Nesting biology and breeding density of Least Flycatchers (Empidonax minimus) in the Beaverhill Natural Area, Alberta, Canada

Authors: Van Brempt, Myrthe, Holroyd, Geoffrey L., Hvenegaard, Glen, and Van Arragon, Jon

Source: The Wilson Journal of Ornithology, 135(4) : 553-560

Published By: The Wilson Ornithological Society

URL: https://doi.org/10.1676/22-00110

The Wilson Journal of Ornithology 135(4):553–560, 2023 DOI: 10.1676/22-00110

Nesting biology and breeding density of Least Flycatchers (*Empidonax minimus*) in the Beaverhill Natural Area, Alberta, Canada

Myrthe Van Brempt,[1] Geoffrey L. Holroyd,[1]* Glen Hvenegaard,[2] and Jon Van Arragon[1]

ABSTRACT—Least Flycatchers (*Empidonax minimus*), like most aerial insectivores, have declined rapidly over the last 50 years in North America, mostly due to the extensive use of insecticides. Since the Least Flycatcher is the most common bird encountered in the Beaverhill Natural Area, located in central Alberta, Canada, likely due to high insect densities, we studied the nesting success and habitat use of this species in the summer of 2022. We monitored 28 nests until fledging and found a high nest success rate and more nesting in trembling aspen trees (*Populus tremuloides*), compared to balsam poplar trees (*Populus balsamifera*). We found that mean host tree height was greater for successful nests than unsuccessful nests. In addition, based on a breeding bird census, we found a high breeding density in our research area. Understanding the relationship between breeding success and habitat is important for conservation actions to be effective in the future. Our results show that the Beaverhill Natural Area has high-quality habitat for Least Flycatchers and is a candidate for critical habitat when designated under the Canadian Species at Risk Act. *Received 10 November 2022. Accepted 27 November 2023.*

Key words: aerial insectivore, critical habitat, nest habitat, nesting success, productivity.

[1] Beaverhill Bird Observatory, Edmonton, AB, Canada
[2] University of Alberta, Augustana Campus, Department of Science, Camrose, AB, Canada
* Corresponding author: chair@beaverhillbirds.com

Biología de anidamiento y densidad reproductiva de mosquero *Empidonax minimus* en el Área Natural Beaverhill, Alberta, Canadá

RESUMEN (Spanish)—El mosquero *Empidonax minimus*, como la mayoría de insectívoros aéreos, han declinado rápidamente en los últimos 50 años en Norteamérica, mayormente debido al uso extensivo de pesticidas. Puesto que el mosquero *Empidonax minimus* es el ave más común encontrada en el Área Natural Beaverhill, localizada en Alberta central, Canadá, posiblemente debido a altas densidades de insectos, estudiamos el éxito de anidamiento y el uso de hábitat de esta especie en el verano de 2022. Monitoreamos 28 nidos hasta su emancipación y encontramos una alta tasa de éxito de nido y más anidamiento en álamo temblón (*Populus tremuloides*), comparado con álamo balsámico (*Populus balsamifera*). Encontramos que el promedio de altura del árbol hospedero era superior para nidos exitosos que para nidos no exitosos. Además, basados en censo de aves reproductivas, encontramos una alta densidad reproductiva en nuestra área de investigación. Entender la relación entre el éxito reproductivo y el hábitat es importante para que las acciones de conservación sean efectivas en el futuro. Nuestros resultados muestran que el Área Natural Beaverhill es un hábitat de alta calidad para el mosquero *Empidonax minimus* y es candidata para ser designada como hábitat crítico bajo el Acta de Riesgo de Especies Canadienses.

Palabras clave: éxito de anidamiento, hábitat crítico, hábitar de nido, insectívoro aéreo, productividad.

Populations of aerial insectivorous birds (including swallows, swifts, nightjars, and flycatchers) in Canada have declined by 59% since 1970 (NABCI-Canada 2019). These population declines seem to vary by region and species (Nebel et al. 2010, Smith et al. 2015, Spiller and Dettmers 2019). For example, Nebel et al. (2010) showed the probability of aerial insectivore declines to be the greatest in northeastern North America and greater for long-distance migrants than short-distance migrants. Conservation planners need more studies on species-specific life history characteristics and population changes, structured by region, in order to make informed decisions about conservation priorities and programs.

