



Least Flycatcher nest success increases at sites with extensive northern hardwood cover at the landscape scale

El éxito de nidificación del Mosquero Mínimo aumenta en sitios con amplia cobertura de bosque latifoliado del norte a escala de paisaje

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ABSTRACT. The Least Flycatcher (*Empidonax minimus*), a small migratory songbird, has experienced significant population declines across its North American range over the past five decades. Whereas the causes of this decline remain complex and multifaceted, habitat loss, fragmentation, and changes in forest composition on the breeding grounds are suspected to play a critical role. To better understand the relationship between breeding habitat and reproductive success, we estimated nesting success across a gradient of increasing forest cover, i.e., 46% to 85%, at seven sites in Minnesota. Data from 171 nests revealed substantial variation in nesting success, ranging from 37% at the site with the lowest forest cover to 94% at the most forested site. Nesting success was significantly higher in landscapes dominated by northern hardwood forests, particularly those with abundant sugar maple (*Acer saccharum*), and in nests located lower in the canopy. These findings suggest that forest composition and landscape-scale forest cover are important predictors of reproductive success in Least Flycatchers. Although limited to a single breeding season, this study contributes to our understanding of the species' breeding ecology and the importance of extensive northern hardwood forest, especially of mixed-age sugar maple and paper birch (*Betula papyrifera*), at both local, i.e., 100-m, and landscape, i.e., 10-km, scales.

RESUMEN. El Mosquero Mínimo (*Empidonax minimus*), un pequeño pájaro cantor migratorio, ha experimentado significativos descensos poblacionales en toda su área de distribución norteamericana durante las últimas cinco décadas. Si bien las causas de este declive siguen siendo complejas y multifacéticas, se sospecha que la pérdida de hábitat, la fragmentación y los cambios en la composición forestal en las zonas de reproducción desempeñan un papel fundamental. Para comprender mejor la relación entre el hábitat de reproducción y el éxito reproductivo, estimamos el éxito de nidificación a lo largo de un gradiente de cobertura forestal creciente, i.e., 46% a 85%, en siete sitios en Minnesota. Los datos de 171 nidos revelaron una variación sustancial en el éxito de nidificación, que va del 37% en el sitio con la cobertura forestal más baja hasta el 94% en el sitio más boscoso. El éxito de nidificación fue significativamente mayor en paisajes dominados por bosques latifoliados del norte, particularmente aquellos con abundante arce azucarero (*Acer saccharum*), y en nidos ubicados en la parte baja del dosel. Estos hallazgos sugieren que la composición del bosque y la cobertura forestal a escala de paisaje son importantes predictores del éxito reproductivo del Mosquero Mínimo. Aunque limitado a una sola temporada reproductiva, este estudio contribuye a nuestra comprensión de la ecología reproductiva de la especie y de la importancia de los extensos bosques latifoliados del norte, especialmente aquellos con arces azucareros y abedules paperíferos (*Betula papyrifera*) de distintas edades, tanto a escala local, i.e., 100 m, como a escala de paisaje, i.e., 10 km.

Key Words: *Least Flycatcher*; nest survival; Great Lakes

INTRODUCTION

The Least Flycatcher (*Empidonax minimus*), a small migratory songbird, has experienced significant population declines across its range. North American Breeding Bird Survey data from 1966 to 2022 reveal average annual declines of 1.2% in the United States, 0.9% in Canada, and 1.0% range wide (Hostetler et al. 2023). Within the Great Lakes region, declines are particularly pronounced, with Minnesota experiencing a 1.16% annual decrease, Michigan 1.85%, Wisconsin 2.47%, and Ontario 1.03%. The designation of the Least Flycatcher as a “common species in steep decline” by Partners in Flight (<https://www.partnersinflight.org/what-we-do/science/databases>) highlights the urgency of identifying the factors contributing to its population decline. Although the species is currently classified as Least Concern by the International Union for Conservation of Nature (<https://www.iucnredlist.org>) because of its extensive range and large

global population, ongoing declines raise concern for future risk and may warrant a reassessment of its conservation status if these trends continue (Spiller and Dettmers 2019). Identifying the precise drivers of population decline remains challenging; however, key factors likely include reproductive success, which is heavily influenced by factors such as predation and nest parasitism, changes in breeding habitat associated with forest succession and fragmentation, and limited understanding of migration and overwintering survival (Robinson et al. 1995, Tarof and Briski 2020, de Zwaan et al. 2022, Van Brempt et al. 2023, Pfannmuller et al. 2024).

