Review and Meta-analyses



# A meta-analysis of edge effects on nesting success in forest and shrubland birds of eastern North America

# Un meta-análisis de los efectos de borde sobre el éxito de la nidificación en aves de bosques y matorrales del este de Norteamérica

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ABSTRACT. Numerous studies report proximity to land cover edges decreases avian nesting success, yet variation among species, sites, and nesting guilds obscures overall patterns. Nest success is a key demographic parameter, and edges are often created from anthropogenic disturbance; therefore, further understanding of nest success and edges should inform bird conservation efforts. We performed a meta-analysis to examine effects of edges on mature forest and shrubland bird nest survival in eastern North America. Sixteen studies fit our inclusion criteria, comprising data for 11 mature forest and 9 shrubland species. Nest success for mature forest birds declined with proximity to edges. Additionally, random effects of species and study explained a relatively large amount of variance in nest survival. We did not find a significant edge effect for shrubland birds, but only two data points (averaged within studies) were greater than 100 meters from an edge. Thus, in studies we compiled, an impact of edges was only apparent for forest species that nested far from edges. An interactive effect of distance-to-edge and nest placement (low vs. higher nesting height) did not significantly influence nest survival. Single-species analyses showed a relationship between distance-to-edge and nesting success for Hermit Thrush (*Catharus guttatus*), though small sample sizes may have limited our ability to detect relationships for other species. Overall, core areas greater than 250 m from edges tend to have higher nest success for mature forest birds, information that will help managers and conservationists when maintaining habitat for both forest and shrubland bird communities.

RESUMEN. Numerosos estudios señalan que la proximidad a los bordes de la cubertura terrestre disminuye el éxito de nidificación de las aves, aunque la variación entre especies, lugares y gremios de nidificación oscurece los patrones generales. El éxito de nidificación es un parámetro demográfico clave y los bordes se crean a menudo a partir de perturbaciones antropogénicas; por lo tanto, una mayor comprensión del éxito de nidificación y los bordes deberían informar los esfuerzos de conservación de las aves. Hemos realizado un meta-análisis para examinar los efectos de borde en la supervivencia de los nidos de aves de bosques maduros y matorrales en el este de Norteamérica. Dieciséis estudios se ajustaron a nuestros criterios de inclusión, incluyendo datos de 11 especies de bosque maduro y 9 de matorral. El éxito de los nidos de aves de bosques maduros disminuyó con la proximidad a los bordes. Además, los efectos aleatorios de la especie y el estudio explicaron una cantidad relativamente grande de la varianza en la supervivencia de los nidos. No encontramos un efecto de borde significativo para las aves de matorral, pero sólo dos puntos de datos (promediados dentro de los estudios) estaban a más de 100 metros de un borde. Así, en los estudios recopilados, el impacto de los bordes sólo fue evidente para las especies forestales que anidaban lejos de los bordes. Un efecto interactivo de la distancia al borde y la ubicación del nido (altura de nidificación baja vs. alta) no influyó significativamente en la supervivencia de los nidos. Los análisis mono-específicos mostraron una relación entre la distancia al borde y el éxito de nidificación para el Zorzal Ermitaño (Catharus guttatus), aunque el pequeño tamaño de las muestras puede haber limitado nuestra capacidad para detectar relaciones en otras especies. En general, las zonas núcleo situadas a más de 250 m de los bordes tienden a tener un mayor éxito de nidificación para las aves forestales maduras, información que ayudará a los gestores y conservacionistas a la hora de mantener el hábitat para las comunidades de aves tanto forestales como de matorral.

Key Words: border; depredation; ecotone; nest predation; review

# INTRODUCTION

Avian populations can be highly influenced by their nesting habitat, including exposure to predators (Martin 1993, Thompson 2007). The existence of an edge environment, such as a road, agricultural field, or a border between a shrubland and a closed-canopy forest, can influence productivity of nesting birds (Gates and Gysel 1978, Flaspohler et al. 2001a, Woodward et al. 2001). Predators of bird nests, such as Blue Jays (*Cyanocitta cristata*) and raccoons (*Procyon lotor*), tend to increase in abundance and activity near edges, which can lead to lower nest survival relative to interior sites (Donovan et al. 1997, Chalfoun et al. 2002a, Barding and Nelson 2008). Thus, effects of edges on

nesting success should be considered when assessing long-term viability of terrestrial birds (Donovan et al. 1995, Robinson et al. 1995, King et al. 2009).

Many individual studies have examined how success of natural avian nests is affected by edges (e.g., Suarez et al. 1997, Conkling et al. 2012, Kaasiku et al. 2022), but individually, these studies are limited in scope. Past studies have been performed at distinct study sites often with a singular edge type (Friesen et al. 1999, Woodward et al. 2001). Additionally, primary studies usually only focus on one or a few bird species (e.g., Moorman et al. 2002, Kaiser and Lindell 2007), and making general inferences from these studies about edge effects on an entire bird community is

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difficult. Furthermore, there is extensive variation in the strength and importance of edge effects on nest survival among studies conducted at different sites, even within the same species (King et al. 2001, 2009, King and Byers 2002).