One species, the Least Flycatcher (*Empidonax minimus*), saw a population decline of 53% since the 1970s across North America (Spiller and Dettmers 2019, de Zwaan et al. 2022), largely due to habitat disturbance and declines in insect populations (Tarof and Briskie 2020). In Canada and Alberta, the Least Flycatcher declined by 1.28% and 1.84% per year, respectively, from 1970 to 2019 (Calvert 2012, Smith et al. 2020). This decline is more than that of most other flycatchers (Calvert 2012) although not as severe as for other aerial insectivores (Smith et al. 2015, Spiller and Dettmers 2019). Least Flycatchers are among the smallest of the aerial insectivores in North America, breeding in the deciduous and mixed forests of southern and western Canada, and northern United States (Tarof and Briskie 2020). Despite its decreasing population trend, the IUCN Red List of Threatened Species assessed the Least Flycatcher as a species of Least Concern because of its large range and extremely large population size globally (IUCN 2021). However, the species may be at future risk if its populations continue to decline rapidly (Spiller and Dettmers 2019, de Zwaan et al. 2022). In Canada, the Least Flycatcher is not a species at risk, although it is a candidate for a detailed status report (COSEWIC 2022). Alberta lists the species as sensitive since it has been declining (Alberta Wild Species General Status Listing 2015). A national workshop on aerial insectivore declines recommended better information on demographic parameters of certain flycatchers, particularly those showing steep declines (Calvert 2012).

The Canadian Species at Risk Act includes a provision to identify and protect critical habitat for endangered and threatened species, with critical habitat defined as "the habitat that is necessary for the survival or recovery of a listed wildlife species" (SARA 2002). Habitat can be described by plant species composition and structure (Warkentin et al 2003). Many studies defined critical habitat based on species at risk occurrence and habitat occupancy and not based on population viability (Camaclang et al. 2014). Population viability includes productivity parameters such as clutch size, fledging rate, and nest success. We need more studies on the Least Flycatcher's productivity in different habitats and how the species interacts with its environment while it is still relatively abundant. Understanding how breeding success is influenced by environmental factors, including weather, food supply, and predation risk, as well as the location of the nest in relation to habitat, is important for conservation actions to be effective in the future (Goodenough 2014). At present, researchers lack knowledge on habitat–productivity relationships for the Least Flycatcher; this information would be valuable for future conservation strategies.

Least Flycatchers generally nest in the lower to mid canopy of deciduous forests and feed on insects by hawking (Robinson and Holmes 1982, Darveau et al. 1993). Nests have been found in a variety of trees, depending on the geographical region, and include birches (*Betula* spp.), maples (*Acer* spp.), poplars (*Populus* spp.), and pines (*Pinus* spp.) (Tarof and Briskie 2020). Least Flycatchers build a small cup nest in branch crotches or forks (Darveau et al. 1993); nests consist mostly of grasses, plant down, and spider webs. Clutch size ranges from 2 to 5 eggs, with 4-egg clutches being the most common

(Briskie and Sealy 1989a). Habitat changes may influence reproductive success by altering nest concealment or altering insect communities (Des-Granges 1987). In addition, breeding density has been negatively associated with forest decline (Darveau et al. 1992).

Despite large-scale population declines, there are large numbers of breeding Least Flycatchers in the Beaverhill Natural Area (BNA), Alberta, Canada. Since the Least Flycatcher is so abundant in the natural area, we sought to determine the productivity of Least Flycatchers, their breeding density, and habitat use in relation to breeding success, and in comparison to other studies. In addition, we aimed to interpret our findings within the context of identifying critical habitat for this declining species.

Methods

Our study site of 0.25 km^2 (length of 500 m, width of 500 m) was located south of Beaverhill Lake within the BNA, 60 km east of Edmonton and 10 km east of Tofield in central Alberta, Canada (53.381°N, −112.529°W). The BNA consists of an early successional trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) forest in the Aspen Parkland Natural Region.

We started searching for nests on 7 June 2022 by moving systematically through the study site, looking and listening for Least Flycatchers. When we found a Least Flycatcher, we observed its behavior and followed the individual in order to find its nest. We used behaviors such as collecting nest material, singing, looking or moving repeatedly toward the same direction, mating, and chasing others away as cues to find the nest. In addition, we scanned trees for nests in likely nesting locations.