Habitat loss, fragmentation, and homogenization on the breeding grounds for many forest birds, including Least Flycatcher, is a significant concern. Overall, these factors have an impact on habitat quality by decreasing the diversity of resources available, affecting foraging success, increasing vulnerability to predators,

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and they can result in decreased breeding productivity of birds (Fahrig 1998, Stephens et al. 2003, de Souza et al. 2022, Wayman et al. 2024). Past forestry practices can influence many current habitat factors such as tree-species composition, age-class distribution, and understory density that can have a direct impact on factors related to breeding productivity such as nest-site availability and foraging opportunities (Annand and Thompson 1997, Burke and Nol 1998, Schulte et al. 2007, Hart and Chen 2008, Cordeiro Pereira et al. 2024). However, observed avian numerical and demographic response to forestry practices is complex and highly contextual (Duguay et al. 2001, Cordeiro Pereira et al. 2024).

Nest success, the proportion of nests that successfully fledge young, is an important component of species' reproductive output and is a key indicator of population health (Etterson et al. 2011). It is influenced by a complex interplay of factors, including habitat quality, resource availability, and environmental conditions (Lebreton et al. 1992, Germain et al. 2015, Crombie and Arcese 2018). High quality habitats provide the necessary resources for successful nesting, such as suitable nest sites, abundant food, and cover from predators (Thompson 2007). Nest-site selection is a key behavior that reduces predation risk (Martin 1993), whereas ample food resources are vital for parents to provision their young (Van Eerden et al. 2025). Habitat fragmentation can have a negative impact on nesting success by increasing predator access (Robinson et al. 1995, Chalfoun et al. 2002), highlighting the importance of landscape context and scale (Donovan et al. 1997). These factors contribute to higher nest success rates (Robinson et al. 1995, Johnson et al. 2012) and increased productivity, ultimately supporting larger and more stable populations. Conversely, low quality habitats or those affected by habitat loss and fragmentation can negatively affect nest success and limit reproductive output (Mattsson and Niemi 2006, Etterson et al. 2014).

Studies focusing on Least Flycatcher have shown a wide range of nest success rates, likely highlighting the importance of habitat quality. For example, Mayfield estimates of nest success for Least Flycatchers have ranged from 20% to 85% in the Great Lakes Region (Hanski et al. 1996, Sammler et al. 1999, Flaspohler et al. 2001). In a large-scale study of nest success and forest fragmentation in the upper Midwest, USA, that included nine bird species, including the Acadian Flycatcher (*Empidonax virens*), congeneric to Least Flycatcher, Robinson et al. (1995) found a positive correlation between daily nest survival and the percentage of forested landscape within 10 km, further emphasizing the link between habitat availability and reproductive success. These findings underscore the importance of conserving and restoring high quality habitats to support healthy bird populations.

This study aimed to clarify how habitat characteristics within a timber-managed forest, which consists of a mosaic of stands of varying ages, influence nesting success in the Least Flycatcher. Specifically, we examined how reproductive outcomes vary among seven sites with differing amount of forest cover in the landscape at the 10-km scale. Percent of common upland forest types, i.e., northern hardwoods and aspen-birch, nest-tree species, nest height, plant height, and nest-tree diameter were also considered as covariates to help identify which features most

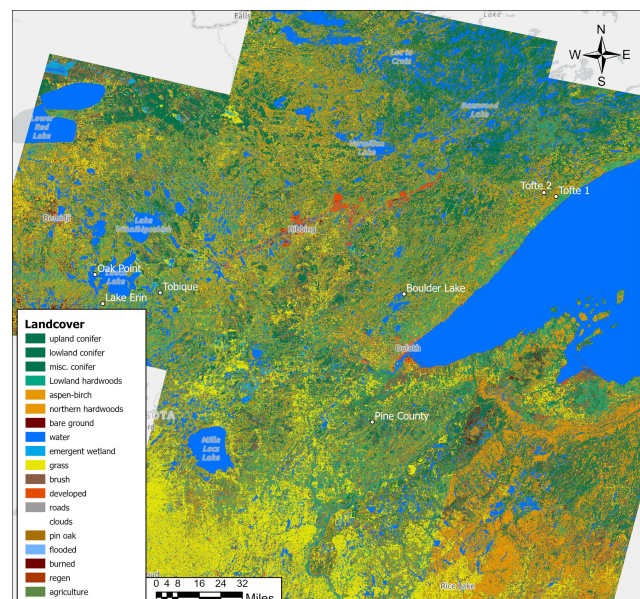
strongly predict success. By focusing on both local and landscape-scale variables, particularly forest cover, this research addresses important knowledge gaps in the species' breeding ecology.

