Of those nests, buffers included 5.8 kilometers of edge with a mean edge density of 54.5 m/ha. When nest buffers without edge were included, mean edge density dropped to 22.9 m/ha (Table 2.1).

Acadian flycatcher nest survival

We monitored 370 Acadian flycatcher nests every 3.56 ± 1.31 days for a total of 1,567 observations (Table 2.1). Forty-one percent of Acadian flycatcher nests were successful. Predation was the primary cause of nest failure, accounting for 93% of failed nests. Little parasitism by brown-headed cowbirds occurred, accounting for only 1% of all nests. The majority of Acadian flycatcher nests were found within the incubation and nestling stages (9% lay, 64% incubation, and 27% nestling).

The effective sample size was 4,406 days for Acadian flycatcher nest survival models. A total of 6 models were in the final model set for Acadian flycatcher nest survival. The best-supported model for Acadian flycatcher nest survival included factors such as edge density, time period (pre- and post-harvest), nest stage (lay, incubation, and nestling), and a quadratic relationship with day of season (Table 2.2, 2.3). As predicted, daily nest survival decreased with an increase in edge density (Fig. 2.1a). Daily nest survival was highest early in the breeding season, decreased as the breeding season progressed, and increased slightly at the end of the breeding season (Fig. 2.1b). During the nesting cycle, daily nest survival was lowest in the laying stage, increased in the incubation stage, and increased even more during the nestling stage (Fig. 2.1c). However, 95% confidence intervals did overlap suggesting no significant change. The 95% confidence intervals for model coefficients overlapped zero for incubation and nestling stages suggesting no effects on daily nest survival (Table 2.3). When adjusted for period nest survival for each stage (2 lay days, 14 incubation days, and 14 nestling days), period survival was highest during the lay stage and declined drastically during the incubation and nestling stages. Contrary to our predictions, daily nest survival increased from the pre-harvest period to the post-harvest period (Fig. 2.1d). However, 95% confidence intervals did overlap suggesting no significant change. Overall daily survival and period survival (30 days) were 0.95 and 0.2, respectively.

Indigo bunting nest survival

We monitored 132 indigo bunting nests every 3.31 ± 1 (Mean ± SD) days for a total of 429 observations (Table 2.1). Sixty-three percent of indigo bunting nests were successful. Predation was the primary cause of nest failure, accounting for 90% of failed nests. No indigo bunting nests were parasitized by brown-headed cowbirds. The majority of indigo bunting nests were found within the incubation and nestling stages (8% lay, 38% incubation, and 55% nestling).

The effective sample size was 1,031 days for indigo bunting nest survival models. A total of 6 models were in the final model set for indigo bunting nest survival. The best-supported model for indigo bunting nest survival was the null model which included nest stage (lay, incubation, and nestling) and day of season (Table 2.2, 2.3). During the nesting cycle, daily nest survival decreased from the laying stage to the incubation stages, then increased during the nestling stage (Fig. 2.2a). However, 95% confidence intervals did overlap showing no significant differences of daily nest survival between nest stages. When adjusted for period survival for each stage (3 lay days, 11 incubation days, and 11 nestling days), period survival was highest during the lay stage and decreased significantly during the incubation and nestling stages. Daily nest survival was highest early in the breeding season, decreased as the breeding season progressed, and increased at the end of the breeding season (Fig. 2.2b). Overall daily survival and period survival (25 days) were 0.96 and 0.36, respectively.

Discussion

Our findings demonstrate edge effects on a species of mature-forest bird do occur in landscapes managed for timber using even- and uneven-aged management practices. They also show that daily nest survival for both Acadian flycatchers and indigo buntings is lowest during the middle of the breeding season. Studies analyzing the effects of forest management on breeding birds typically measure bird abundances rather than nest survival (review by Thompson et al. 1995, Sallabanks and Arnett 2005, Perry and Thill 2013, Kendrick et al. 2015). Nest survival and other reproductive measures allows for a greater understanding of the underlying mechanisms that drive population growth rates. Several studies have evaluated the relationship between forest management and breeding bird nest survival (Duguay et al. 2001, Moorman et al. 2002, Dellinger et al. 2007, Leblanc et al. 2011, Richmond et al. 2012). Responses are typically species-specific and vary depending on scale and forest management practice used. Forest management can create edge that may attract nest predators and, as a consequence, increases rates of nest predation for mature-forest and shrubland species (Chalfoun et al. 2002, Weldon and Haddad 2005, Cox et al. 2012a, Cox et al. 2012b).