When we found a nest, we recorded the location with a GPS, marked the closest nearby tree with blue flagging tape (with knot in direction of nest), and recorded the nest site and habitat characteristics. We visited nests every 3 d (or 4 due to rainy or windy weather) to monitor egg laying, incubation, hatching, nestling period, and fledging. We observed the nest with a pole camera connected to a smartphone, using a USB camera app. We used a homemade pole camera similar to ones made by Hudson and Bird (2006) and Huebner and Hurteau (2007). We could not monitor nests located at heights more than 8 m with the pole camera; we did not use these nests in our analysis. We recorded the number of eggs (i.e., clutch size), number of nestlings, and adult behavior when we visited the nest. We aged young based on pictures taken with the pole camera using Jacklin's (2017) aging guide. We assumed a nest was successful when fledglings were observed leaving the nest, when the empty nest showed signs of fledging (e.g., droppings), or when the young were capable of leaving the nest at the previous nest visit (12 d old). We did not observe fledglings out of the nests. All nests were empty by 21 July.

After the last young had fledged (21 July), we visited each nest to measure nest site and habitat characteristics (Martin 1992). For the nest site characteristics, we determined the species of the host tree (which were only trembling aspen or balsam poplar). We estimated the height of the nest tree and height of the nest with a clinometer or with a measuring tape for low nests. We measured the circumference of the nest tree at 1.3 m above ground to calculate diameter at breast height (DBH) according to the formula: $DBH = circumference/\pi$. We recorded the number of branches on which the nest was built (other than the trunk). We recorded the distance between the nest and the trunk, and the overhead leaf cover within 20 cm above the nest, suggesting a relationship with nest predation.

For the habitat characteristics, we counted all trees within a 5 m radius of the nest tree, identified each tree to species, and measured each tree for DBH. We hypothesized that Least Flycatchers prefer to nest in trees with a large DBH, which are more stable against winds and other inclement weather, as well as provide more structure such as branches to hold a nest. We considered all stems with a DBH larger than 3 cm to be trees, while we counted smaller woody stems as saplings. In addition, we estimated ground cover (%), shrub cover (%), and shrub height (m), and recorded the number of dead standing snags. We estimated canopy cover with a densiometer and measured canopy height with a clinometer. We measured shrub height as the height of the tallest shrub within the 5 m radius area around the nest tree. We visually

Table 1. Comparison of nest locations and productivity parameters across the range of Least Flycatchers.

Location	Dominant nest tree species	Mean nest height (m) and/or range	Clutch size (*n* of eggs)	Nest success rate (%)	Breeding density (pairs/ha)	Reference
Beaverhill Natural Area, AB, Canada	Trembling aspen	3.6 (1.5–10)	3.89	79	3.64	Current study
Michigan, USA	Maples	7.2 (1.5–20)	3.95	52	2.0	Walkinshaw (1966)
Quebec, Canada	Sugar maple	8.4 (1–18)	3.97	53	–	Darveau et al. (1993)
Delta Marsh, MB, Canada	Manitoba maple, green ash	4.1 (0.6–10)	3.92	38	–	Briskie and Sealy (1989a), Tarof and Briskie (2020)
Winnipeg, MB, Canada	Balsam poplar, trembling aspen	3.5 (0.8–12.2)	3.89	–	–	Prairie Nest Records Scheme
Queen's Biology Station, ON, Canada	Deciduous	–	3.9	–	–	Tarof and Briskie (2020)
Ontario, Canada	Deciduous	0.6–15	3.41	–	–	Peck and James (1987)
Eastern Ontario, Canada	Sugar maple	2–20				Tarof and Briskie (2020)
New Hampshire, USA	–	13.7	–	–	1.4	Tarof and Briskie (2020)
Minnesota, USA	Maples, oaks	–	–	–	1.5	Tarof and Briskie (2020)
Virginia, USA	–	4.8–8.5	3.6	–	2.0–3.0	Davis (1959), Johnston (1970)
Entire range north of Mexico	–	–	3.64	–	–	Murphy (1989)

estimated ground cover and shrub cover in percentages with increments of 5%. We calculated basal area (BA) for each tree in each plot according to the formula: $BA = \pi * (DBH/2)^2$. To describe the forest structure, we calculated BA per hectare by adding all of the trees' BAs and dividing by the area of the plot (= 78.54 m^2).