Meta-analyses are an important tool for synthesizing findings from multiple studies (Arnqvist and Wooster 1995); yet prior meta-analyses on the effects of edges on nest success included both natural nests as well as artificial nests and combined results across all species (Paton 1994, Hartley and Hunter 1998, Lahti 2001, Batáry and Báldi 2004, Stephens et al. 2004, Vetter et al. 2013). Given that artificial nests lack the presence and activity of adults and young, which serve as cues for predators, these artificial nest studies may not functionally indicate the effects of edges on predation of actual nests (King et al. 1999, Thompson and Burhans 2004, King and DeGraaf 2006). Moreover, artificial nests may have lower survival rates than natural nests (Stuart-Smith and Hayes 2003, Burke et al. 2004) and may not exhibit seasonal or temporal variation in nest survival (Buler and Hamilton 2000, Burke et al. 2004). Previous nest survival metaanalyses also examined all bird species and communities together, sometimes across ecosystems worldwide (e.g., Batáry and Báldi 2004). Combining across ecological communities may be valuable for illustrating overall edge effects on nesting success but can fail to test for differences among bird communities or specific regions (Flaspohler et al. 2001b).

In eastern North America, a distinct set of avian species nest in open-canopy, early-successional forests and shrublands (Conner and Adkisson 1975, Hunter et al. 2001, Dettmers 2003, Schlossberg and King 2007), while a second set of birds nest in older, closed-canopy forests (Annand and Thompson 1997, King and DeGraaf 2000, Schlossberg 2009), and edge effects may influence these species guilds differently (Woodward et al. 2001). Shrublands may have different nest predators, predator abundances, or predator activity levels compared to forests, with potentially more snake-related nest depredation in shrublands and more corvid depredation in forests (DeGregorio et al. 2016, Diaz and Blouin-Demers 2018). Additionally, a mature forest edge is often functionally and ecologically different from an interior forest (e.g., in microclimate, food resources, light levels, and vegetation cover; Palik and Murphy 1990, Matlack 1993, Jokimäki et al. 1998), but depending on the edge type, an edge of a shrubland may be similar in vegetation density and food resources compared to a shrubland interior (Weldon and Haddad 2005, Shake et al. 2011). Predators cuing in on functional differences or similarities among forest interiors, edges, and shrubland interiors (Chalfoun et al. 2002b, Benson et al. 2010a, Cox et al. 2013) could in turn cause variation in observed edge effects of nest survival between forest and shrubland nesting birds.

Additional variation, such as nest placement (e.g., ground vs. above-ground nests; Wilcove 1985, Martin 1993) can also influence edge effects and should be accounted for in analyses. Bird nests on the ground may be more likely to be depredated by species that have higher activity levels near the ground, such as snakes and ants, whereas nests higher up in vegetation may have increased depredation by raptors (DeGregario et al. 2016). Given that certain predators also have higher abundance near edges (Chalfoun et al. 2002a), nest placement and distance to edge can interact to influence nest survival (Flaspohler et al. 2001b).

We performed a meta-analysis examining effects of distance-toedge and interactions with nest placement on nesting success of mature forest and shrubland birds in eastern North America to synthesize existing data in this region. Our study is unique in that we examined natural nests, conducted separate analyses for mature forest and shrubland bird communities in a single region, and tested relationships for individual species. The shrubland bird community is declining and of conservation concern in eastern North America (King and Schlossberg 2014), and some forest bird populations are declining as well (Rushing et al. 2016). Past studies have found edge effects on nest survival can impact both forest and shrubland birds (e.g., Burke and Nol 2000, King et al. 2009, Etterson et al. 2014), but there have been some mixed or inconclusive findings (e.g., Rodewald and Yahner 2001, Newell and Kostalos 2007, Benson et al. 2010b), and a meta-analysis is needed to synthesize the literature and elucidate patterns. Our presented quantitative relationships can be used as a tool for forest managers and conservationists to better manage for both mature forest and shrubland birds (Lott et al. 2021).

# METHODS

We selected focal bird species based on a review of avian habitat preferences and included birds that breed in shrubland and forested habitats in eastern North America (Annand and Thompson 1997, King and DeGraaf 2000, Schlossberg and King 2007, Lott et al. 2019), using the same species lists as in Akresh et al. (2023). Shrubland birds specifically nest in open-canopy, early successional forest stands and shrublands (Dettmers 2003, Chandler et al. 2009, King et al. 2011, King and Schlossberg 2014). Our classification of "mature forest birds" occurs primarily during the nesting season, because birds that nest in mature forests disperse to shrubland habitats during the post-fledging period in this region (Akresh et al. 2009, Stoleson 2013). We also use the term "mature forest" to denote closed-canopy forest stands within primary studies that were not recently managed, but note that almost all forests in our study area of eastern North America have had some tree harvesting in the previous 150-200 years (Litvaitis 1993, Foster et al. 1998). We only examined and included studies in eastern North America, which is an ecologically cohesive area bounded to the west by the Great Plains and defined by the United States Forest Service (USFS) regions R8, R9, as well as New Brunswick, Nova Scotia, southern Ontario, and Quebec (King and Schlossberg 2014).

Data for our meta-analysis came from a literature search of studies that analyzed nest survival for individual mature forest and shrubland birds in relation to nests' distance-to-edge. We found relevant studies by searching published papers on Web of Science, Academic Search Complete, OAlster, Oxford Scholarship Online, Taylor and Francis Journals, WorldCat.org, and Google Scholar. We conducted our search in 2019 and 2020. We searched with the following key phrases: "edge," "nest success," "species specific," "nest survival," "distance to edge," "daily nest survival," "eastern North America," and/or "avian". Additional studies were found by consulting a systematic map of forest bird species-environment relationships (Lott et al. 2019). We also used snowballing techniques to search for studies (Wohlin 2014). For example, we reviewed articles cited by lists in Google Scholar, relevant meta-analyses, and primary source studies to find additional publications (Lahti 2001, Stephens et al. 2004). We did not search for studies in other languages (e.g., French).

