

Least Flycatcher nest reuse in the Beaverhill Natural Area

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Introduction

Between season nest reuse is rarely observed and remains understudied in open-cup nesting birds (Otterbeck et al. 2019, Wuczyński & Hałupka 2024). Despite the significant energetic costs involved, new nests are constructed annually, particularly by tree nesting songbirds (Mainwaring and Hartley 2013, Lack 1954). Nest reuse offers potential benefits, such as saving time and energy and increased overall nest success (McIvor and Healy 2017). Previous studies indicate that nest reuse allows for earlier egg-laying, reduces the likelihood of brood parasitism, and facilitates the quick establishment of replacement clutches in cases of nest failure (Batisteli et al. 2021, Cavitt et al. 1999, Otterbeck et al. 2019). Conversely, both Cancerelli and Murphy (2013) and Redmond et al. (2007) found no reproductive advantage to nest reuse in Eastern Kingbird (*Tyrannus tyrannus*) populations in Malheur National Wildlife Refuge in Oregon, United States. Instead, their study indicates frequent nest reuse is a response to a shortage of high-quality nesting sites, which corroborates results found by Wysocki (2004) about European Blackbirds (*Turdus merula*) and Wuczyński & Hałupka (2024) about multiple passerine species in Poland.

Historically, the lack of nest reuse has been attributed to ectoparasite avoidance (Clark and Mason 1985, Wiebe et al. 2007). However, most studies employing this hypothesis analyze cavity nesting species, due to their inherently limited nest sites, and consequent nest reuse (Barclay 1988, Brawn and Balda 1988). Research focusing on cavity nesters has shown that increased nest parasites in reused nests are detrimental to nestling survival and fitness and reduce reproductive success, especially in colonially nesting species (ie. Moss and Camin 1970, Shields and Crook 1987, Brown and Brown 1986). It has also been acknowledged that costs and benefits of nest reuse vary geographically between populations (ie. based on breeding season length) (Barclay 1988).

Nest re-use in open-cup nesting passerines is uncommon, and therefore not well understood (Wuczyński & Hałupka 2024, Batisteli et al. 2021). The absence of nest reuse in open-cup nesters may be attributed to exposure to the elements, which degrade the structural quality of nests between years (Batisteli 2021). Reduced structural stability can pose additional risks in adverse weather, if the nest is unable to withstand high winds or precipitation (Mazgajski 2007). However, even in the presence of structurally adequate nests from previous years, nest reuse is uncommon (Lack 1954). Additionally, open-cup nests are highly susceptible to predation, deterring individuals from returning to the same nesting location in consecutive years (Weidinger and Kočvara 2010, Martin 1995). New nests are often built in different locations within the same breeding territory, to avoid repeated nest failure due to local predators' memorization (Sonerud and Fjeld 1987, Sonerud 1985, 1993, Weidinger and Kocvara 2010). Predation risk may also be increased by accumulated olfactory cues over several breeding seasons, or more vocal young due to elevated parasite abundance in reused nests (Otterbeck et al. 2019, Christie et al. 1996, Leech and Leonard 1997). Some evidence has been found that implies that, in addition to open-cup nesters, species with small body size and canopy nesting species

also face higher predation risks (Erckmann et al. 1990, Redmond et al. 2007, Martin 1995, Lack 1954). Based on the threat-sensitive predation avoidance hypothesis, the predisposition to predation risk based on life history could discourage nest reuse in some species (Chuard et al. 2020).

Least Flycatchers (*Empidonax minimus*) are abundant breeding birds in the Beaverhill Natural Area in central Alberta, Canada. They build open-cup nests in upright crotches, or on the proximal end of horizontal limbs (Briskie 1988). Their nests are commonly constructed from fine grasses or other plant material, reinforced with spiderwebs, and lined with cotton, grasses, feathers, or hair (Bent 1942, Harrison 1978, Briskie 1988). Least Flycatchers display opportunistic preferences in nesting material, notably demonstrated in 1986 where a Least Flycatcher lined its nest with several layers of dragonfly wings (Briskie 1988). The biodiverse and abundant arthropod populations in the Beaverhill Natural Area therefore may increase the likelihood that more spiderwebs are incorporated into nest building. Since spiderwebs serve to re-enforce the structural integrity of the nest, more spiderwebs could improve the longevity of Least Flycatcher nests between breeding seasons.

Least Flycatcher nesting behavior has previously been studied and monitored for nesting success and habitat use in the Beaverhill Natural Area (Van Brempt et al. 2023, Jorgensen 2023). Due to their small body size and mid-canopy, open-cup nesting behaviour, Least Flycatchers are not ideal candidates for nest reuse, based on predation risk explored in previous literature (Erckmann et al. 1990, Redmond et al. 2007, Martin 1995, Lack 1954). However, during two years of monitoring in Beaverhill (2022, 2023), at least five nests were found to be reused by Least Flycatchers between breeding seasons. This study aims to determine if the local population of Least Flycatchers consistently reuses nests and whether this behavior provides advantages such as earlier initiation of egg laying and more efficient replacement clutches, or if it's a reflection of high-quality nest sites. It also seeks to identify any enhanced susceptibility to failure through predation or weathering associated with nest reuse, and if nest success is correlated to nest success in previous years. Here, it is hypothesized that the increased structural integrity provided by spiderwebs will enhance the number of nests that remain inhabitable between breeding seasons, increasing the amount of nest reuse in the breeding area.