We mapped breeding territories of Least Flycatchers based on singing individuals recorded within a 0.25 km^2 area and using a 10×10 m point grid system. Individual points were located 50 m apart and we replicated the survey 6 times between 8 June and 21 July. We recorded all locations of detected Least Flycatchers on a map of the grid, as well as the method of detection (song, call, or sight). We mapped the territory boundaries based on the location of counter-singing individuals (birds singing in response to singing neighbors of the same species). Territories on the edge of the study plot were counted as partial territories (½ territory). We calculated breeding density by dividing the number of territories by the census area.

Using SPSS 28.0.1.1, we tested for relationships between nest productivity (i.e., clutch size, brood size, number of fledglings, and the nest outcome) and both nest site and habitat characteristics. When exploring relationships between dichotomous variables, we used chi-square tests. When exploring relationships between continuous dependent variables and dichotomous independent variables, we used independent samples *t*-tests. When exploring relationships between continuous variables, we used Pearson's correlations. We used an alpha level of 0.05.

Results

Clutch size

We monitored 28 nests with the pole camera (<8 m high). We determined clutch size for 15 nests, of which 2 (13%) had 5 eggs, 11 (73%) had 4 eggs, and 2 (13%) had 2 eggs. We could not determine clutch size for 13 other nests since they contained young (mean age = 6 d old) when we found them. Assuming that the number of eggs equals the number of young, we inserted the brood size for these nests (predicted clutch size) and expanded our sample size for later analyses involving clutch size. Of 28 nests monitored, 5 (18%) had a predicted clutch size of 5 eggs, 17 (61%) had 4 eggs, 4 (14%) had 3 eggs, and 2 (7%) had 2 eggs. Overall, the mean clutch size was 3.87 eggs (SD = 0.83) and mean predicted clutch size was 3.89 (SD = 0.79). Since these values were so similar, we continued to use predicted clutch size in further analyses.

Brood size and number of fledglings

Of 28 nests, 5 (18%) produced 5 young, 14 (50%) produced 4 young, 4 (14%) produced 3 young, and 1 (4%) produced only 2 young. Of 28 nests, 4 (14%) failed at the egg stage and did not produce any young. Twelve (43%) of the nests produced 4 fledglings, while 5 (18%) produced 5 fledglings and another 5 (18%) produced 3 fledglings. Two (7%) of the nests failed during the nestling stage; adding 4 (14%) of the nests that did not produce any young resulted in 6 (21%) of the nests that did not produce any fledglings. Overall, we found a mean brood size of 3.39 (SD = 1.57) and a mean number of fledglings of 3.14 (SD = 1.78).

Nest outcome

Out of the 28 monitored nests, 22 nests were successful (79%). Of the 6 nest failures (21%), 2 nests contained eggs from a Brown-headed Cowbird (*Molothrus ater*), 1 nest was depredated by a House Wren (*Troglodytes aedon*), and 3 nests failed from unknown causes. In the 22 successful nests, all young that hatched also fledged.

Nest site characteristics

Twenty-one (75%) nests were placed in trembling aspen trees and 7 (25%) were placed in balsam poplar trees. Of the 21 nests in aspen trees, 16 (76%) were successful and 5 (24%) failed. Of the 7 nests in balsam trees, 6 (85%) were successful and 1 (15%) failed. However, there was no significant association between nest tree species and nest outcome.

The mean height of nests was 3.63 m (SD = 1.67), the mean height of the nest tree was 10.14 m (SD = 2.41), the mean DBH of the nest tree was 9.85 cm (SD = 2.87), and the mean cover over the nest was 7% (SD = 14.15). The mean number of branches supporting each nest was 1.9. These variables did not differ between nests in aspen and balsam trees. The nest trees for successful nests were taller on average (mean = 10.67 m, SD = 2.13) than for failed nests (mean = 8.17 m, SD = 2.55; $t = 2.46$, $N = 28$, $P = 0.021$). There were no significant relationships between height of the nest tree and the predicted clutch size, the brood size, or the number of fledglings. We did not find significant associations between the other nest site variables (host tree species, height of the nest, DBH of the nest tree, number of branches, and nest cover) and the predicted clutch size, brood size, number of fledglings, or nest outcome.