We screened potential studies for our meta-analysis with inclusion criteria. We only included studies that presented species-specific nest survival data in discrete distance-to-edge bins (e.g., 0-50 m from an edge, 50-100 m from an edge), because continuous distance-to-edge relationships within primary studies were not suitable for our analyses. Studies that did not have data on daily nest survival or nest success within discrete distance-to-edge categories were excluded, with a few exceptions of re-analyzing continuous data from our own studies. We excluded studies that had only artificial nest data. We also excluded studies that only presented apparent nest survival without accounting for the number of nest observation days (Mayfield 1975). Lastly, studies with only community nest survival rates were excluded because we could not examine variation of individual species nest survival from these data, and a few of these studies grouped shrubland and forest birds together (Rodewald and Yahner 2001, Knutson et al. 2004).

Biases related to literature searching or due to the publication of studies are possible when conducting meta-analyses (Woodcock et al. 2014). A "file drawer effect" can sometimes occur when unpublished data are excluded (or are unknown to the authors), if unpublished data and studies have proportionally fewer significant findings than data from published studies (Arnqvist and Wooster 1995, Gurevitch and Hedges 1999). However, we did find a number of published studies that presented non-significant results (e.g., King et al. 2001, Moorman et al. 2002) and included these in our meta-analysis. Additionally, we included a random effect of study in our analyses, which can account for variation among studies. Although we could not quantitatively examine publication biases via funnel plots, given that we were not examining effect sizes in our analyses, similar meta-analyses have found no evidence for publication bias when examining nest survival and edge effects (Batáry and Báldi 2004, Vetter et al. 2013). Nevertheless, we cannot completely rule out that publication bias was present in our study, and the relationships we observed could potentially be exaggerated (Yang et al. 2023).

We collected a suite of variables from each study, including bird species, nest survival, mechanism of nest survival (e.g., depredation, abandonment), distance-to-edge bin, edge type, and the year of the study and its location. For each bird species and distance-to-edge bin within each study, we recorded the nest survival or depredation rate (including daily nest survival, daily nest predation, nest success across a nesting cycle), and the number of nests. Most studies had data presented in tables, but for some studies, data were only presented in figures. We used Web Plot Digitizer Version 4.1 (Rohatgi 2018) to obtain data from figures. One author (SLM) screened the articles and extracted data from the studies, and another author (MEA) reviewed the extracted data.

Studies recorded daily survival rates, nest survival during a given nesting cycle, or other nest survival metrics, and they used a variety of methods (e.g., Mayfield 1975, Dinsmore et al. 2002, Hazler 2004, Shaffer 2004) to analyze nest success. We standardized all presented values to nest survival calculated for the entire nesting cycle (which better fit a normal distribution than daily nest survival). To convert daily nest survival (DNS) into nest survival during a given nesting cycle, we obtained nesting interval length in days for each species of interest (Billerman et al. 2022). We then calculated nest survival for a nesting cycle with the following equation: Nest survival = DNS<sup>Nesting days</sup>. Daily nest survival values were highly correlated with our standardized nest success metric (nest survival during a nesting cycle; r = 0.95).

We standardized distance-to-edge values using midpoints of the distance-to-edge bins within each study. For instance, if the original study had a distance-to-edge bin of 100-200 m for a set of nests, the midpoint we assigned to the nests was 150 m. When the distance-to-edge bins were open-ended (e.g., > 200 m from the edge), we reached out to the original authors of the study in an attempt to determine the end of the range. For the small percentage of data points for which we were unable to determine the farthest distance from an edge in a given study (7%), we used an estimated midpoint value by adding 50 m to the start of the bin (e.g., > 200 m from the edge was assigned a midpoint distanceto-edge value of 250 m). The midpoint values of distance-to-edge bins within each primary study were then used as our main predictor variable in our analyses. Although our analysis method did not allow us to include studies that examined a continuous distance-to-edge relationship with nest success, many studies were still applicable and had nest survival values grouped in discrete distance-to-edge bins (Table 1).

Using *Birds of the World* (Billerman et al. 2022) species accounts, we also classified the nest placement of each species as either lownesting, often ground-nesting species, or higher-nesting, shruband tree-nesting species. We defined low-nesting species as nesting on average < 1.0 m in height, while higher-nesting species nesting on average > 1.0 m (DeGregorio et al. 2016). We note that a minority of the species included in our study, e.g., Yellow-breasted Chat (*Icteria virens*), Prairie Warbler (*Setophaga discolor*), often nest along a gradient of heights both above and below 1 m, but these species and data points represent a small percentage of the species and data examined overall.

We were originally also interested in examining edge type (e.g., silvicultural, agricultural, or road edges) in our analyses. However, most (75%) of our included primary studies solely examined silvicultural edges (e.g., clearcut and mature forest border), and a few additional studies combined edge types (Burke and Nol 2000, Newell and Kostalos 2007). Thus, comparisons among edge types were not feasible in our meta-analysis.

