SURVIVAL AND HABITAT USE OF THE KIRTLAND’S WARBLER IN THE BREEEDING AND POST-BREEDING PERIODS

BY

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THESIS

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ABSTRACT

The post-breeding period is an important yet understudied phase of the annual cycle for migratory birds. Emerging evidence suggests that survival and habitat use may be unequal between the breeding and post-breeding periods. The breeding period historically has received disproportionate attention, perhaps resulting in misleading conclusions about the ecology of the post-breeding period. Similarly, juvenile birds are often studied for only a few weeks after fledging, and rarely tracked through their independence period until migratory departure. I leverage both hand-held and automated telemetry, taking advantage of the restricted breeding range of Kirtland's Warbler *(Setophaga kirtlandii)* a habitat specialist, to contrast the ecology in two periods of this migratory bird's annual cycle. Estimates for adult survival were lower at the beginning of the study, with weekly survival increasing throughout, and not significantly different between the breeding and post-breeding periods. Juvenile survival was initially low but increased substantially by six weeks. We found that for both adults and juveniles habitat use differed in the post-breeding period in respect to habitat selected for nesting. Not all adults moved after breeding, but on average, those that did relocated to stands were 8.6 years older than the stand they bred in. Nearly all juveniles were observed to move from their natal areas before migration, and though typically moving more frequently, were also more likely to be resighted in older stands. For all juveniles and many adults, the individual's post-breeding period was longer than the breeding period. Our findings support the importance of studying the ecology of birds during the post-breeding period. For migratory species that exhibit complex life-history strategies over multiple spatial scales, understanding the dynamics of habitat use and survival is

critical for effective conservation, and especially for imperiled species and those with declining or obligate habitats.

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DEDICATION

To all of the creatures. Especially the wildest of ones, and most especially to those that have unwilded and rewilded once more.

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CHAPTER 1: GENERAL INTRODUCTION

Migratory birds employ complex habitat-use strategies throughout their annual cycle, including the often-overlooked post-breeding period. This phase, distinct from migration or breeding, requires many individuals to undergo molt, improve body condition for migration, adapt to changes in predator composition, and explore new areas for food and future dispersal (Ausprey and Rowald 2013, Rappole 2013, Züst 2023, Hays et al. 2024). Despite its potential importance, the post-breeding period remains relatively neglected in migratory bird studies (Rappole 2013). Tracking individuals across these periods poses significant challenges, often precluding even basic descriptions of survival rates and specific habitat use outside of the breeding period. The timing and duration of the post-breeding period are influenced by nesting timing and success, making it essential to confirm both specific cessation of breeding and parental care until migratory departure on an individual basis (Burke 2013). Despite continuous advancements in tracking technologies, comprehensive descriptions of differences in breeding and post-breeding ecology are rare for migratory North American passerines and almost nonexistent for juvenile birds.

Previous studies have highlighted that strategies of habitat use in the post-breeding period may diverge from those in the breeding period for some migratory birds (Vega Rivera et al. 1998, Vega Rivera et al. 2003. Shipley 2013 et al., Vitz and Rodewald 2006, Wilson and Marten 2005, Pagen et al. 2000, Dittmar et al. 2014). Access to appropriate post-breeding habitat may be crucial for survival and migration preparation, potentially offering safer environments for molting and better food availability. (Rivera Vega et al. 1998, McDermott and Wood 2010, Burke 2013, Gow and Stutchbury 2013, Rappole 2013).

Survival rates of migratory birds across different periods of the annual cycle show considerable variation, with migration typically identified as the period with the lowest survival (Sillett and Holmes 2002, Marra et al. 2015, Paxton et al. 2017, Rockwell et al. 2017, Robinson et al. 2020, Newton 2024). The post-breeding period, while less studied, presents its own survival challenges. Juvenile birds face increased mortality immediately after fledging and possibly again post-independence (Rush and Stutchbury 2008, Cox et. al. 2014, Evans et al. 2020, Jones and Ward 2020) though the latter period is far less studied. Adults, too, may experience different survival pressures during the post-breeding period compared to the breeding period due to changing habitat needs and predator dynamics (Vitz and Rowald 2010, Rappole 2013, Shipley et al. 2013).