Nest habitat

We found a mean canopy height of 12.47 m (SD = 1.53), a mean canopy cover of 98% (SD = 2.72), a mean shrub cover of 8% (SD = 8.10), and a mean ground cover of 95% (SD = 13.74). The mean total basal area was 29.22 m^2 per hectare (SD = 11.05). The mean number of trees in the plots was 21.82 (SD = 7.53), the mean number of saplings in the plots was 14.93 (SD = 11.34), and the mean number of snags in the plots was 9.50 (SD = 5.61). We did not find a significant relationship between any of the habitat variables (canopy height, canopy cover, shrub cover, ground cover, total basal area, total number of trees, total number of saplings, and number of dead snags) and the predicted clutch size, brood size, number of fledglings, and the nest outcome. The mean total number of aspen trees in the 5 m radius plot was 15.11, while the mean total number of balsam trees was 6.71. The mean number of aspen saplings was 12.82 and the mean number of balsam saplings was 2.11.

When separating the number of saplings by tree species, we only found a significant association between the number of aspen saplings and the brood size ($R = -0.38$, $P = 0.044$). We did not find any significant relationship between the number of aspen or balsam trees within the 5 m radius plot and the productivity variables.

Breeding density

We found 91 Least Flycatcher territories in the census area. This is equal to a breeding density of 364 territories/km^2 or 3.6 territories/ha.

Discussion

We assessed productivity of Least Flycatchers in the BNA and aimed to understand breeding success in relation to nest site characteristics and habitat. This study's mean clutch size of 3.89 was comparable to the mean clutch size found in other studies across North America (Table 1). Hatching success is generally high for Least Flycatchers, and we observed this trend in the BNA (Table 1).

We recorded a nest success rate of 79%, which is much higher than success rates recorded in other studies in North America (Table 1). The high success rate we observed might be a result of high food availability in the BNA. Dunn (1989) sampled insect abundance in the BNA and found higher food abundance throughout the breeding season relative to findings in Ontario. No recent studies have investigated insect abundance in the BNA, although information on this would be valuable since the environment has changed considerably since 2016, when water returned to Beaverhill Lake after it dried up over the period 2005–2015. A continental review of clutch size in Tree Swallows (*Tachycineta bicolor*) showed that clutch size increased with latitude, with the maximum clutch size in the BNA (Winkler et al. 2014). There was a positive correlation between clutch size and summer evapotranspiration (as a measure of terrestrial primary productivity), which was assumed to be correlated with resource abundance (Dunn et al. 2000). The high insect abundances in combination with long days optimized breeding conditions, resulting in high success rates and breeding densities of Tree Swallows (Hussell 1985, Winkler et al. 2014). Similarly, breeding conditions (day length and food abundance) in the BNA might be optimal for Least Flycatchers and could explain the high success rate we observed. We found that mean host tree height was greater for successful nests than unsuccessful nests.

Overall, nest sites had dense canopy cover and low shrub cover; these results are similar to earlier studies that found Least Flycatchers nesting in semi-open, mid-successional deciduous forests with moderate understories and well-developed canopies (DellaSala and Rabe 1987, Darveau et al. 1992, Tarof and Ratcliffe 2004). Earlier studies showed that habitat changes might influence reproductive success by altering nest concealment or adjusting local insect communities (DesGranges 1987). Ongoing forest succession in the BNA, from grassland to willow stands to forest, increased suitable habitat for Least Flycatchers over the past years and may contribute to the high breeding density and high productivity found in our study area. Most previous studies documented Least Flycatcher nests in maples and other tall deciduous trees, while our study was in an early successional trembling aspen and balsam poplar forest (Table 1). Consequently, the mean nest height was in the lower range compared to other studies. While we found that nests were on 1 or 2 branches immediately next to the tree trunk, many other studies found nests in forks in branches with 2–5 branches holding the nest. The tree trunk likely provides visual protection from predators in our forest with sparse tree branching in the understory.

In addition, the breeding density of 3.6 territories/ha found in our research area is double the magnitude of breeding densities recorded in most other studies (Table 1) and likely reflects good breeding conditions in the BNA.

We acknowledge that our sample size of 28 monitored nests is small and future studies in our research area should do similar analyses with a larger sample size to obtain greater statistical power. To understand breeding success better in relation to habitat, future research should compare productivity and habitat variables in low-density versus high-density sites, and between sites of high failure and low failure rates. Future studies that assess habitat availability with use by Least Flycatchers would allow for an understanding of habitat preferences. Furthermore, assessments of food availability, potential predation, and clustered breeding behavior would aid in interpreting rates of nest success and productivity.