Methods

Survey methods

The study area covered approximately 28ha (~700m x ~400m), located in the Beaverhill Natural Area. The habitat in all nest locations was mixed age deciduous forest, dominated by trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.) in the Aspen Parkland Natural Region.





To determine locations of nests built in previous years, saved GPS points from 2023 and 2022 were visited in May 2024. Where nests could be identified, images were taken using a CIMELR brand ALS5005 dual lens industrial endoscope camera, affixed to a telescopic pole in May 2024. Nests found were rated on a scale from one to four (Table 1) based on images taken. Additionally, a Canon SX40 HS PowerShot camera was used to take photos three metres from either side of the nest from the ground, to document the side profile of the nests upon discovery.

New nests were found by following Brown-headed Cowbirds (*Molothrus ater*), a Least Flycatcher brood parasite, and territorial singing, contact calls, and defense displays of Least Flycatchers (Briskie et al. 1990). Other behaviours such as carrying food or nesting material were also used as cues to locate nests, following methods as described by Van Brempt et al. (2023). Search efforts for new nests began in the second week of June 2024 and continued until the end of June 2024 and were assumed to be newly constructed for the 2024 breeding season. 2024 nests were flagged at the base of the tree and the location was recorded with a GPS. New nests were added to the survey route as they were discovered.

Due to inclement weather, regular nest surveys began one month after the first Least Flycatcher capture during the Beaverhill Bird Observatory's (BBO) Spring migration monitoring program. The first Least Flycatcher of the season was banded on May 9th, 2024, and regular nest surveys began on June 9th, 2024. Surveys were conducted every two to five days (mean = 4 days), depending on staff availability and weather, and continued until July 23, 2024 (when all nests were empty). Surveys typically took one day, but sometimes spanned two days. On June 9th and 10th, 40 nests (new and old) were surveyed and evaluated based on their condition (see Table 1). Subsequent surveys included only nests in good condition (rated three or four) and new nests found after June 9th. Two weeks after regular nest surveys began, a second sweep of all previous years' nests was completed to ensure no reused nests were occupied after the first survey. This secondary evaluation was completed with binoculars only, as completed and lined nests were conspicuous without utilization of the pole camera.

Egg-lay dates were estimated within one day when clutches were discovered before completion, based on the laying behavior of Least Flycatchers (one egg per day) and an average clutch size of three to five eggs. If the exact lay date could not be determined for complete clutches, the latest possible lay date was estimated by subtracting the number of eggs in the clutch from the observation date. The estimated lay dates were never more than two days after the actual lay date due to frequent surveys. For nests with nestlings, the lay date was estimated by subtracting the age of the nestlings (in days) from 14 days prior to observation, assuming a 14-day incubation period (Davis, 1959). Nestling age was assessed using photos taken with the pole camera and an aging guide developed by Jacklin (2017). Once nestlings were old enough to flap their wings and potentially fledge (12-15 days), age was assessed using binoculars to avoid premature fledging.

Table 1. Class variable scale of Least Flycatcher nest condition, assigned at every survey based on image taken.

Condition		Example
1	Extremely damaged; walls slumped or missing	
2	Slightly damaged; not round or completely intact, some holes or slumping	
3	Good condition; mostly round or slightly misshapen with walls completely in-tact	
4	Complete and lined; mostly round with new lining of feathers and nesting material	

Nest success was classified as nests that had successful fledging of all hatched eggs. Partial success was classified as nests that had less than half of the eggs hatch, or only some of the nestlings successfully fledged. Complete and partial success was pooled for analysis, given the restricted sample size. Nest failure was classified by eggs leaving the nest (by predation or falling from the nest, ie. in a storm), or all nestlings failing to fledge. Failed nests continued to be monitored if they failed due to predation, but not if they were damaged in a weather event, due to differences in structural quality.

Statistical Methods

Statistical analysis was completed using Excel data analysis tools (Microsoft Corporation 2018), and RStudio using the R base package (R Core Team 2022) and *ggplot2* (Wickham 2016).

Results

A total of 38 nests from previous years were surveyed for presence and condition between May 15th and May 23rd. Based on their structural condition (Table 1), 17 of these nests were regularly monitored. Additionally, 10 new nests were discovered through targeted nest searches, which continued until the end of June 2024. These new nests were added to the regular survey route as they were found, except for two nests that were too high to observe using the pole camera and were excluded from surveys.