Most studies analyzing edge effects on the nest survival of breeding birds use distance to edge as their edge metric (Benson et al. 2010, Bakermans et al. 2012, Jenkins et al. 2016). Distance to edge is important for understanding how far within a tract of continuous forest that disturbances such as agriculture and forest management have on breeding bird populations (Hoover et al. 2006, Wallendorf et al. 2007). Studies using distance to edge as their edge metric have found that nests that are closer in proximity to edge show increased rates of nest predation and brood parasitism (Hoover et al. 2006, Benson et al. 2010). Several species of both mature-forest and shrubland species have shown increases in densities within 100 meters of clearcut edges (Wallendorf, et al. 2007). Although important, distance to edge does not address the configuration or intensity of harvest, or the amount of edge created by harvests. Using edge density as the edge metric can reveal how the shape and placement of harvests created can affect breeding bird populations.

Although we did not find effects of treatment type on daily survival rates, it is possible that edge effects were greater in sites that received group-selection cuts than those that received clearcuts. From our results, group-selection cuts had higher edge densities (28.31 m/ha) than clearcuts (18.61 m/ha). Despite the fact that effects of time period (pre- vs. post-harvest) were minimal, our results show that the edge created by forest management negatively affects rates of Acadian flycatcher daily nest survival. As predicted, Acadian flycatcher daily nest survival decreased with an increase in edge density. Declines in daily nest survival are likely due to an increase in nest predation rates which coincides with the 93% of failed nests that were depredated (Chalfoun et al. 2002, Allen et al. 2017). The decrease in daily nest survival could also be attributed to the shape of clearcuts. Irregularly shaped cuts typically contain more edge than more rectangular cuts (Weldon and Haddad 2005). Additionally, group-selection cuts within the MOFEP framework are spread throughout the uneven-aged sites in relatively close proximity to one another, potentially increasing edge density within 100 meters of a nest.

As predicted, Acadian flycatcher and indigo bunting daily nest survival was lowest toward the middle of the season. This is mostly like due to an increase in nest predation rates from raptors, nonraptorial birds, and snakes. Although this was not a nest camera study, we are aware of the nest predators in the region from other studies looking directly at nest predators (Cox et al. 2012a, Cox et al. 2012b). For example, predation from blue jays, western ratsnakes, and broad-winged hawks can increase midseason (Cox et al. 2012a). Black ratsnakes and broad-winged hawks, two generalist species, are more likely to depredate a nest during the middle of the breeding season when more birds are nesting. As the season progresses, fewer birds are nesting and searching for nests becomes less effective than looking for other prey items (Schmidt 1999).

Acadian flycatcher period nest survival rates were comparable to nest survival estimates in landscapes fragmented by agriculture (Peak et al. 2004). This was unanticipated because large forest tracts and continuously forested landscapes like the MOFEP study area are typically viewed as a population source for mature-forest species like the Acadian flycatcher (Donovan et al. 1995, Burke and Nol, 2000). However, we can only speculate these conclusions. Peak et al. only had 4 Acadian flycatcher nests that were pooled with other mature-forest species. Therefore, studies with larger numbers of nests are required to confirm these findings. Additionally, Acadian flycatchers almost always renest regardless of whether or not their first nest succeeded or failed (Fauth and Cabe 2005, Allen et al. 2017). As a consequence, it is not known how many of the Acadian flycatchers with failed nest went on to renest and be successful.

Management Implications

We found no direct effects of treatment type on the nest survival of Acadian flycatchers and indigo buntings. Nonetheless, some important conclusions about forest management can be made from our results. First, edge created by timber harvest can have negative effects on a species of mature-forest bird species of conservation concern in the Midwest. It is possible that edge created by management increases rates of nest predation especially during the middle of the breeding season when more birds are nesting. Our results show that it is important to account for edge created by forest management and midseason peaks of nest predation when managing for breeding birds.

To mitigate edge effects on Acadian flycatchers, managers could decrease edge densities created by forest management. Within the current MOFEP framework, group-selection cuts are spread out uniformly across the uneven-aged sites where any given nest is likely to be in close proximity to one of the cuts. Managers could concentrate these cuts to leave larger tracts of undisturbed canopy. However, more information on how group-selection cuts directly affect nest success should be explored across more species.

Table 2.1. Summary statistics of nest monitoring data and edge density for Acadian flycatcher and indigo bunting nests. Edge density values are from post-harvest nests.