The Kirtland's Warbler *(Setophaga kirtlandii*), a habitat specialist with a very restricted breeding range, makes it an ideal system for targeted investigations into post-breeding ecology. Despite extensive studies during the breeding season (Walkinshaw 1983, Sykes 1989, Petrucia et al. 2013, Rockwell et al. 2017, Cooper et al. 2019, Cooper et al. 2020, Boccetti and Mayfield 2020), little is known about ecology during the post-breeding period for this species.

Understanding differences in habitat use and survival in different periods of a migratory bird's annual cycle is critical for effective conservation management. Differentiating survival rates across the breeding and post-breeding periods helps identify potential survival bottlenecks and informs habitat management to optimize survival in multiple periods in the annual cycle. Insights into post-breeding habitat use could also illuminate dispersal trends among juveniles, revealing movement patterns and the potential for subsequent range expansion. The availability of quality post-breeding habitat may impact population viability, especially for species such as the Kirtland's Warbler with small populations, restricted ranges, and specific habitat requirements. Thus, elucidating post-breeding survival rates and habitat use is crucial for the conservation of vulnerable avian species.

CHAPTER 2: SURVIVAL OF ADULT AND JUVENILE KIRTLAND’S WARBLERS IN THE BREEDING AND POST-BREEDING PERIODS: AN EXPLORATION OF AN UNDERSTUDIED YET IMPORTANT STAGE OF THE ANNUAL CYCLE

ABSTRACT: The complicated annual cycles of migratory bird species have created formidable barriers to understanding the factors that limit their populations. For migratory birds, the post-breeding period is likely an important part of the annual cycle yet has received little attention. To fill this critical information gap, we investigated the behavior and ecology of adult and juvenile Kirtland's Warblers (*Setophaga kirtlandii*). We tracked 96 adults and 93 juveniles with radio-tags during the breeding and post-breeding periods until fall migration. Both handheld and automated telemetry were used to build detection histories to estimate survival. Adult survival was not significantly different in the breeding or post-breeding periods. However, the duration of the breeding period was likely longer than the breeding period for nearly half of individuals. Juvenile survival was initially low but rapidly improved. This research enhances our understanding of post-breeding ecology by providing separate survival estimates for the breeding and post-breeding periods. Understanding the durations of different periods of the annual cycle and differences in seasonally specific survivorship can improve survival estimates for migratory birds.

INTRODUCTION

Bird populations in North America have experienced dramatic declines with an estimated net loss of 3 billion individuals since 1970, and with migratory birds experiencing some of the greatest declines (Rosenberg et al. 2019). Despite conservation efforts and the identification of some factors which limit populations (e.g., climate change, loss of habitat, unregulated harvest, and other anthropogenic activities), detailed information on where and when in the annual cycle a given population is most at risk remains unknown for most species (Marra et al. 2015, Rosenberg et al. 2019, Flack et al. 2022,). A critical step in identifying the factors that limit populations of migratory birds is estimating survival throughout the annual cycle. Migratory birds exhibit a suite of species-specific breeding and migration strategies that vary both spatially and temporally, which complicates survival estimates both across species and parts of the annual cycle (Hostetler 2015, Marra et al. 2015). The annual cycle of a migratory bird is commonly depicted as having four components: breeding, a spring migration, a wintering period, and a fall migration; each being governed by its own set of factors that impact survival (Marra et al. 2015). However, for many species, the breeding period is composed of two distinct periods: breeding and post-breeding (Rappole 2013). The post-breeding period - the portion of the annual cycle beginning with the termination of reproductive activities (adults) or independence from adults (juveniles) and ending with departure on migration (Rappole 2013) – has received relatively little attention, which has led to a significant knowledge gap in our understanding of avian ecology at this time. Though juvenile birds do not have a 'breeding period', for simplicity, we refer to the period of juvenile parental dependence also as the breeding period.