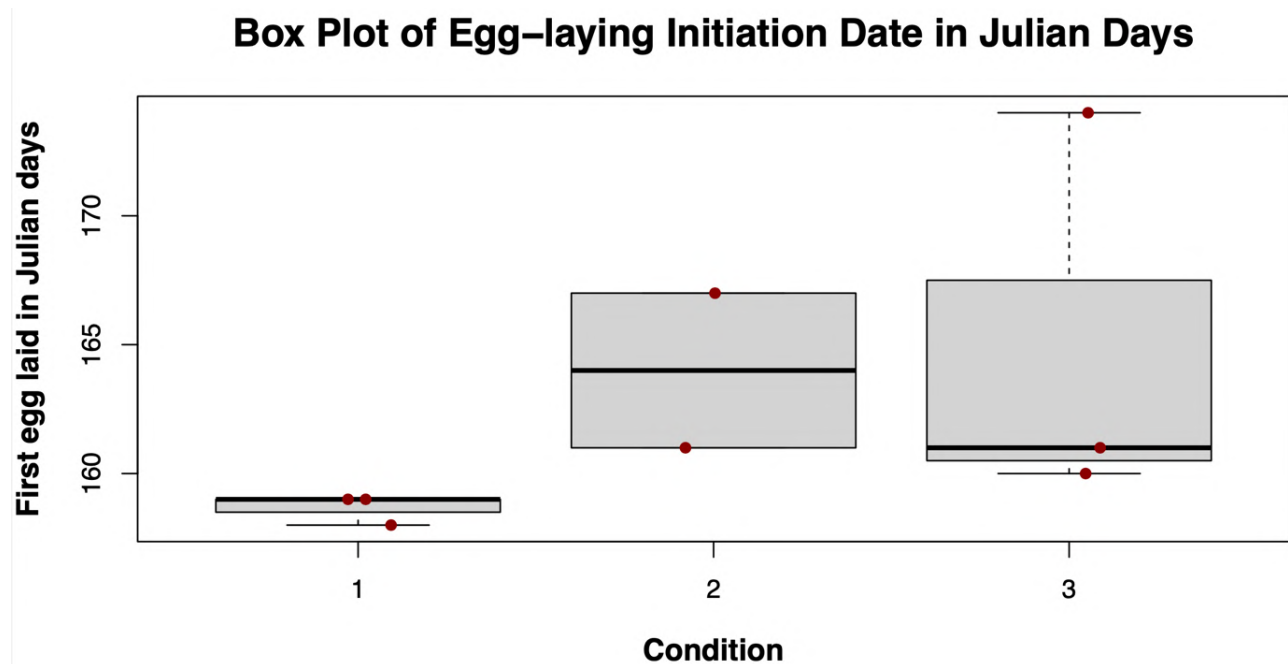
In total, 16 observed nests were active, established asynchronously. Six of the active nests failed, four due to predation, and two due to damage in inclement weather (evidenced by nest damage and eggs recovered on the ground). The active nests included one established in 2022, seven in 2023, and eight in 2024. Notably, one nest established in 2024 was in the same location as a Least Flycatcher nest from 2021 (anecdotal evidence, BBO). Overall, 50.0% of monitored active nests were reused from previous years. However, the small sample size ($n = 16$) should be acknowledged and reduce the certainty of this result. Of the 38 old nests surveyed, 21.05% were reused.

Initiation of egg laying

The difference in lay date between old nests and new nests was not statistically significant (ANOVA, $P = 0.659$, $F = 0.204$). The average first egg lay date for re-used nests was 162.4 Julian days (June 10) whereas the average first egg lay date for new nests was 164.3 Julian days (June 12).

The difference in initiation of egg laying between initial conditions of reused nests was also not statistically significant (ANOVA, $P = 0.769$, $F = 0.381$). Variance increased with increasing structural quality (Table 1.). Condition one nests ($n = 3$) had a variance of 0.33 (ANOVA), condition two nests ($n = 2$) had a variance of 18.0 (ANOVA), and condition three nests ($n = 3$) had a variance of 61.0 (ANOVA, Figure 1.).

Figure 1. Box plot of nest establishment date in Julian days, showing mean date, variance, and jitter showing individual nests in red points.



The average first egg lay date for condition one nests was 158.7 Julian days (June 6), condition two nests was 164 Julian days (June 12), and condition three nests was 165 Julian days (June 13).

The difference in lay date between failed reused nests and condition two and three nests was statistically significant (ANOVA, $P = 0.04750$, $F = 5.7574$). Failed nests established in 2022 or 2023 ($n = 5$) had a mean egg laying initiation date of 158.4 Julian days (June 6), and condition two and three nests ($n = 4$) had a mean egg laying initiation date of 165.5 Julian days (June 13).

The difference in lay date between all failed nests ($n = 6$) and condition two and three nests was not statistically significant (ANOVA, $P = 0.45435$, $F = 0.61826$). Failed nests of all conditions had a mean egg laying initiation date of 161.7 Julian days (June 9).

Susceptibility to failure events

Proportions of reused versus new nests that failed were visually analyzed using bar graphs generated in R using *ggplot2* (Wickham 2016) (Figure 2, 3). Of the failed nests, one was established in 2022, two in 2023, and three in 2024. Of the predated nests, two were established in 2023 and two were established in 2024. Of the weather damaged nests, one was established in 2022 and one was established in 2024. Overall nest outcome was not significant between years of establishment and required no further analysis. Origin of nest failure was also not significant between years of establishment and was not analyzed further.

Figure 2. Bar graph showing numbers of failed and successful nests in 2024, coloured by initial year the nest was built.