#### Data Analysis

We conducted a regression-type meta-analysis (Schlossberg and King 2009, Akresh et al. 2021, 2023) using primary data rather than examining effect sizes (Hedges et al. 1999). Effect sizes and common meta-analytical metrics such as Hedges' d or Cohen's d are calculated with sample sizes and standard deviations (Hedges et al. 1999). However, studies identified in our literature search presented and computed nest survival data in a variety of different formats (e.g., daily survival rates, nest survival during a given nesting cycle). Because sample sizes could not be standardized across all studies as daily observation days versus as nests, and some studies had missing information for standard deviations or standard errors, it was not possible to generate consistent effect sizes among studies that conducted different analyses. Several previous examinations of nest survival studies and forestry metaanalyses have also noted similar issues with standardization using common meta-analytical metrics (Lahti 2001, Stephens et al. 2004, Spake and Doncaster 2017). We therefore conducted linear mixed models, using standardized, primary data of nest survival values within distance-to-edge bins.

 Table 1. Studies included in our meta-analysis examining nest survival and distance-to-edge in mature forest and shrubland avian species in eastern North America.

Study	Location	Year	Number of nests in study	Species <sup>†</sup>	Distance-to-edge bins (m)	Nest failure due to depredation in study's nes survival values (%)	
Akresh 2012	MA 2008–2011		265	PRAW	0–10, 10–20, 20–50, 50–100, 100–250	$100^{*}$	
Akresh and King 2016	MA	2008-2013	21	EWPW	0-50, 50-250	100	
Burke and Nol 2000	Ontario	1996–1997	298	OVEN, RBGR, REVI, VEER, WOTH	0–50, 50–100, 101–200, > 200	$100^{\ddagger}$	
Driscoll and Donovan 2004	NY	1998-2000	230	WOTH	0-200, > 200	$100^{\ddagger}$	
Flaspohler et al. 2001b	WI	1995–1997	392	BTNW, HETH, LEFL, OVEN, RBGR, REVI, SCTA	0–100, 101–200, 201–300, 301–400, 401–950 or 0–300, 300–950	$100^{\ddagger}$	
Friesen et al. 1999	Ontario	1996–2002	217	RBGR, WOTH	0-5, 5-25, 25-50, 50-100, > 100	92 for RBGR, 75 for WOTH	
King and Byers 2002	MA	1999-2000	42	CSWA	0-10, 10-20, 20-50	$100^{\ddagger}$	
King et al. 1996	NH	1992	91	OVEN	0-200, 201-400	89	
King et al. 2001	NH	1994-1996	156	CSWA	$0-10, 10-110^{\$}$	Unknown	
King et al. 2009	MA	2002-2003	199	COYE, CSWA, GRCA, PRAW, EATO	0-10, 10-20, 20-50	94	
Manolis et al. 2002	MN	1992-1998	349	HETH, OVEN	0–140, 141–274, 275–531 <sup>§</sup>	$100^{\ddagger}$	
Moorman et al. 2002	SC	1996-1999	99	HOWA	0-50, 51-100, > 100	83	
Newell and Kostalos 2007	PA	2003-2004	127	WOTH	0-200, 200-536 <sup>§</sup>	Unknown	
Robinson and Wilcove 1994	IL	1989	196	ACFL, WOTH	0–99, 100–199, 200–399, 400–800	$100^{\ddagger}$	
Streby and Anderson 2011	MN	2007-2008	185	OVEN	0-100, 100-1356	90	
Woodward et al. 2001	МО	1997–1999	311	FISP, INBU, PRAW, YBCH	0-20, 21-40, 40-123	$100^{\ddagger}$	

<sup>†</sup>Shrubland species: AMRO = American Robin (*Turdus migratorius*), COYE = Common Yellowthroat (*Geothlypis trichas*), CSWA = Chestnut-sided Warbler (*Setophaga pensylvanica*), EATO = Eastern Towhee (*Pipilo erythrophthalmus*), EWPW = Eastern Whip-poor-will (*Antrostomus vociferus*), FISP = Field Sparrow (*Spizella pusilla*), GRCA = Gray Catbird (*Dumetella carolinensis*), INBU = Indigo Bunting (*Passerina cyanea*), PRAW = Prairie Warbler (*Setophaga discolor*), and YBCH = Yellow-breasted Chat (*Icteria virens*).

Forest species: ACFL = Acadian Flycatcher (*Empidonax virescens*), BTNW = Black-throated Green Warbler (*Setophaga virens*), HETH = Hermit Thrush (*Catharus guttatus*), HOWA = Hooded Warbler (*Setophaga citrina*), OVEN = Ovenbird (*Seiurus aurocapilla*), RBGR = Rose-breasted Grosbeak (*Pheucticus ludovicianus*), REVI = Red-eyed Vireo (*Vireo olivaceus*), SCTA = Scarlet Tanager (*Piranga olivacea*), VEER = Veery (*Catharus fuscescens*), and WOTH = Wood Thrush (*Hylocichla mustelina*). <sup>†</sup> Other failure types (besides nest depredation) were not included in nest survival analyses of the primary study.

<sup>§</sup> Maximum distance-to-edge of a nest in this study was obtained from author communication.

We primarily examined published data that could be directly used in our meta-analysis, but to increase sample sizes, we also used three raw datasets from studies with nest survival data, but the data were not previously examined with distance-to-edge bins (King et al. 2009, Akresh 2012, Akresh and King 2016). Using these raw datasets, we first analyzed the effects of distance-toedge in categorical bins on daily nest survival for individual species using the program MARK through the R package "RMARK" (Laake 2013). A nest survival model was run for any species with more than 10 nests in each raw dataset used. Although we had continuous distance-to-edge measurements for each nest in our data, we grouped nests in distance-to-edge bins to allow for the combination of these data with the other published studies in our meta-analysis. Distance-to-edge bin sizes were selected to encompass a suitable number of nests per bin for the nest survival analysis and varied by each dataset. For Akresh (2012), we used bins of 0-10, 10-20, 20-50, 50-100, and 100-250 m; for King et al. (2009), we used bins of 0-10, 10-20, and 20-50 m; and for Akresh and King (2016), we used bins of 0-50 and 50-250 m because of small sample sizes. When conducting the nest survival models on these raw individual-nest data, our predictor was the categorical variable of distance-to-edge bins, with the response variable of daily nest survival. The daily nest survival values per bin obtained from these models were then included in the overall meta-analysis dataset, standardized into nest survival during a given nesting cycle, and matched with midpoint values of the distance-toedge bins, similar to the data used from other studies.