METHODS

Study area

The primary breeding range of Least Flycatcher in Minnesota includes the upland forested regions of the state (Green and Janssen 1975, Pfannmuller et al. 2024). Our site selection aimed to capture the gradient of fragmentation that exists from north-central to northeastern Minnesota, with sites also representing a range of mature, i.e., > 60 years post stand-replacing disturbance, forest cover, which is dominated, i.e., > 50%, by aspen-birch and northern-hardwood cover types (Mladenoff et al. 1997). Leveraging existing breeding-bird count data, we identified seven study sites within this gradient where Least Flycatchers had been previously observed and where breeding populations were known to exist (Niemi et al. 2016). Sampling efforts focused on the north-central region ($n = 3$ sites, i.e., Oak Point, Tobique, and Lake Erin, all within Chippewa National Forest). Oak Point and Tobique were randomly selected from sites with Least Flycatchers detected during 1991 to 1995 in the course of a long term monitoring program (Niemi et al. 2016), whereas nest success at Lake Erin had been previously studied (Hanski et al. 1996). In east-central Minnesota, one site, i.e., Pine County, was selected based on breeding-bird monitoring data and, in northeastern Minnesota, two sites, i.e., Tofte 1 and Tofte 2, were randomly selected from sites within the Superior National Forest that had Least Flycatcher detections during 1991-to-1995-point count surveys. Last, we chose Boulder Lake, a site with a previously studied Least Flycatcher population, for its intermediate location between the north-central and northeastern sites (Fig. 1).

Fig. 1. Map of the study area and forest-cover types in northern Minnesota, displaying the locations of the seven study sites surveyed for Least Flycatcher nest success.



Forest structure at these sites has been heavily influenced by historical and ongoing forest management practices in Northeastern Minnesota (Schulte et al. 2007). Virtually all the forests of the region were logged during the late 19th and early 20th century (Friedman and Reich 2005). Remaining forest stands, including the sites investigated herein, are managed for diverse objectives, including hunting, fishing, outdoor recreation, and timber production (<https://www.fs.usda.gov/r09/chippewa>, <https://www.fs.usda.gov/r09/superior>). Clearcutting remains a common practice across the state in aspen-birch stands whereas single-tree selection or group selection methods are commonly used in northern hardwood stands. In general, these activities have left a landscape with forests shifted toward mixed-age deciduous forests (Table 1) in the upland habitats preferred by Least Flycatchers and where our sites occurred (Mladenoff et al. 1997, Friedman and Reich 2005), with the oldest trees ranging from 60 to 80 years.

Table 1. Percent composition of each forest type and total forest cover within 10 km of each site based on remote sensing data 1987–1992.

	Percent of total forest within 10 km in each cover class					Total forest area within 10 km (km ²)
	Upland conifer	Lowland conifer	Lowland hardwoods	Aspen-birch	Northern hardwoods	
Lake Erin	5.5	2.9	0.4	65.1	26.0	153
Oak Point	4.7	9.1	0.5	53.6	32.1	100
Tobique	5.8	12.8	2.1	51.1	28.2	193
Pine County	16.9	15.5	9.7	29.8	28.2	221
Boulder Lake	11.9	13.8	3.8	54.3	16.2	214
Tofte 1	7.1	6.8	2.1	55.6	28.4	220
Tofte 2	11.3	9.8	2.1	51.8	25.0	258

At each of the seven sites, we established plots of at least 60 ha overlaid by a 50 x 50 m grid to systematically search the site and determine nest locations. Locational data for grid corners were measured with a global positioning system with a base station to an accuracy of about 10 m and entered in ArcMap Geographic Information System (ESRI 1987). Following Robinson et al. (1995), we used classified satellite imagery (Wolter et al. 1995) to quantify the proportion of forest cover within a 10-km radius surrounding each study site. Forest cover was defined as any mature, i.e., > 60 years, or secondary, i.e., < 60 years but with closed canopy, forested areas, and excluded recently logged sites, such as residential or agricultural areas, roads, and non-forested wetlands.

Nesting data

In 1996, from mid-May to the end of July, teams of two to four individuals systematically searched each site at two-to-three-day intervals. The location of each nest was marked with flagging placed at least 10 m from the nest. Nests were monitored every three to four days until just before fledging, when they were checked daily. After locating nests or when checking nests, we avoided damaging vegetation or making dead-end trails to the nest. Successful nests were defined as (1) those that fledged at least one young; or (2) for very high nests, if the parents were seen feeding nestlings or tending the nest throughout the incubation and nestling periods (Hanski et al. 1996). The following data were gathered at each nest: (1) species of tree or shrub used for nesting; (2) measured height of nest; (3) estimated height of nest tree; and

(4) measured diameter at breast height (dbh) of nest tree or shrub. Canopy cover types surrounding each nest within a 100-m radius circle (31,400 m², 3.14 ha) were identified and classified into one of three cover types, i.e., northern hardwood, aspen-birch, or other, using GIS.