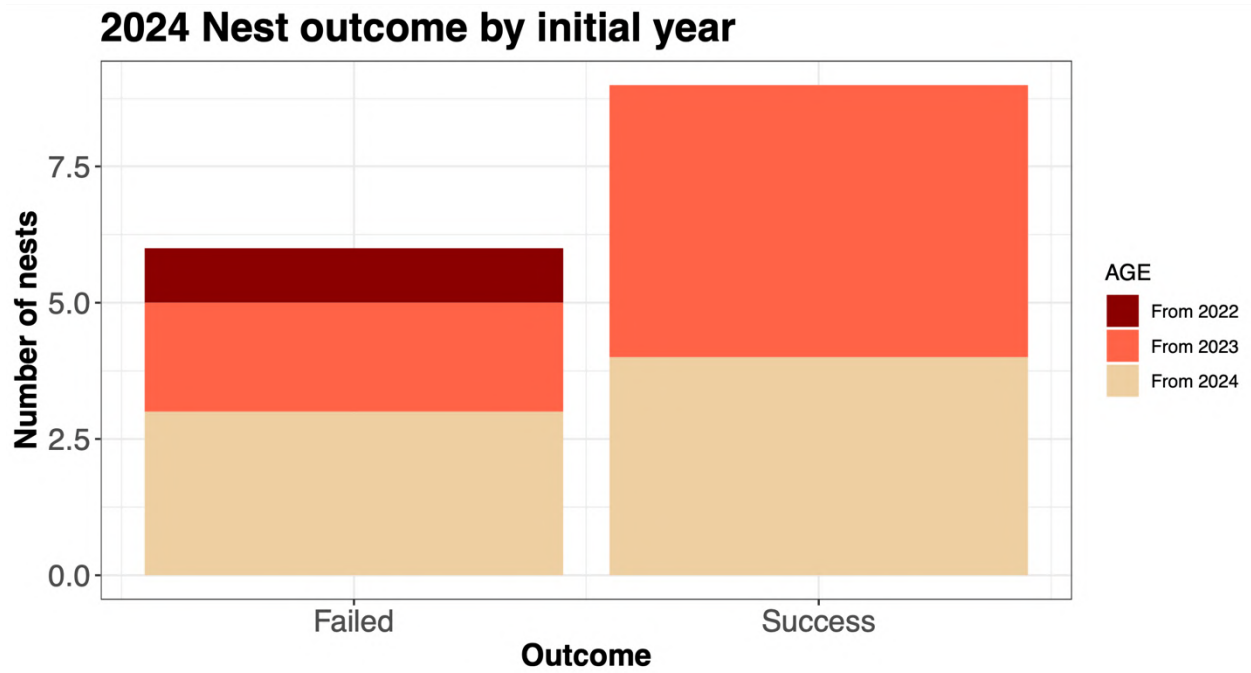
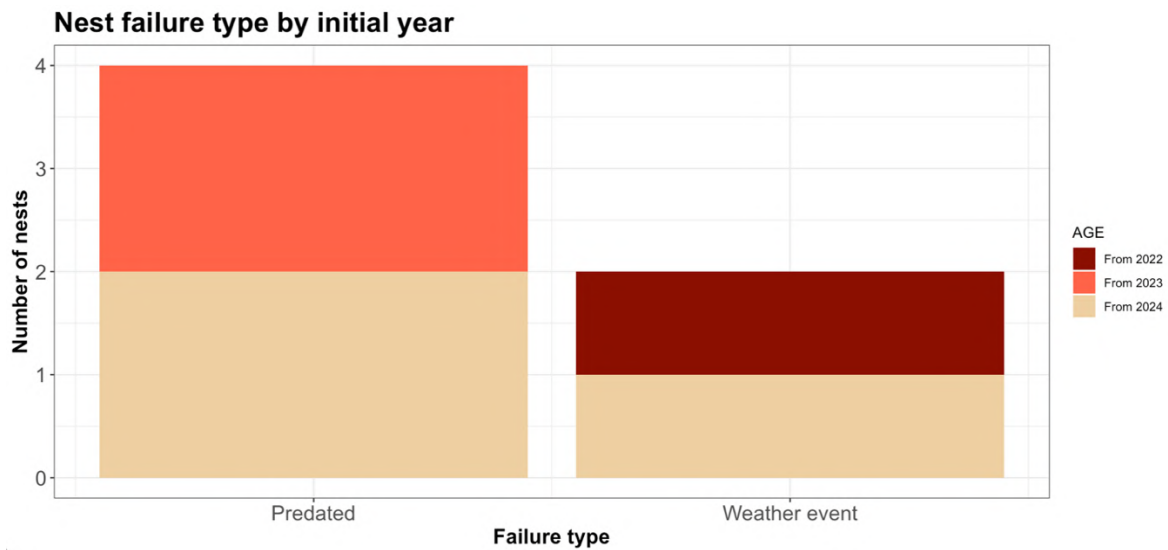