Nebel et al. (2020) called for habitat conservation to benefit aerial insectivores. In Canada, if Least Flycatchers continue to decline, researchers will need to identify the species' critical habitat according to the Species at Risk Act. A review of critical habitat in North America and Australia concluded that the term was used inconsistently (Camaclang et al. 2014). They recommended that population viability parameters need to be included in the identification of critical habitat even though only 1% of the articles that they reviewed did that. We suggest that habitats with high densities of highly productive nesting Least Flycatchers can help define the species' critical habitat. In general, researchers should rely on productivity and density data as credible for critical habitat, rather than presence/absence data. Future research is needed to define a level of density and productivity that would be appropriate for defining critical habitat. Our data show that the BNA could qualify as critical habitat for Least Flycatchers based on our density and productivity measures. We recommend that researchers repeat this 1-year study at the BNA and that researchers conduct similar studies elsewhere to identify other productive habitats for Least Flycatchers and other species, before they reach an endangered status, which increases the difficulty of obtaining useful productivity information.

Acknowledgments

We thank the BBO staff, S. Pearce-Meijerink, J. Teefy, and S. Abernethy, as well as volunteer R. Denn for their help during the field season. This project of the Beaverhill Bird Observatory was co-funded by the European Union. The Beaverhill Bird Observatory thanks its major funders, including the Alberta Conservation Association, Edmonton Community Foundation, TD Friends of the Environment, Canada Summer Jobs, Cabela's Outdoor Fund, and private donors. We thank 2 anonymous referees and the editor for comments on an earlier draft of this article.

Literature cited

Alberta Wild Species General Status Listings. 2015. Government of Alberta. 1 May 2017, last updated 22 October 2019. https://open.alberta.ca/dataset/ad0cb45c-a885-4b5e-9479-52969f220663/resource/763740c0-122e-467b-a0f5-a04724a9ecb9/download/sar-2015wildspeciesgeneralstatuslist-mar2017.pdf

Briskie JV, Sealy SG. 1989a. Determination of clutch size in the Least Flycatcher. Auk. 106:269–278.

Briskie JV, Sealy SG. 1989b. Nest-failure and the evolution of hatching asynchrony in the Least Flycatcher. Journal of Animal Ecology. 5:653–665.

Calvert AM. 2012. Research priorities to support the conservation of aerial insectivores in Canada. Port Rowan (ON) and Ottawa (ON): Bird Studies Canada and Environment Canada.

Camaclang AE, Maron M, Martin TG, Possingham HP. 2014. Current practices in the identification of critical habitat for threatened species. Conservation Biology. 29:482–492.

[COSEWIC] Committee on the Status of Endangered Wildlife in Canada. 2022. COSEWIC Candidate Wildlife Species. https://www.cosewic.ca/index.php/en-ca/reports/candidate-wildlife-species.html#toc5

Darveau M, DesGranges J, Gauthier G. 1992. Habitat use by three breeding insectivorous birds in declining maple forests. Condor. 94:72–82.

Darveau M, Gauthier G, DesGranges J-L, Mauffette Y. 1993. Nesting success, nest sites, and parental care of the Least Flycatcher in declining maple forests. Canadian Journal of Zoology. 71:1592–1601.

Davis DE. 1959. Observations on territorial behavior of Least Flycatchers. Wilson Bulletin. 71:73–85.

DellaSala DA, Rabe DL. 1987. Response of Least Flycatchers *Empidonax minimus* to forest disturbances. Biological Conservation. 41:291–299.

DesGranges J. 1987. Forest birds as biological indicators of the progression of maple dieback in Québec. International Council for Bird Preservation Technical Publication. 6:249–257.

de Zwaan DR, Alavi N, Mitchell GW, Lapen DR, Duffe J, Wilson S. 2022. Balancing conservation priorities for grassland and forest specialist bird communities in agriculturally dominated landscapes. Biological Conservation. 265:109402.

Dunn PO. 1989. The maintenance of monogamy in Black-billed Magpies and Tree Swallows [dissertation]. Edmonton (AB): University of Alberta.

Dunn PO, Thusius KJ, Kimber K, Winkler DW. 2000. Geographic and ecological variation in clutch size of Tree Swallows. Auk. 117:215–221.