Nest success values for each species within a study were weighted based on the number of nests and the range of the distance-to-edge bin. We first computed a weight based on the number of nests for each species  $(W_n)$ : fewer than 10 nests in a distance-to-edge bin were assigned a W<sub>n</sub> of 0.33, between 10 and 30 nests a W<sub>n</sub> of 0.66, and more than 30 nests were weighted 1. If the study did not specify the number of nests within each distance-to-edge bin, we assigned a W<sub>n</sub> of 0.33 for these values. We did not use the actual number of nests on a continuous scale for W<sub>n</sub> because we suspected the accuracy in the values of nest survival would plateau after more than 30 nests (Akresh 2012). Additionally, if there were lower numbers of nests (e.g., < 30), only 1–2 individual nests could dramatically alter the nest success rate (e.g., by 5-20%), but nest success would be less influenced by individual (and potentially outlier) nests when the sample size was greater than 30. Our second weight metric (W<sub>2</sub>) attempted to account for how well the midpoint of the distance-toedge bin was actually reflecting the distance-to-edge. We were determined by proximity to edge and width of the distance-to-edge bin. For any distance-to-edge bin recorded in studies that was greater than 150 m from the edge (e.g., 150-300 m, 200-400 m, etc.), these values were given a  $W_{e}$  of 1. For nest success values in bins < 150 m from the edge, data with 50 m bin widths or smaller were given a  $W_e$  of 1, data with 50–100 m bin widths were 0.66, and data with a 0–150 m range were 0.33  $W_e$ . We set these  $W_e$  values because midpoints of a distance-to-edge bin of 50–100 m and a distance-to-edge bin of 0–150 m are both 75 m, but these bins differ in precision. Especially for distance bins close to edges (< 150 m from the edge), bins with low precision may be less useful in assessing edge effects. To obtain an overall weight for each data point ( $W_o$ ), we multiplied the number of nests weight by the distance-to-edge weight ( $W_o = W_n \ge W_e$ ).

Mixed models were fit to Gaussian distributions separately for each bird species guild, i.e., mature forest and shrubland. Our standardized nest success metric (nest survival for the entire nesting cycle) was the response variable. We also included random effects of species and study in all models, which allowed us to account for various analysis methods, geographical locations, and designs of different studies (Zuur et al. 2009). Model assumptions such as linearity, normality and homoscedasticity of residuals, and influential points were checked via exploring the data and model output in scatterplots, histograms, residuals versus fitted plots, normal Q-Q plots, and residuals versus leverage plots (Zuur et al. 2010, Lüdecke et al. 2021). We used weighted regression models and therefore, each data point was weighted via the aforementioned weight classifications. Direction and significance of results were similar with and without including weights in the models, yet we chose to present our findings with weights to account for the number of nests and the range of distance-to-edge bins in the primary studies.

Akaike's information criterion corrected for small sample sizes (AIC<sub>a</sub>) and Akaike's model weights were used to compare models within candidate model sets for each bird guild (Burnham and Anderson 2002). In each model set, we fit a "null" linear mixed model (with random effects). A second model included a fixed continuous predictor variable of distance-to-edge (using midpoint values of the distance-to-edge bins), and two additional models examined additive and interactive effects (with distance-to-edge) of nest placement. To assist with model convergence and to incorporate interactions, we standardized the continuous distanceto-edge predictor variable to a mean of 0 and SD of 1 (Bates et al. 2015). We defined the top-supported models for each bird guild as models within 2 AIC, of the best-ranking model and presented model parameters and 95% confidence intervals (using the Wald method) from the top models. We defined significant predictor variables as those that did not have 95% confidence intervals overlapping 0 in the top models. We also examined the amount of variance explained by the fixed and random effects, i.e., R<sup>2</sup> values and unadjusted intra-class correlation coefficients (ICC) in the top models (Nakagawa et al. 2017).

In addition to examining effects of edges in bird guilds, we were also interested in testing effects in individual species. We tested the effect of distance-to-edge on nest success for the following species that had at least nine observational units (nest survival values at a given distance-to-edge bin midpoint): Wood Thrush (*Hylocichla mustelina*), Ovenbird (*Seiurus aurocapilla*), Hermit Thrush, Prairie Warbler, and Rose-breasted Grosbeak (*Pheucticus ludovicianus*). Given small sample sizes and concern about overfitting models, we did not include other fixed predictor variables in the individual species models but did include a random effect of study (Schielzeth et al. 2020, Gomes 2022, Oberpriller et al. 2022). We examined  $R^2$  and ICC values for each species.

All analyses were conducted using the R Statistical Program, version 4.2.1 (R Core Team 2022); the lme4 package was used to conduct mixed models (Bates et al. 2015), the MuMIn package was used to compute  $AIC_c$  values (Bartoń 2022), and the performance package to compute  $R^2$  and ICC values (Lüdecke et al. 2021). A post-hoc "loess" smoothing curve of the mature forest bird relationship of distance-to-edge and nest success was created using the ggplot2 package, with the loess method and a span of 0.95 (Wickham 2016). The ggeffects package was used for plotting predictions from model outputs (Lüdecke 2018).