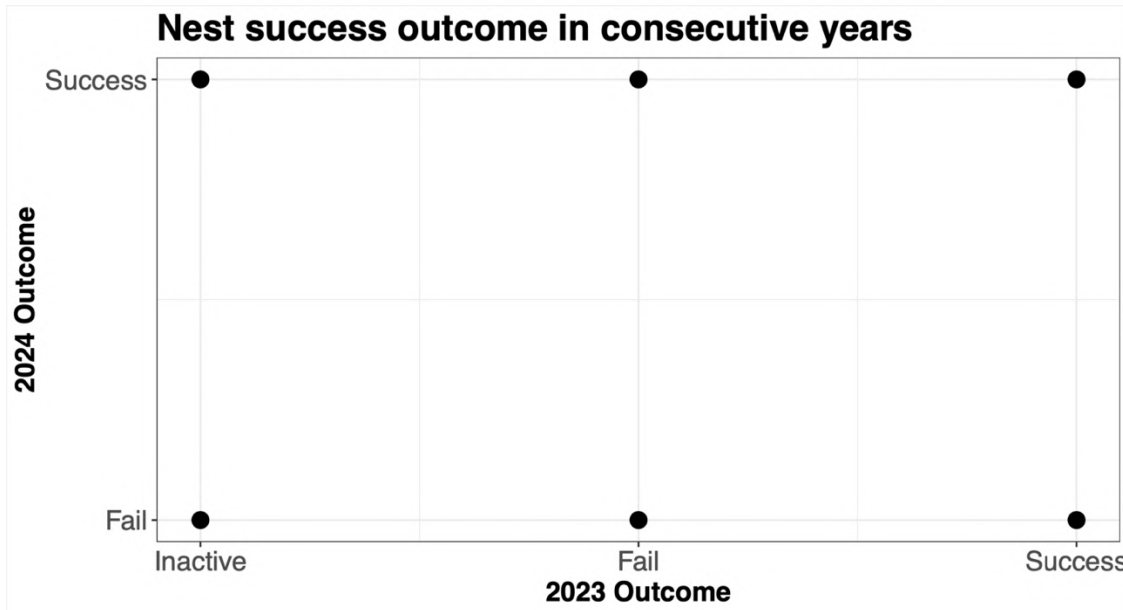
Figure 3. Bar plot showing type of nest failures in 2024, predation and weather events. The graph is coloured by initial year the nest was built.



Previous outcome

The outcome of reused nests in 2023 was plotted against the 2024 outcome in a scatterplot (Figure 4). The distribution was such that the slope was 0°, meaning that there was no correlation at all between the outcomes between years. Nests that were inactive in 2024 were not analyzed to increase clarity of results.

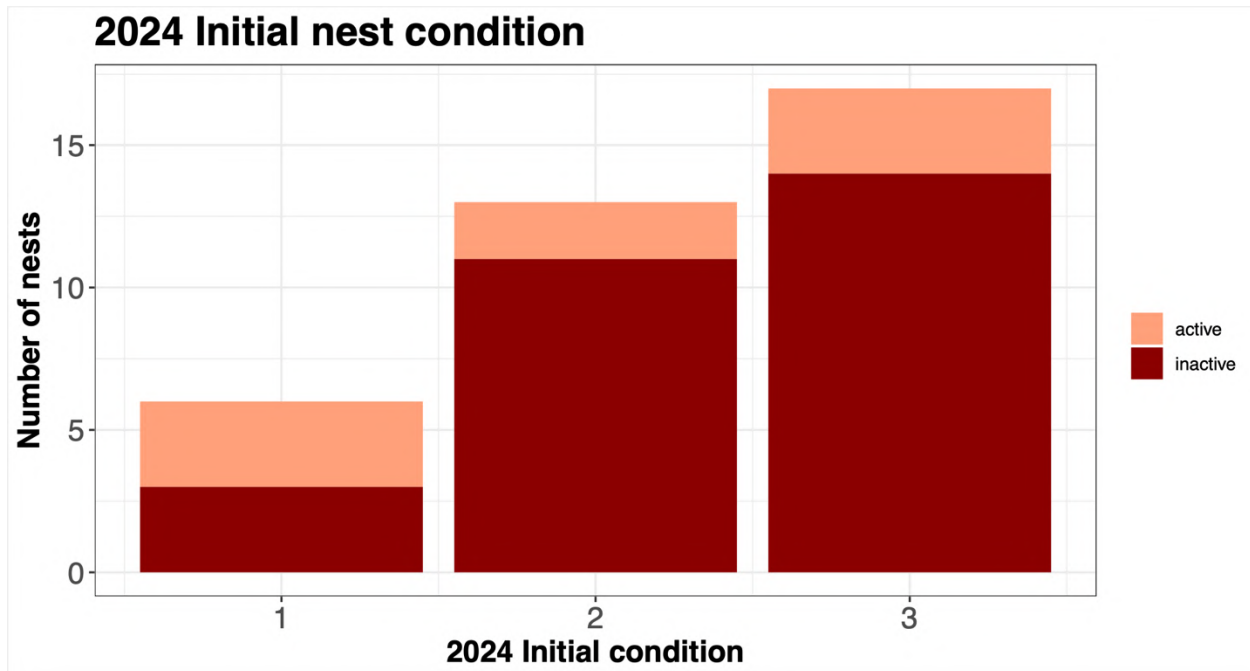
Figure 4. Scatterplot showing 2024 outcome as a function of 2023 outcome.



Initial condition

36 nests were evaluated that had persisted at least one winter (established in 2022 or 2023). Six nests (16.66%) were determined to be condition one, 13 nests (36.11%) were determined to be condition two, and 17 nests (47.22%) were determined to be condition three (Table 1., Figure 5.) Three condition one nests were active (33%), two condition two nests were active (15%), and three condition three nests were active (18%).

Figure 5. Bar graph showing the initial condition of old nests found in 2024. The second colour shows the proportion of each condition of nest that was active in 2024.