Nesting data analysis

Daily nest-survival probability was estimated using the software MCEstimate, a multistate nest-survival analysis program that treats daily nest survival as a Markov process (Etterson and Bennett 2005, Etterson et al. 2014). MCEstimate allows specification of covariates to nest survival and comparison among competing models using AIC and associated statistics such as AICc and QAICc. The software is freely available online at <https://www.epa.gov/chemical-research/markov-chain-nest-productivity-model-estimating-tool>.

To investigate factors influencing nest success, we incorporated site, total forest cover at the 10-km scale, nest-tree species, and cover type surrounding nests as covariates in our analysis. At the study-site scale, we included site as a categorical covariate with six levels, with Boulder Lake being absorbed into the intercept term, and included total forest cover at each site as a continuous variable in the models (Table 2). The two most common nest-tree species were sugar maple, i.e., 76 nests, and paper birch, i.e., 41 nests, accounting for 68% of all nests discovered, and the remaining 54 nests, i.e., 32%, were distributed among nine tree species (Table 2). Because these data were highly skewed, the latter were combined into a single category, i.e., other, against which nest survival in sugar maple and paper birch were compared using a categorical covariate with two levels, with sugar maple being absorbed into the intercept term. We included two cover types within the 100-m buffer of the nest in the models, percentage of aspen-birch and the percentage of northern hardwoods in which sugar maple is the dominant species. Nest height, nest-tree height, and nest-tree dbh were also included and treated as continuous covariates. Not all covariates were measured at all nests, with two sites, i.e., Boulder Lake and Oak Point, lacking GPS positioning data for nests, preventing calculation of percentage-cover statistics. Therefore, for each covariate, a maximal data set was created including all nests with a measured value for the covariate, and statistical tests were restricted to likelihood ratio tests for each covariate against the null model of homogeneous nest survival, using the maximal data set for that covariate.

Following the likelihood ratio analyses with maximal univariate datasets, a single consensus dataset was created as the maximal set of nests for which all covariates were measured. This eliminated two sites, i.e., Oak Point and Boulder Lake, at which GPS locations were not collected, preventing calculation of the Northern Hardwoods and Aspen-Birch variables. For this analysis, the same covariates were analyzed, again as univariate models, and were compared to each other using AICc and associated model weights.

MCEstimate provided estimates of daily survival rates conditional on specific covariate values, e.g., site, nest height, etc. These daily values were used to calculate period survival for each site for incubation, i.e., 18 days including egg laying, nestling rearing, i.e., 13 days, and the full nest cycle, i.e., 31 days, by exponentiation. Standard errors for period-survival estimates were calculated using the delta method with the covariance matrix from the daily survival estimates.

Table 2. Study-area locations, percentage of forest area around study site, number of Least Flycatcher nests found per site, mean nest-tree measurements with standard deviation (sd), and number of tree species used per site.

Study site	Lake Erin	Oak Point	Tobique	Pine County	Boulder Lake	Tofte 1	Tofte 2	Totals
Latitude	47.01977	47.175966	47.083967	46.390176	47.077847	47.588167	47.610581	
Longitude	-94.502703	-94.569026	-94.052913	-92.389057	-92.131409	-90.914341	-91.008682	
Percent forest area in 10-km buffer	54	46	59	69	73	85	84	
Number of nests with nesting data	18	19	37	28	18	19	32	171
Nests lost with no nesting data	9	6	20	3	11	1	10	60
Mean nest tree dbh in cm (sd)	24.5 (26.6)	20.5 (10.7)	14.9 (6.5)	16.9 (10.5)	not measured	24.4 (14.8)	26.8 (12.1)	
Mean tree height in m (sd)	16.7 (5.3)	17.3 (8.0)	14.3 (4.2)	16.4 (7.0)	not measured	15.4 (3.8)	18.1 (6.1)	
Nest height in m (sd)	10.3 (5.2)	10.4 (5.8)	10.4 (3.4)	9.8 (3.9)	not measured	10.4 (3.3)	11.3 (4.4)	
Nest tree species								
Sugar maple (<i>Acer saccharum</i>)	1	2	17	18	0	18	22	78
Beaked hazel (<i>Corylus cornuta</i>)	0	1	0	4	0	0	0	5
Red pine (<i>Pinus resinosa</i>)	0	0	0	0	6	0	0	6
White pine (<i>Pinus strobus</i>)	0	0	0	0	9	0	0	9
Red maple (<i>Acer rubrum</i>)	0	1	10	1	0	0	0	12
Paper birch (<i>Betula papyrifera</i>)	14	8	6	6	2	0	6	42
Bur oak (<i>Quercus macrocarpa</i>)	3	4	0	0	0	0	0	7
Red oak (<i>Quercus rubra</i>)	1	1	4	0	0	0	0	6
Silver maple (<i>Acer saccharinum</i>)	0	1	0	0	0	0	0	1
Black ash (<i>Fraxinus nigra</i>)	0	0	0	1	0	0	0	1
Mountain maple (<i>Acer spicatum</i>)	0	0	0	0	0	0	1	1
Total identified to species in each site	19	18	37	30	17	18	29	168