Variable	**Mean ± SD**	**Minimum**	**Maximum**	**Median**
Acadian flycatcher				
Julian date	167.55 ± 9.82	142	200	167
Observation interval (days)	3.56 ± 1.31	1	13	3
Edge density (m/ha)	12.43 ± 24.74	0	108.3	0
Indigo bunting				
Julian date	164.9 ± 11.44	143	202	163
Observation interval (days)	3.31 ± 1	1	9	3
Edge density (m/ha)	35.96 ± 37.13	0	178.33	2.71

Table 2.2. AIC results for Acadian flycatcher and indigo bunting nest survival in the Missouri Ozark Forest Ecosystem Project. The model parameters are described in the text. Models include a combination of edge, management, time period, nest stage, and day of season. *K* = number of parameters in each model. ΔAIC_c = the difference between the AIC values for the best-supported model and a given model. w_i = weight of evidence for models

Model	***K***	$\boldsymbol{\Delta AIC_c}$	$\boldsymbol{w_i}$
Acadian flycatcher (n = 4,409)			
Edge + Period + Stage + Date + Date^2	7	0	0.64
Edge + Stage + Date + Date^2	6	3.02	0.14
Null (Stage + Date + Date^2)	5	3.49	0.11
Period + Stage + Date + Date^2	6	3.71	0.1
Edge + Treatment × Period + Stage + Date + Date^2	17	12.96	<0.01
Treatment × Period + Stage + Date + Date^2	16	13.54	<0.01
Indigo bunting (n = 1,031)			
Null (Stage + Date + Date^2)	5	0	0.46
Edge + Stage + Date + Date^2	6	1.27	0.24
Period + Stage + Date + Date^2	6	1.72	0.19
Edge + Period + Stage + Date + Date^2	7	3.25	0.09
Management × Period + Stage + Date + Date^2	10	6.85	0.01
Edge + Management × Period + Stage + Date + Date^2	11	8.75	0.01

Table 2.3. Estimated coefficients for the best-supported models for Acadian flycatcher and indigo bunting nest survival. Significant effects are in bold.

Parameter	**Coefficient**	**Standard Error**	**Lower 95% CI**	**Upper 95% CI**
Acadian flycatcher				
Intercept	**5.64**	**0.69**	**4.29**	**6.99**
Edge density	**-0.01**	**0.004**	**-0.02**	**-0.002**
Pre-harvest	**-0.35**	**0.16**	**-0.66**	**-0.04**
Incubation	0.03	0.22	-0.41	0.47
Nestling	0.19	0.27	-0.35	0.72
Date	**-0.11**	**0.04**	**-0.20**	**-0.03**
Date^2	0.001	0.0006	-0.0002	0.002
Indigo bunting				
Intercept	**5.3**	**1.05**	**3.24**	**7.36**
Incubation	-0.04	0.49	-1	0.92
Nestling	0.02	0.53	-1.01	1.05
Date	**-0.15**	**0.07**	**-0.29**	**-0.003**
Date^2	0.002	0.001	-0.0003	0.004