Discussion

Initiation of egg laying and clutch replacement

Although the difference in initiation of egg laying was not statistically significant ($\alpha = 0.05$) between old nests and new nests or between nest condition ($P = 0.6591$, $P = 0.7693$, respectively), relative to Least Flycatchers lifecycle, the time interval is significant. The difference between re-used nests and new nests was insignificant, at only two days. However, the difference between condition one nests and condition two, three, and four nests is five, six, and five days, respectively. Since incubation of eggs can be assumed to last 14 days, a difference of five/six days accounts for nearly half of the incubation time (Davis 1959). Surprisingly, the earlier clutch initiation occurs at nests of lower structural quality, indicating that Least Flycatchers may initially be selecting based on site quality, not nest quality. This also corroborates findings by Cancerelli and Murphy (2013), Redmond et al. (2007), who determined

nest reuse in Eastern Kingbirds (*Tyrannus tyrannus*) to be a function of high-quality nesting site availability. Wysocki (2007) also found nest reuse to be correlated with increasing nest site quality. Although this study did not measure, and therefore cannot make inferences about, site conditions, the reuse of old nests that are extremely structurally damaged offers little other advantage to nesting pairs in the breeding season.

Later initiation dates of structurally superior nests could reflect the use of old nests to re-clutch following brood failure or late arrival to the breeding grounds, similar to findings by Otterbeck et al. (2018) in Eurasian sparrowhawks (*Accipiter nisus*). Based on the significant difference in initiation dates between failed reused nests and high-quality reused nests ($P = 0.0475$, seven days), higher quality nest structures are reused following nest failure. This could be advantageous to compensate for a delayed brood following a nest attempt failure due to inclement weather or predation (Otterbeck et al. 2018). However, new nests had a similar initiation date to high quality old nests, indicating that there is no significant advantage to reusing a nest instead of constructing a new one.

There were two major weather events during the survey period, at 163 Julian days (June 11), and 173 Julian days (June 21). On June 11, a thunderstorm with strong winds swept through the natural area, followed by a hailstorm on June 21 that also affected the study site. Nests damaged by these weather events were identified by broken tree branches that had impacted the nests and shattered eggs found at the base of the trees. No further weather-related nest damage occurred after June 21. After Julian day 158 (June 6), no nests rated below condition two were reused. This implies that if the parents of the two clutches damaged by wind attempted nesting again, they may have opted for higher quality nests or built new ones. Without identifying individual Least Flycatchers (e.g., through color banding), this hypothesis cannot be confirmed. However, it is clear that no breeding pair attempted a second brood in a highly damaged nest from previous years, as evidenced by the early initiation dates of the observed nests.

Susceptibility to failure events

Six active nests failed in total over the course of the study. One failed nest was originally built in 2022, two in 2023, and three in 2024. Interestingly, one of the failed nests established in 2024 was in a location where a nest had previously resided in 2021 but had been destroyed completely in previous years. Only half of the observed nest failures occurred in reused nests, which does not suggest that nest reuse significantly amplifies the risk of failure (Figure 3).

Weather damage caused nest failure in two nests, one established in 2022 and one established in 2024. This may indicate that the structural degradation between breeding seasons is not significant enough to increase the likelihood of failure in inclement weather. Predation caused nest failure in four nests, two established in 2024 and two established in 2023. Therefore, failure by predation did not occur more in reused nests than in new nests, indicating that predation risk

is not higher in reused (Figure 4.) Ultimately, nest failure does not appear correlated to nest reuse, although the small sample size ($n = 6$) should be acknowledged and lower the certainty of this result.

Previous Outcome

Of the active reused nests in the Beaverhill Natural Area, the 2023 outcome was unknown in two nests (not monitored), inactive in two nests, successful in two nests, and failed in two nests. Both nests unknown in 2023 were successful in 2024. For the other nests, one nest from each category (inactive, successful, and failed in 2023) succeeded in 2024, while the other nest in each category failed. Overall, no correlation or pattern was observed in the outcomes of reused nests between the two years (Figure 5).

Structural Integrity

Many nests from previous years were intact following one or two winters between breeding seasons. 30 of the 36 (83.33%) evaluated nest sites were recognizable Least Flycatcher open-cup nests, and 17 (47.22%) of them showed very little signs of wear at all. Structural retention between years of Least Flycatcher nests has not been previously examined in literature, and so the results found in the Beaverhill Natural Area have significant implications in the study of nesting behaviours. Additionally, winter conditions between breeding seasons, and spring weather at the start of the breeding season could influence renesting behaviour, as suggested by Wuczyński & Hałupka (2024). This result is geographically and temporally unique because weather conditions vary from year to year and can affect ecological processes in different ways.

Although this result might be specific to the 2024 breeding season in the Beaverhill Natural Area, the high percentage of nests that were structurally maintained between years suggests that exposure to the elements may not be the reason why open-cup nesters avoid reusing nests. Alternately, this could suggest that nests in the Beaverhill Natural Area contain more spiderwebs, used for structural reinforcement, and are able to withstand more weathering. High arachnid diversity in the study area suggests that nest builders, such as Least Flycatchers, could include more spiderwebs in their nests. More study would be needed to draw conclusions about these hypotheses, such as nest component analysis between the Beaverhill Natural Area and other Least Flycatcher nesting grounds. Replicating this study in other years may also provide insight to whether the results found here are unique to this season, or if they have implications for the Natural Area.