RESULTS

A total of 171 nests with nesting data were located ranging from 18 at Boulder Lake and Lake Erin to 37 at Tobique (Table 2); an additional 60 nests were abandoned or destroyed before any nesting data were gathered. A smaller set of 129 nests had measured values for all covariates. Nesting trees used by Least Flycatchers ranged from a dbh of 14.9 cm and a height of 14.3 m at Tobique to 26.8 cm dbh and 18.1 m at the Tofte 2 site. Mean nest height among the study sites was consistent and only ranged from 9.8 m to 11.3 m but was variable within each site. Eleven tree or shrub species were used for nesting with the majority, i.e., 68%, found in sugar maple, i.e., 44%, or paper birch, i.e., 24%.

Average daily nest-survival rate among all Least Flycatcher nests was 0.983 (+/- 0.002 SE), yielding an estimated average nest-success rate, i.e., probability of fledging at least one fledgling, over 31 days of 0.59 (+/- 0.04; Table 3). Nesting success ranged from 0.37 (+/- 0.12) at the Lake Erin study area to 0.94 (+/- 0.06) at the Tofte 1 study area and differed significantly among study sites (Table 3, Fig. 2). Nesting success was also high at the Pine County site (0.84 +/- 0.08), and lower at Tofte 2 (0.59 +/- 0.09) and Oak Point (0.57 +/- 0.13). Predicted nest success was low at Tobique (0.45 +/- 0.08) and Boulder Lake (0.41 +/- 0.11). The contrast in survival rates during incubation, nestling rearing, and nesting success through the entire nest cycle separated by site is well illustrated by the high nesting success at Tofte 1 versus Lake Erin (Fig. 2).

Across all seven study sites, predicted nest success was highest for nests located in sugar maple (0.72 ± 0.05), compared to those in paper birch (0.55 ± 0.08) or in all other tree species combined (0.42 ± 0.07). The latter two groups were not statistically different from each other. This pattern is illustrated across all nesting phases, including incubation, nestling, and the full nest cycle, indicating that tree species play a key role in reproductive outcomes in Least Flycatchers (Fig. 3).

Likelihood ratio tests for maximal subsets of nests for each covariate support the conclusions that nest survival differed by site, nest-tree species, area of northern hardwood cover within 100 m of the nest (Fig. 4), nest height (Table 4, Fig. 5), and the percent of total forest cover among terrestrial vegetation types within 10 km of the study site (Table 4, Fig. 6). In contrast, nest survival was not correlated with the amount of aspen-birch forest type within 100 m of the nest, dbh of the nest tree, or with height of the nest tree (Table 4; all $P > 0.05$). Nesting success was highest at the three sites with the greatest surrounding forest cover at the 10 km scale (Table 4, Fig. 6).

Univariate models compared using AICc on the consensus dataset with values for all covariates (129 nests) broadly agreed with results from the maximal covariate datasets (Table 5). The categorical variable site was the strongest predictor of nest success, receiving 86% of AICc weight. Forest cover within 10 km of the site and area of northern hardwoods within 100 m of the nest each received 7% of AICc weight. Together, these three covariates accounted for > 99% of AICc model weight.