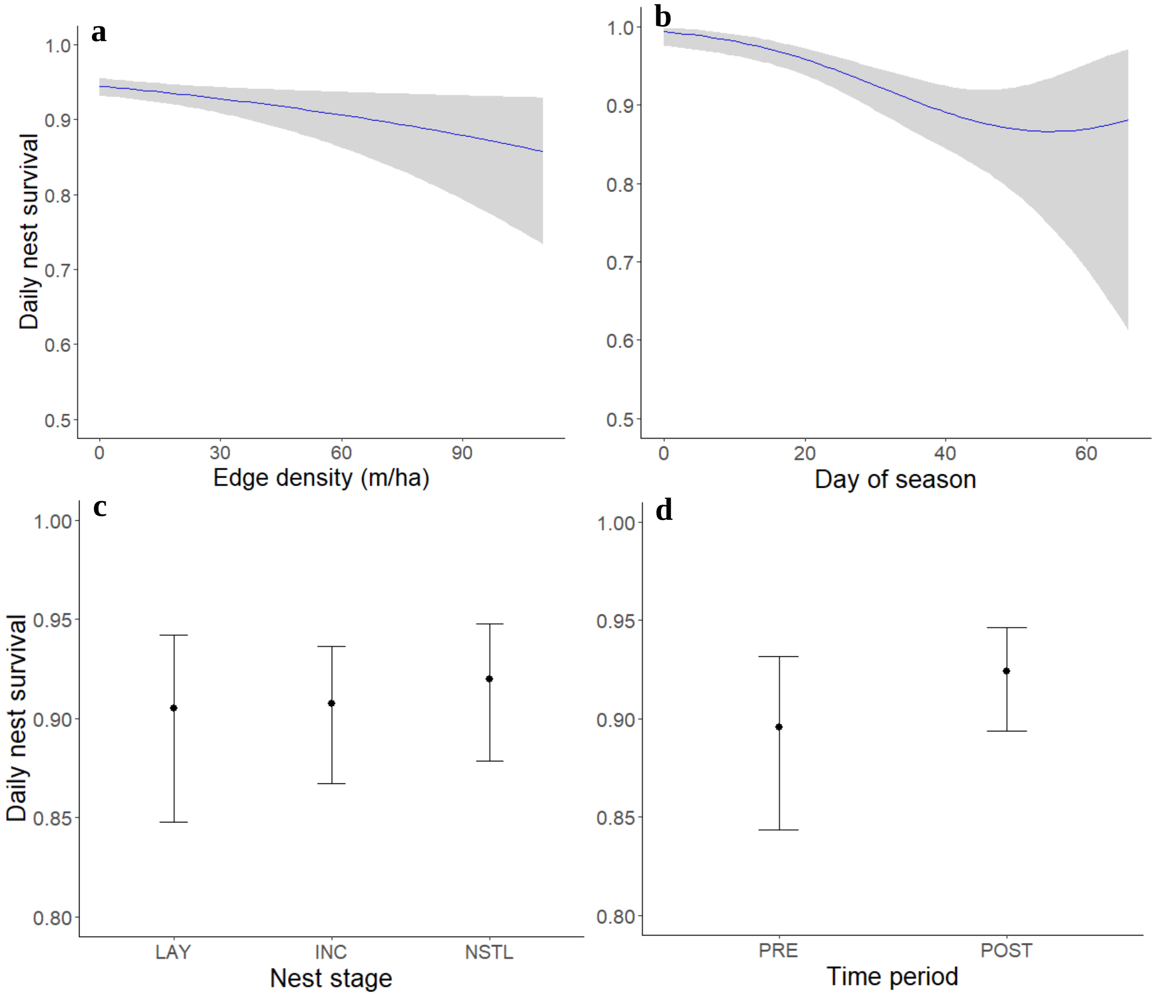

Figure 2.1. Predictions from the best-supported model of the relationship between Acadian flycatcher daily nest survival and (a) edge density, (b) day of season, (c) nest stage, and (d) time period. Bars and shaded areas represent 95% confidence intervals. Factor of interest varied across range of values while other variables were held at their mean.

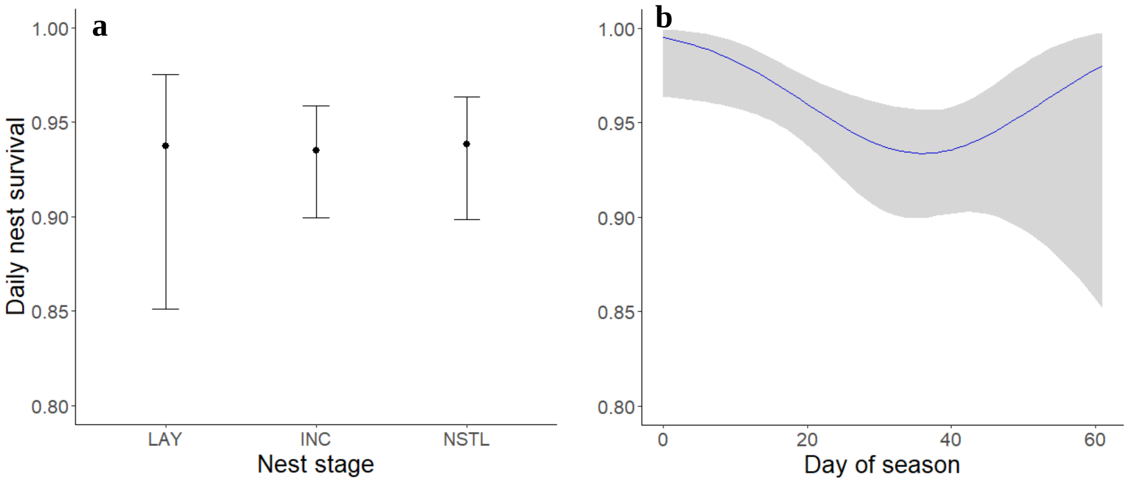

Figure 2.2. Predictions from the best-supported model of the relationship between indigo bunting daily nest survival and (a) nest stage and (b) day of season. Bars and shaded areas represent 95% confidence intervals. Factor of interest varied across range of values while other variables were held at their mean.

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