Conclusion

Least Flycatchers are an abundant breeding passerine in the Beaverhill Natural Area (BNA). Nest monitoring in successive years has revealed nest reuse as a relatively frequent breeding strategy within the BNA. Earlier nest reuse likely occurs in high quality nest sites, where the previous structure has been compromised. Later nesting occurs more frequently in higher quality nest structures from previous years and in newly constructed nests. This behaviour is likely to make up for late arrival to the breeding grounds, or to attempt a second clutch if the first one fails. However, nest reuse doesn't appear to offer a distinct advantage over building a new nest.

The significantly later initiation of nests of higher structural quality and new nests (between five and six days) compared to lower quality nests indicates that using nests from previous years may be a strategy to combat a late start to breeding. Instead of an initial advantage, nest reuse appears to be a compensation tactic for overcoming obstacles during the breeding season. However, there is no evidence of any reproductive advantage compared to building new nests. The earlier initiation in low-quality reused nest structures could indicate an advantage in using evidence of previous nests to locate high-quality nest sites. Nest site quality has been speculated to be a motivating factor in nest reuse in other literature, and this study finds evidence supporting this conclusion (Cancerelli and Murphy 2013, Redmond et al. 2007, Wuczyński & Hałupka 2024, Wysocki 2004).

The analysis in this study shows that there is no increased risk of predation or adverse weather events with nest reuse, conflicting with current literature (Mazgajski 2007, Sonerud and Fjeld 1987, Christie et al. 1996, Leech and Leonard 1997). The predation observed in this study may be a result of Least Flycatcher's predisposition to predation risk due to their body size and nesting habits, though the small sample size should encourage further research (Erckmann et al. 1990, Redmond et al. 2007, Martin 1995, Lack 1954). This study also found that the outcome of the nest in previous years is not correlated with nest success during reuse.

The structural integrity of most nests was found to be maintained between breeding seasons. 83.3% of nests surviving through one or two winters were found to retain their shape and structural stability in May 2024. Several interacting factors could have impacted this result, including arthropod abundance and spiderweb use in nest building, winter conditions, spring conditions, and microhabitat at the nest site. While no conclusions can be drawn from this result, the high percentage of nests surviving between years and conspicuous nest reuse could have implications for open-cup nesting species. The structural retention between years conflicts with current literature, indicating that degraded structural quality is not the reason for low nest reuse in open-cup nesting species (Batisteli 2021).

This study's success depended on consecutive years of nest monitoring but was limited by the small sample size. Continuation of the Least Flycatcher nest monitoring project should

broaden search effort for new nests, to expand the sample size and increase the certainty of conclusions drawn from the project.

Ultimately, nest reuse by Least Flycatchers in the Beaverhill Natural Area between breeding seasons is a frequent occurrence, with 50.0% of observed active nests in 2024 being reused from 2022 or 2023. Nest failure, both by predation and by inclement weather occurred equally in old and new nests, indicating that there is no correlation between nest reuse and nest failure. Despite the complex ecological interactions impacting nest longevity, and the small sample size, the relatively high percentage of active reused nests indicates that nest reuse is at least as common as nest building by Least Flycatchers in the Beaverhill Natural Area. Additional research to expand sample size and account for environmental stochasticity should be considered to make further conclusions.

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Literature Cited

- Barclay, R. M. (1988). Variation in the costs, benefits, and frequency of nest reuse by Barn Swallows (*Hirundo rustica*). *The Auk*, 105(1), 53-60.
- Batisteli, A. F., Sarmiento, H., & Aurélio Pizo, M. (2021). Nest reuse by Pale-breasted Thrushes reduces the chance of cowbird parasitism and allows earlier initiation of breeding. *Journal of Field Ornithology*, 92(2), 105-114.
- Bent, A.C. (1942). Life histories of North American flycatchers, larks, swallows and their allies. *U.S. National Museum Bulletin*. 179
- Brawn, J. D., & Balda, R. P. (1988). Population biology of cavity nesters in northern Arizona: do nest sites limit breeding densities?. *The Condor*, 90(1), 61-71.
- Briskie, J. V. (1988). Least Flycatcher lines nest with dragonfly wings. *Blue Jay*, 46(3).
- Briskie, J. V., & Sealy, S. G. (1989a). Nest-failure and the evolution of hatching asynchrony in the Least Flycatcher. *The Journal of Animal Ecology*, 653-665.
- Briskie, J. V., & Sealy, S. G. (1989b). Determination of clutch size in the least flycatcher. *The Auk*, 106(2), 269-278.
- Briskie, J. V., Sealy, S. G., & Hobson, K. A. (1990). Differential parasitism of least flycatchers and yellow warblers by the brown-headed cowbird. *Behavioral Ecology and Sociobiology*, 27, 403-410.
- Brown, C.R., & Brown, M.B. (1986). Ectoparasitism as a cost of coloniality in Cliff Swallows (*Hirundo pyrrhonota*). *Ecology* 67: 1206-1218.
- Cancellieri, S., & Murphy, M.T. (2013). Experimental examination of nest reuse by an open-cup-nesting passerine: time/energy savings or nest site shortage? *Animal Behaviour* 85: 1287–1294.
- Cavitt, J.F., Pearse, A.T., & Miller, T.A. (1999). Brown Thrasher nest reuse: a time saving resource, protection from search-strategy predators, or cues for nest-site selection? *Condor* 101: 859–862.
- Christie P., Richner H., & Oppliger A. (1996). Begging, food provisioning, and nestling competition in great tit broods infested with ectoparasites. *Behav Ecol* 7:127–131
- Chuard, P. J., Grant, J. W., Ramnarine, I. W., & Brown, G. E. (2020). Exploring the threat-sensitive predator avoidance hypothesis on mate competition in two wild populations of Trinidadian guppies. *Behavioural Processes*, 180, 104225.