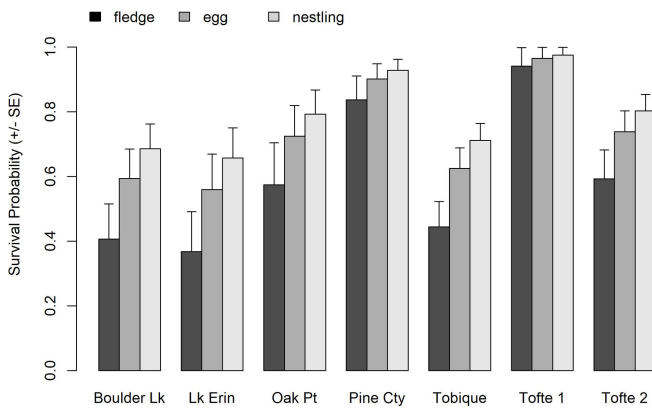
DISCUSSION

Our results indicated that Least Flycatcher nests located in sugar-maple trees and within landscapes at the 10-km scale that are dominated by northern hardwood forests, specifically those composed of sugar maple, had the highest probability of fledging young. This suggests that both nest-tree species and surrounding forest composition play important roles in reproductive success, likely because of a combination of factors such as food availability, protection from predators, and differences in the predator community in large, relatively unfragmented forest stands. Although sugar maple was associated with the highest nest success, Least Flycatchers also used at least 10 other tree species for nesting, including those in aspen-birch forest types. However, because of resource constraints, we were unable to conduct formal plant surveys, limiting our ability to assess nest success relative to

Table 3. Estimates of nesting success of Least Flycatchers by study site, including number of nests, days of exposure, and daily, incubation, nestling, and nesting success with standard error (se).

	Lake Erin	Oak Point	Tobique	Pine County	Boulder	Tofte 1	Tofte 2
Number of nests	18	19	37	28	18	19	32
Exposure days	303	352	804	704	402	515	733
Effective sample size	266	326	748	696	369	514	705
Daily survival - standard error (se)	0.968 (0.010)	0.982 (0.010)	0.974 (0.010)	0.994 (0.003)	0.971 (0.009)	0.998 (0.002)	0.983 (0.004)
Incubation survival (se)	0.560 (0.108)	0.725 (0.095)	0.625 (0.066)	0.902 (0.046)	0.594 (0.093)	0.966 (0.034)	0.739 (0.062)
Nestling survival (se)	0.658 (0.092)	0.793 (0.075)	0.712 (0.054)	0.928 (0.034)	0.686 (0.078)	0.975 (0.025)	0.803 (0.048)
Nest survival (se)	0.368 (0.11)	0.575 (0.13)	0.445 (0.08)	0.837 (0.07)	0.407 (0.11)	0.942 (0.06)	0.593 (0.09)

Fig. 2. Period survival rates for full nest cycle (fledge, 31d), laying and incubation (egg, 18d), and post-hatch (nestling, 13d) phases by site. Error bars represent 1 SE.



availability, which should be a topic of future studies. The high performance of the Site model (Table 4) also suggests that there is residual variation in nest success that is not explained by nest-tree species or landscape scale forest cover. Other causal factors, including forest structural components at meso and local scales, cannot be eliminated, but we suspect this variation is, at least in part, due to random variation by site.

This study was designed to evaluate how habitat characteristics, particularly forest cover at multiple spatial scales, influence nesting success in Least Flycatchers across a forest landscape. Our findings provide a broader geographic perspective than previous research, which has largely focused on the Chippewa National Forest in north-central Minnesota. Earlier studies reported variable nesting success, with Hanski et al. (2006) documenting a low rate of 24%, and Perry et al. (2008) reporting a range of 38% to 58%. In contrast, our study encompassed seven sites across Minnesota and revealed that three sites exhibited notably higher nesting success than previously reported. Overall, our findings are consistent with Flaspohler et al. (2001), who reported high nesting success rates of 79% to 90% in northern Wisconsin, and align with more recent work by Tarof and Briskie (2020), which documented a wide range of Mayfield nesting success estimates, i.e., 20% to 85%, further emphasizing the influence of regional habitat conditions on reproductive outcomes. By expanding the spatial scope of investigation, our study contributes important new insights into the variability of reproductive success across the

Fig. 3. Period survival rates for full nest cycle (fledge, 31d), laying and incubation (egg, 18d), and post-hatch (nestling, 13d) phases by nest-tree species. Error bars represent 1 SE.