#### RESULTS

In total, we downloaded and reviewed 62 manuscripts, of which 16 studies fit our selection criteria (Table 1). Of the 16 studies, 56% were on a single species, whereas 44% had data for multiple species. From a total of 20 species with nest survival data, we classified Chestnut-sided Warbler (*Setophaga pensylvanica*), Common Yellowthroat (*Geothlypis trichas*), Eastern Towhee (*Pipilo erythrophthalmus*), Eastern Whip-poor-will (*Antrostomus vociferus*), Field Sparrow (*Spizella pusilla*), Hermit Thrush, Hooded Warbler (*Setophaga citrina*), Indigo Bunting (*Passerina cyanea*), Ovenbird, Veery (*Catharus fuscescens*), and Yellowbreasted Chat as low-nesting species and the other remaining species as higher-nesting species. Distance-to-edge bin sizes and ranges varied greatly among studies (Table 1) and were often smaller in shrubland habitats (e.g., King and Byers 2002).

Nest failure was primarily due to nest depredation in all studies included in our analyses (Table 1). Seven of the primary studies did not include nest failures due to other mechanisms (e.g., brood parasitism, abandonment, weather events) in their original nest survival analyses or values per distance-to-edge bin. For the remaining studies, depredation accounted for 75-100% of nest failures depending on the study and species within the study (Table 1).

We compiled 83 data points of nest survival from 10 studies on 11 mature forest bird species. For mature forest birds, the best-supported models included a model with additive terms of distance-to-edge and nest placement, and a model with just distance-to-edge (Table 2). However, the additive variable of nest placement was not significant ( $\beta = 12.472$ , SE = 6.993, CI = -1.234 to 26.178).

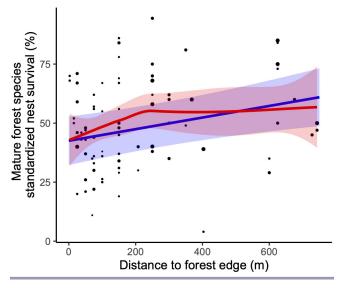
In the simpler, more parsimonious mature forest birds' model with only distance-to-edge (for fixed effects), nest success significantly decreased closer to edges (B = 5.098, SE = 1.701, CI = 1.765– 8.432; Fig. 1). In this simpler model, the proportion of variance explained by the random effects of species and study was relatively high (0.58) compared to the variance explained by the fixed effect of distance-to-edge (0.09). A post-hoc loess smoothing curve fit to the data showed a distinct threshold of nest success increasing steadily from 0 m up to approximately 250 m from the edge, after which nest success remained fairly constant as distance to edge increased past 250 m (Fig. 1). **Table 2.** Comparison of linear mixed models examining effects on nest survival in mature forest birds. Presented are the models, number of parameters (K), Akaike's information criterion value corrected for small sample sizes (AIC<sub>c</sub>), difference in AIC<sub>c</sub> from the top model ( $\Delta$ AIC<sub>c</sub>), and model weight (W<sub>i</sub>).

Model	K	AIC	$\Delta AIC_{c}$	W,
Distance-to-edge + nest placement	5	713.33	0	0.52
Distance-to-edge	4	714.46	1.01	0.31
Distance-to-edge * nest placement	6	715.79	2.34	0.16
Null	3	720.66	7.22	0.01

**Table 3.** Linear mixed models examining effects on nest survival in shrubland birds. Presented are the models, number of parameters (K), Akaike's information criterion value corrected for small sample sizes (AIC<sub>c</sub>), difference in AIC<sub>c</sub> from the top model ( $\Delta$ AIC<sub>c</sub>), and model weight (W<sub>i</sub>).

Model	K	AIC	$\Delta AIC_{c}$	W
Null	3	338.38	0	0.71
Distance-to-edge	4	340.80	2.42	0.21
Distance-to-edge + nest placement	5	343.18	4.79	0.06
Distance-to-edge * nest placement	6	345.62	7.23	0.02

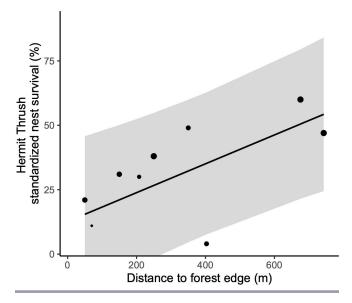
Fig. 1. Relationship between distance to forest edge and standardized nest survival for mature forest bird species. The blue line is the predicted relationship from a weighted linear mixed model (LMM), while the red line is predicted from a loess smoothing curve with a span of 0.95. Shading represents the 95% confidence intervals. Points indicate values from individual studies, with larger points indicating higher weights in the LMM (range of weights = 0.11-1.00).



We compiled 39 data points from 6 studies on 9 shrubland bird species. For shrubland birds, the null model was the top model (Table 3), and thus our examined predictors did not influence nest success for shrubland species (Appendix 1, Fig. A1). Similar to mature forest birds, the variance explained by the random effects of species and study was high (0.73) for shrubland birds.