- Clark L., & Mason J.R. (1985). Use of nest material as insecticidal and anti-pathogenic agents by the European Starling. *Oecologia* 67:169–176
- Davis, D. E. (1959). Observations on territorial behavior of Least Flycatchers. *The Wilson Bulletin*, 73-85.
- Erckmann W.J., Beletsky L.D., Orians G.H., Johnsen T., Sharbaugh S., & D’Antonio C. (1990). Old nests as cues for nest-site selection: an experimental test with Red-winged Blackbirds. *Condor* 93:113– 117. <https://doi.org/10.2307/1368389>
- Harrison C. (1978). A field guide to the nests, eggs and nestlings of North American birds. *Collins*, London.
- Jacklin, M. (2017). Aging Guide for Least Flycatcher chicks in the Beaverhill Natural Area. [Report published on the website of the Beaverhill Bird Observatory.]. <http://beaverhillbirds.com/publications/papers-reports-manuals/>
- Jorgensen, C. (2023). 2023 Least Flycatcher (LEFL) Nest Monitoring Report. Beaverhill Bird Observatory website
- Lack D .(1954). The natural regulation of animal numbers. Clarendon press, Oxford
- Leech S.M., & Leonard M.L. (1997). Begging and the risk of predation in nestling birds. *Behav Ecol* 8:644–646
- Mainwaring, M. C., & Hartley, I. R. (2013). The energetic costs of nest building in birds. *Avian biology research*, 6(1), 12-17.
- Martin T.E. (1995). Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol Monogr* 65:101–127. <https://doi.org/10.2307/2937160>
- Mazgajski T.D. (2007). Effect of old nest material on nest site selection and breeding parameters in secondary hole nesters — a review. *Acta Ornithologica* 42(1):1–14. DOI: 10.3161/068.042.0107.
- McIvor, G.E., & Healy, S.D. (2017). Nest site selection and patterns of nest re-use in the Hooded Crow *Corvus cornix*. *Bird Study* 64: 374– 385.
- Microsoft Corporation. (2018). *Microsoft Excel*. Retrieved from <https://office.microsoft.com/excel>
- Moss, W.W., & Camin, J.H. (1970). Nest parasitism, productivity, and clutch size in Purple Martins. *Science* 169: 1000-1003.

- Otterbeck, A., Selås, V., Tøttrup Nielsen, J., Roualet, É., & Lindén, A. (2019). The paradox of nest reuse: early breeding benefits reproduction, but nest reuse increases nest predation risk. *Oecologia*, *190*, 559-568.
- Redmond L.J., Murphy M.T., & Dolan A.C. (2007). Nest reuse by Eastern Kingbirds: adaptive behavior or ecological constraint? *Condor* *109*:463–468. <https://doi.org/10.1650/0010-5422>
- R Core Team. (2022). *R: A language and environment for statistical computing* [Manual]. <https://www.R-project.org/>
- Shields, W.M., & Crook, J.R. (1987). Barn Swallow coloniality: a net cost for group breeding in the Adirondacks? *Ecology* *68*: 1373-1386.
- Sonerud G.A. (1985). Nest hole shift in Tengmalm's owl *Aegolius funereus* as defence against nest predation involving long-term memory in the predator. *J Anim Ecol* *54*:179–192. <https://doi.org/10.2307/4629>
- Sonerud G.A. (1993). Reduced predation by nest box relocation: differential effect on Tengmalm's Owl nests and artificial nests. *Ornis Scand* *24*:249–253. <https://doi.org/10.2307/3676742>
- Sonerud G.A., Fjeld PE (1987). Long-term memory in egg predators: an experiment with a Hooded Crow. *Ornis Scand* *18*:323–325. <https://doi.org/10.2307/3676904>
- Van Brempt, M., Holroyd, G. L., Hvenegaard, G., & Van Arragon, J. (2023). Nesting biology and breeding density of Least Flycatchers (*Empidonax minimus*) in the Beaverhill Natural Area, Alberta, Canada. *The Wilson Journal of Ornithology*, *135*(4), 553-560.
- Weidinger, K., & Kočvara R. (2010). Repeatability of nest predation in passerines depends on predator species and time scale. *Oikos* *119*: 138– 146.
- Wickham H (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. ISBN 978-3-319-24277-4, <https://ggplot2.tidyverse.org>.
- Wiebe, K. L., Koenig, W. D., & Martin, K. (2007). Costs and benefits of nest reuse versus excavation in cavity-nesting birds. In *Annales Zoologici Fennici* (pp. 209-217). Finnish Zoological and Botanical Publishing Board.
- Wuczyński, A., & Hałupka, L. (2024). Multiple nest reuse by three passerine species. *The European Zoological Journal*, *91*(1), 298-304.
- Wysocki, D. (2004). Nest re-use by Blackbirds—the way for safe breeding?. *Acta Ornithologica*, *39*(2), 164-168.