Goodenough AE. 2014. Effects of habitat on breeding success in a declining migrant songbird: The case of Pied Flycatcher *Ficedula hypoleuca*. Acta Ornithologica. 49:157–173.

Hudson MR, Bird DM. 2006. An affordable computerized camera technique for monitoring bird nests. Wildlife Society Bulletin. 34:1455–1457.

Huebner DP, Hurteau SR. 2007. An economical wireless cavity-nest viewer. Journal of Field Ornithology. 78:87–92.

Hussell DJ. 1985. Clutch size, daylength, and seasonality of resources: Comments on Ashmole's hypothesis. Auk. 102:632–634.

[IUCN] International Union for Conservation of Nature. 2021. *Empidonax minimus*. The IUCN Red List of Threatened Species 2021. https://www.iucnredlist.org/species/22699854/138003012

Jacklin M. 2017. Aging guide for Least Flycatcher chicks in the Beaverhill Natural Area. Edmonton (AB): Beaverhill Bird Observatory. http://beaverhillbirds.com/publications/papers-reports-manuals

Johnston DW. 1970. High density of birds breeding in a modified deciduous forest. Wilson Bulletin. 82:79–82.

Martin TE. 1992. Breeding productivity considerations: What are the appropriate habitat features for management? In: Hagan JM, Johnston DW, editors. Ecology and conservation of Neotropical migrant landbirds. Washington DC: Smithsonian Institution Press; p. 455–473.

Murphy MT. 1989. Life-history variability in North American breeding tyrant flycatchers: Phylogeny, size or ecology? Oikos. 54:3–14.

[NABCI-Canada] North American Bird Conservation Initiative Canada. 2019. The state of Canada's birds. Ottawa (ON): Environment and Climate Change Canada. http://nabci.net/resources/state-of-canadas-birds-2019/

Nebel S, Casey J, Cyr MA, Kardynal KJ, Krebs EA, et al. 2020. Falling through the policy cracks: Implementing a roadmap to conserve aerial insectivores in North America. Avian Conservation and Ecology. 15:23.

Nebel S, Mills A, McCracken J, Taylor P. 2010. Declines of aerial insectivores in North America follow a geographic gradient. Avian Conservation and Ecology. 5:1.

Peck GK, James RD. 1987. Breeding birds of Ontario: Nidology and distribution. Volume 2. Toronto (ON): Royal Ontario Museum.

Robinson SK, Holmes RT. 1982. Foraging behavior of forest birds: The relationships among search tactics, diet, and habitat structure. Ecology. 63:1918–1931.

Smith AC, Hudson MA, Downes CM, Francis CM. 2015. Change points in the population trends of aerial-insectivorous birds in North America: Synchronized in time across species and regions. PLOS One. 10: e0130768.

Smith AC, Hudson MA, Aponte VI, Francis CM. 2020. North American Breeding Bird Survey - Canadian trends website, data-version 2019. Gatineau (QC): Environment and Climate Change Canada. https://wildlife-species.canada.ca/breeding-bird-survey-results

[SARA] Species At Risk Act. 2002. An act respecting the protection of wildlife species at risk in Canada. https://laws.justice.gc.ca/eng/acts/s-15.3/

Spiller KJ, Dettmers R. 2019. Evidence for multiple drivers of aerial insectivore declines in North America. Condor. 121:duz010.

Tarof SA, Briskie JV. 2020. Least Flycatcher (*Empidonax minimus*), Version 1.0. In: Poole AF, editor. Birds of the world. Ithaca (NY): Cornell Lab of Ornithology. https://doi.org/10.2173/bow.leafly.01

Tarof SA, Ratcliffe LM. 2004. Habitat characteristics and nest predation do not explain clustered breeding in Least Flycatchers (*Empidonax minimus*). Auk. 121: 877–893.

Walkinshaw LH. 1966. Summer observations of the Least Flycatcher in Michigan. Jack Pine Warbler. 44:150–168.

Warkentin IG, Reed JM, Dunham SM. 2003. Nest site characteristics of American Robins breeding in desert riparian habitat. Wilson Bulletin. 115:16–23.

Winkler DW, Ringelman KM, Dunn PO, Whittingham L, Hussell DJ, et al. 2014. Latitudinal variation in clutch size–lay date regressions in *Tachycineta* swallows: Effects of food supply or demography? Ecography. 37:670–678.