Examining individual species, Hermit Thrush had a significant positive relationship of increasing nest success as distance-to-edge increased (Fig. 2; Table 4). We did not detect a significant relationship of nest success with distance-to-edge for Ovenbird, Wood Thrush, Prairie Warbler, or Rose-breasted Grosbeak, although the Rose-breasted Grosbeak model had a moderately high (> 0.3) R<sup>2</sup> value (Table 4). There was also considerable variation explained in each individual-species model by the random effect of study (ICC values; Table 4).

**Fig. 2.** Predicted relationship from a weighted linear mixed model with distance to forest edge and standardized nest survival for Hermit Thrush (*Catharus guttatus*). The black line represents the predicted linear regression curve, and the gray shading represents the 95% confidence interval. Points indicate values from individual studies, with larger points indicating higher weights in the model (range of weights = 0.11-0.66).



# DISCUSSION

Our meta-analysis of natural avian nest survival across eastern North America upheld patterns of edge effects observed in previous literature reviews and primary studies (Paton 1994, Batáry and Báldi 2004, Vetter et al. 2013), and presented new synthesized findings in that mature forest bird nest success increases farther from edges, but shrubland specialists do not exhibit the same trend. Our results on mature forest birds are consistent with previous individual studies that have found edges can impact nest survival at some sites, and proximity to edges may indicate less suitable habitat for certain avian species (King et al. 1996, Friesen et al. 1999, Flaspohler et al. 2001a, Poulin and Villard 2011). For shrubland birds, our meta-analysis complements individual studies that have found varied and inconsistent results of the effect of edges on nest survival (e.g., Woodward et al. 2001, Burhans et al. 2002, Weldon and Haddad 2005, Shake et al. 2011).

**Table 4.** Linear mixed model results for individual bird species examining the relationship between distance-to-edge and nest success. We present the number of data points (n), the number of studies that had data for the given species, model parameter estimates of the slope ( $\beta$ ), SE, and 95% CI, percent of the variance accounted by the fixed predictor of distance-to edge ( $R^2$ ), and percent of variance accounted for by the random effect of study (ICC).

Species	n	No. studies	ß	SE	95% CI	R <sup>2</sup>	ICC
Ovenbird (Seiurus aurocapilla)	20	5	2.704	3.017	-3.209 to 8.617	0.04	0.46
Wood Thrush (Hylocichla mustelina)	20	5	4.116	2.932	-1.630 to 9.862	0.09	0.57
Prairie Warbler (Setophaga discolor)	11	3	-6.432	4.206	-14.677 to 1.812	0.17	0.59
Rose-breasted Grosbeak (Pheucticus ludovicianus)	11	3	10.361	6.053	-1.502 to 22.225	0.33	0.37
Hermit Thrush ( <i>Catharus guttatus</i> )	9	2	13.931	3.340	7.385 to 20.476	0.44	0.47

Nest failures within studies were primarily due to nest depredation, and lower nest predation rates farther from edges may be due to lower numbers or activity of predators within interior forests and under increased canopy cover (Marini et al. 1995, Zanette and Jenkins 2000). Edge environments often host abundant nest predators, including avian predators and snakes (Weatherhead and Charland 1985, Chalfoun et al. 2002a, 2002b). Predators might be more abundant or more active near edges because they favor thermal environments, increased food, or other preferred resources in open habitats and these predators encroach into adjacent forest edges (Diaz and Blouin-Demers 2018, Akresh et al. 2022). Predators may also use forest edges for movement, resulting in increased activity near edges (Pedlar et al. 1997, Barding and Nelson 2008).

We observed that nest survival does not continue to increase past 250 m from an edge for mature forest birds, which contrasts with some past global meta-analyses on primarily artificial nests that have noted a cutoff of edge effects at 50 m from an edge (Paton 1994, Batáry and Báldi 2004). However, Flaspohler et al. (2001b), in a natural nest survival study of mature forest birds in Wisconsin, observed a threshold of 300 m. Potentially avian, mammalian, and snake predators that prey on natural nests (Chalfoun et al. 2002b, Cox et al. 2012a), at least in eastern North America, have higher abundance and activity patterns up to 250-300 m from edges, due to their home range sizes and movement patterns along edges (Durner and Gates 1993, Billerman et al. 2022). Further studies identifying the specific predators depredating nests along edges would be useful to elucidate the mechanisms behind observed edge effects on nest survival (Benson et al. 2010a, Cox et al. 2012b, DeGregorio et al. 2014).

One potential reason nest predation on shrubland birds was unrelated to distance from edges was because most of the shrubland nests in studies we examined were found within 50 m of an edge and were thus within an area of high predation risk. Few studies of shrubland species included nests greater than 100 m from edges, probably due to the relatively small size of most shrubby openings examined within primary studies, and therefore analyses on more interior nest success for these birds was not possible. Nonetheless, many studies have found a lack of edge effects on shrubland bird nest survival (Woodward et al. 2001, Riddle and Moorman 2010, Weatherhead et al. 2010), perhaps because increased small mammal and snake abundance or increased activity of other predators are often throughout shrubland habitats, rather than being concentrated on edges (Fantz and Renken 2005, Schlossberg and King 2007, Akresh et al. 2017).