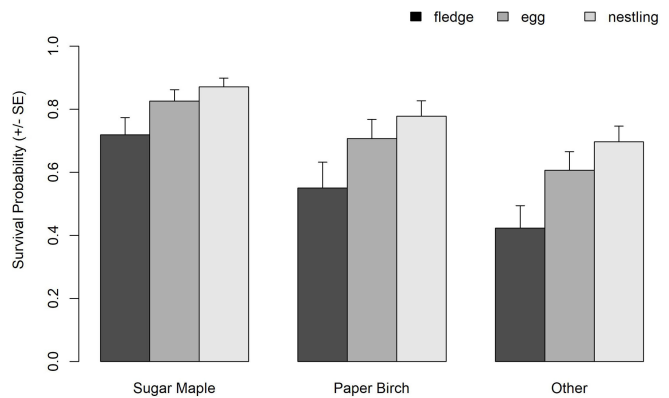
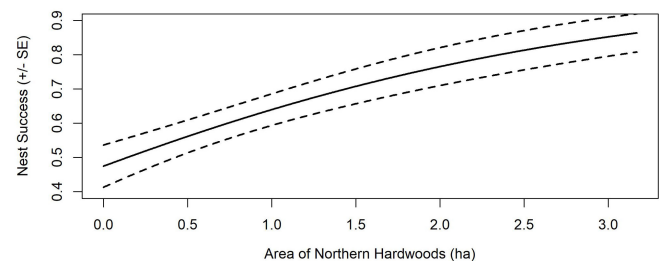


Fig. 4. Predicted nest success (+/- SE) versus area (ha) of northern hardwoods within 100 m of the nest, generated using the maximal data set for area of northern hardwoods (n = 152).



species' breeding range. This broader context is critical for informing conservation strategies, especially given the species' long-term population declines.

Interestingly, despite the widespread presence of aspen (*Populus* spp) in Minnesota's forests, especially in the northeast, it was not frequently used for nesting by Least Flycatchers. This contrasts with findings from the Canadian Prairies, where Tarof and Briskie (2020) reported frequent use of *Populus* spp. Similarly, balsam fir (*Abies balsamea*), another common species in northeastern Minnesota, was not used in our study and was also absent from the nest-tree species reviewed by Tarof and Briskie (2020). Their

Table 4. Likelihood ratio tests for each variable against an intercept-only null model. NLL = negative log-likelihood. K = number of estimated parameters. Δ AICc was calculated in comparison to the sample-size specific null model and cannot be compared across rows.

Variable	Nests	Effective sample size	Null NLL	Null K	Alt NLL	Alt K	Diff	df	ChiSq prob	Δ AICc
Site	171	3813	236.12	1	222.6	7	27.04	6	<0.0002	15.02
Forest cover within 10 km	171	3813	236.12	1	233.98	2	5.86	1	0.015	3.86
Northern hardwoods	134	3059	179.02	1	172.6	2	12.84	1	<0.0004	10.83
Nest tree species	165	3494	227.15	1	221.9	3	10.5	2	0.0053	6.48
Nest height	152	3383	199.13	1	197.04	2	4.18	1	0.041	2.17
Aspen-birch	134	3059	179.02	1	178.32	2	1.4	1	0.24	0.61
Plant height	151	3203	198.74	1	198.15	2	1.18	1	0.28	0.81
Nest Tree DBH	150	3179	198.36	1	198.36	2	0	1	>0.9999	2

Fig. 5. Predicted nest success (+ / - SE) versus nest height, generated using the maximal data set for nest height (n = 152).

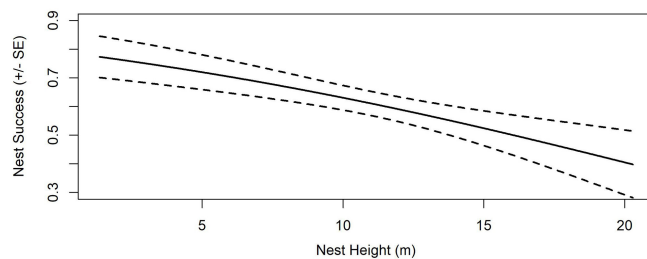
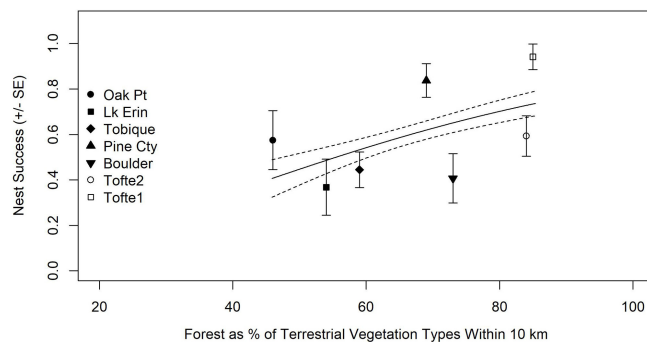