Similar to previous meta-analyses (Murcia 1995, Lahti 2001, Batáry and Báldi 2004, Vetter et al. 2013), a relatively large amount of variation in nest survival was explained by the random effects of species and study in our meta-analysis. Examining individual species, only Hermit Thrush had a significant increase in nest success as distance-to-edge increased, consistent with past studies on this species (Flaspohler et al. 2001b, Manolis et al. 2002). Flaspohler et al. (2001b) reported ground-nesters, such as the Hermit Thrush, were more vulnerable to edge effects than above-ground nesters; however, nest placement (low versus higher nesting species) did not significantly interact with edge distance to influence nest survival in our meta-analysis. The other individual species analyses did not show significant trends in nesting success relative to edge distance, but small samples size within species likely hindered our ability to detect significant relationships based on the CIs of the parameters. Overall, variation of edge effects among species or sites in our metaanalysis was not unexpected and could be due to other aspects we did not examine, such as other landscape- and local-scale patterns at sites (varying forest types, vegetation structure, alternative prey availability, or predator composition), or other avian species' behaviors and susceptibility to predators unrelated to nest placement (Chalfoun et al. 2002b, Thompson et al. 2002, 2007).

Most of the studies included in our meta-analysis were situated in forest-dominated landscapes with silvicultural edges (due to group-selection cuts or clearcuts), or otherwise had edges between open-canopy shrublands and closed-canopy mature forest (e.g., power line corridors). We therefore could not compare distanceto-edge effects among other edge types, such as agricultural edges, roads, lakes, or urban development. Nonetheless, past studies have found edge type can influence nest survival (Suarez et al. 1997, King and DeGraaf 2002, Falk et al. 2011, Shake et al. 2011), and this variation in nest survival among edge types may be specific to individual sites and predator compositions (DeGregorio et al. 2014, 2016). In addition, some past studies have found that surrounding land cover can influence edge effects, i.e., decreased edge effects in more forested sites (Hanski et al. 1996, Duguay et al. 2001, Driscoll and Donovan 2004, Cox et al. 2012b), but most of the included studies in our analyses were in forest dominated landscapes with < 15% agricultural cover in the surrounding 1-km of the study site. We thus could not adequately examine landscape effects, especially at individual nests, in our analyses, despite the possibility that interactions with land cover could potentially influence the impact of edges on nest survival (Chalfoun et al. 2002b, Chapa-Vargas and Robinson 2013).

Concerns have been raised against using nest success values as a sole indicator of productivity (Thompson et al. 2001, Jones et al. 2005, Donovan et al. 2008), but there is a lack of existing data on the impacts of edges on other fecundity metrics. Nest survival only examines a single nesting cycle and does not consider partial brood losses (Hoover 2003) or any re-nesting attempts after nest failure (King et al. 1996). Our study also did not consider postfledging survival, an important metric of seasonal fecundity (King et al. 2006, Streby and Anderson 2011, Cox et al. 2014). Unfortunately, relatively few studies have examined full-season productivity measures in relation to edges, and the studies that have looked at edge effects and full-season productivity have found inconsistent results. Petersen et al. (2016) found a reduction of edge habitat led to an increase in full-season productivity for Golden-winged Warblers (Vermivora chrysoptera), but other studies have found edge habitats may increase (Jenkins et al. 2016) or have no effect on survival of post-fledging birds (Schlossberg et al. 2018). Post-fledging habitat selection and survival can differ from nesting habitat and survival (Jenkins et al. 2016, Adalsteinsson et al. 2018), and most mature forest bird species select and disperse to shrubland habitat during the post-fledging period (Akresh et al. 2009, Chandler et al. 2012). Additional studies of post-fledging survival will provide further information on the influence of edges for more species.

# CONCLUSION

Our meta-analysis of edge effects on nest survival supported the results of many individual studies indicating nest survival is typically lower for mature forest birds nesting near edges in temperate mature forests (Vetter et al. 2013). Forest stands greater than 250 m from edges can be classified as core areas, in which edge effects on avian nests are absent for mature forest breeding birds of conservation concern. Nevertheless, although the creation of edges through forest management or other human activities can be expected to reduce nest success, these edge effects may be compensated to some extent through renesting (King et al. 1996), or the provision of post-fledging habitat in harvested areas (Chandler et al. 2012). A diversity of forest age classes in the landscape created by forest management, which can form some forest edges, may still overall benefit the entire community of shrubland and forest birds (Twedt 2020, Akresh et al. 2021, 2023), and many other taxa that are adapted to natural and historic disturbances in eastern North American forests (Litvaitis et al. 2003, Leuenberger et al. 2016, Roberts et al. 2017).

# **Author Contributions:**

All authors conceived the manuscript idea. SLM conducted the literature search, and MEA and SLM curated the dataset, conducted statistical analyses, and wrote the paper. DIK obtained funding, led the project administration, and assisted with revising and editing the manuscript.

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# **Data Availability:**

The data and code are archived with Harvard Dataverse at the following link: <u>https://doi.org/10.7910/DVN/MBVRNT</u>

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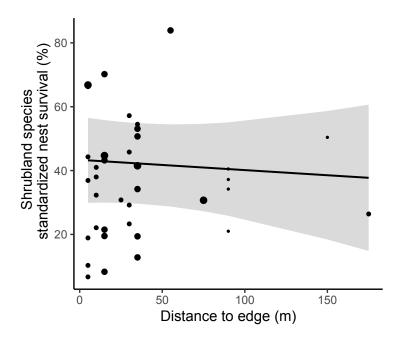
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**Appendix 1.** A meta-analysis of edge effects on nesting success in forest and shrubland birds of Eastern North America.

Supplemental figure.



**Fig. A1**. Relationship between distance to edge and standardized nest survival for shrubland bird species. The black line represents the predicted linear regression curve, and the grey shading represents the 95% confidence interval ( $\beta = -0.033$ , SE = 0.069, CI = -0.168 - 0.103). Points indicate values from individual studies, with larger points indicating higher weights in the model (range of weights = 0.22-1.00).