Fig. 6. Estimated Least Flycatcher nest success versus area of total forest cover within 10 km of each site. Slope of daily survival probability with Total Forest Cover within 10 km is 0.0231 (+ / - 0.008 SE). Dashed lines represent 1 SE around nest success. Values from the categorical Site model (+ / - SE) also shown for comparison.



synthesis highlights sugar maple, ash (*Fraxinus* spp.), oaks, and birch (*Betula* spp.) as commonly used nesting trees across various regions, including Ontario and Michigan (Tarof and Briskie 2020). These patterns suggest that whereas Least Flycatchers exhibit some flexibility in nest-tree selection, certain species, particularly sugar maple, may offer structural or ecological advantages that enhance nesting success. Interestingly, sugar maple and paper birch are both predicted to change significantly in northeast Minnesota with climate change, with sugar maple predicted to increase in relative abundance, but paper birch predicted to decrease (Handler et al. 2014).

Table 5. AICc and model weights for all univariate models of the eight covariates using the consensus data set created as the maximal set of nests (n = 129) for which all covariates had been measured. Note that nest-specific GPS locations were not collected at two sites (Boulder Lake and Oak Point), reducing the number of estimated parameters (K) for the Site model in this dataset.

Model	Δ AICc	Weight	K
Site	0	0.86	5
Forest cover within 10 km	5.06	0.07	2
Northern hardwoods	5.06	0.07	2
Nest tree species	16.3	0	3
Aspen-birch	16.6	0	2
Null	18.6	0	1
Nest height	19	0	2
Nest Tree DBH	19.53	0	2
Plant height	20.6	0	2

Nest height was a significant predictor of nesting success, with lower nests being more successful than those placed higher in the canopy. This pattern is consistent with the range of nest heights reported by Tarof and Briskie (2020) and may reflect increased vulnerability of higher nests to avian predators like Blue Jays (*Cyanocitta cristata*) or raptors, as well as greater susceptibility from wind and precipitation during storm events. Whereas this interpretation is plausible, it remains speculative and highlights the need for future field studies that directly assess predation and weather-related nest failures. Our study represents one of the few replicated investigations of Least Flycatcher nesting success across a broad geographic region. The results reveal substantial spatial variability in reproductive outcomes, with the highest success observed in northern hardwood forests, particularly in sugar-maple trees and at lower canopy positions. Notably, the three study sites with the highest nest success, Tofte 1 (94% success, 85% forested), Pine County (84%, 69%), and Tofte 2 (59%, 84%), were among the four sites, excluding Boulder, with the greatest forest cover within a 10-km radius around the site. These findings are consistent with previous studies that suggest forest fragmentation and reduced contiguous forest area negatively affect nesting success of Least Flycatchers (Manolis et al 2000, Flaspohler et al. 2001). However, it is also noteworthy that results from the two Tofte sites are highly influential (Fig. 6) in the relationship between forest cover and nest survival. These two sites are both Lake Superior coastal sites, where forest

characteristics may have differed from inland sites. Our results also suggest a need for future studies at intermediate scales, from 500 m to 2 km, to further inform the scale at which management for this species would be most effective.

Our data showed a high proportion, i.e., 26%, or 60 of 231, of potential nesting attempts were abandoned by the nesting pair or destroyed from other causes likely due to storm events. Tarof and Briskie (2020) reported nest desertion during incubation was rare, i.e., 1.2% of 162 nests. A Manitoba study estimated up to 14.5% of nests destroyed by wind damage (9.7%), nest-tree falling (1.9%), and abandonment (2.9%). A Wisconsin study identified a total of 46%, or 61 of 133, of nesting failures were due to predation, weather, abandonment, and adult mortality. Our data fall within these ranges. Note also that these 60 nests never had any verified eggs present nor observed incubation activity, and were abandoned post construction, but prior to when such nests would normally be included in nest survival analyses.

Our findings reinforce long-standing concerns about the conservation of neotropical migrant birds in forested habitats. Robbins et al. (1989) and Terborgh (1989) emphasized the importance of large, contiguous forest tracts for maintaining viable populations of forest-dependent species. Robinson et al. (1995) similarly reported higher nest success and lower parasitism rates in more forested landscapes across the Midwest, even though their study did not include Least Flycatchers. Our results extend these conclusions by demonstrating that Least Flycatchers, too, benefit from extensive forest cover, particularly in landscapes dominated by northern hardwoods. Continued research on nest survival in the upper Midwest and Canada is essential, especially studies that integrate post-fledging survival to provide a more complete picture of reproductive success and population dynamics.

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Data Availability:

The data for this study will be available at the Data Repository for the University of Minnesota upon publication of the manuscript: <https://hdl.handle.net/11299/278983>

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