Past studies have typically assumed that the post-breeding period is much shorter than the breeding period and that survival during breeding and post-breeding periods is equivalent (Sillett and Holmes 2002, Rockwell et al. 2017, Sergio et al. 2019), However, both of these assumptions may be false, at least for some species. For example, several studies have shown that the post-breeding period may last several months and, in some cases, can be longer than the breeding period (Vega Rivera et al. 2003, Burke 2013, Tsuru 2023). Moreover, the post-breeding period imposes different physiological demands than the breeding period as migratory birds must undergo molt and otherwise prepare for fall migration, sometimes relocating to habitat different than those necessary for breeding (Pyle 1997, Vega Rivera et al. 1998a, Pagen et al. 2000, Vega Rivera et al. 2003, King et al. 2006, McDermott and Wood 2010, Gow and Stutchbury 2013, Rapple 2013).

Additionally, species vary widely in their behaviors during the post-breeding period. Blackpoll (*Setophaga striata*) and Yellow-rumped Warblers (*Setophaga coronata*), for example, exhibit landscape-scale movements (Cormier 2011, Brown and Taylor 2017) whereas other species are known to engage in pre-migratory and night flights (Züst et al. 2023, Hays et al. 2024), and some remain in their territory until migratory departure (Vega Rivera et al. 1998a). For juveniles, the post-breeding period is likely crucial to gain information on habitat quality to inform future dispersal (Baker 1993, Vega-Rivera et al. 1998b, Rappole 2013). Despite the known variation among and within species in post-breeding behavior, there are relatively few studies on the topic or of the potential demographic consequences of these differences.

Given the potential for differences in behavior and habitat use, survival may vary significantly between these periods. For juvenile birds, survival rates are usually lowest during the first few days after fledgling from their nest but rapidly improve thereafter (Rush and Stutchbury 2008, Jones and Ward 2020, Jones et al. 2020). However, a secondary phase of increased mortality following independence from parental care has been observed for juvenile Barn Swallows (*Hirundo rustica*) as well (Evans et al. 2020). For adults, little is known of how survival may differ between the breeding and post-breeding periods. Lacking information on the duration and survival of the post-breeding period, but assuming that it is short with equal survival to the breeding period is problematic because it may result in estimates that misalign with estimates for migratory duration and survival.

Both adults and juvenile birds have been shown to change habitat between the breeding and post-breeding periods (Vega Rivera et al. 1998a, Vega Rivera et al. 1998b, Vega Rivera et al. 2003, Vitz and Rodewald 2011, Burke 2013). Habitat selected by adults for nesting may feature different associated risks to survival than habitat which is selected after breeding (Vitz and Rodewald 2007, Stoleson et al. 2013), and may misalign with habitat optimal for juvenile survival (King et al. 2006, Vitz and Rodewald 2010, Shipley et al. 2013, Streby et al. 2014, Raybuck et al. 2019). However, for most species, challenges in relocating either adults which are no longer exhibiting conspicuous breeding behaviors, or highly mobile juveniles in the post-breeding period have created significant barriers to estimating survival during this time.

The Kirtland's Warbler (*Setophaga kirtlandii*) is an ideal species for investigating the post-breeding period owing to its limited distribution within a primarily managed habitat matrix. This warbler breeds almost exclusively in stands of young jack pine (*Pinus banksiana*) in northern Lower Michigan and overwinters primarily in the Bahamian Archipelago (Cooper et al. 2019). Its geographically restricted breeding range allows for precise determination of migratory departure timing for individuals within the population (Cooper et al. 2023a, b). The combination of a relatively small population and the restrictiveness of this breeding area allows for a unique opportunity to study survival throughout the breeding and post-breeding periods. Leveraging the Kirtland's Warbler as a study system, we investigated survival of adult and juvenile birds in the breeding and post-breeding periods.

METHODS

Study Sites

We carried out our research from May – October of 2022 and 2023 at four study sites that were centrally located within the Kirtland's Warbler breeding range in the northern Lower Peninsula of Michigan (Figure 1, Table 6). Occupied breeding habitat at these four study sites included 7–17-year-old jack pine habitat planted by the Michigan Department of Natural Resources and the U.S. Forest Service for Kirtland's Warblers (Huber et al. 2001). At two sites, we also used 8–17-year-old jack pine habitat that was created through natural or unintentional fire, with some planting efforts in areas where jack pine did not naturally regenerate to desired densities (3,588 trees/ha).

Each season, we operated 12-13 solar-powered automated-telemetry stations (Lotek Model SRX800, Lotek Wireless Inc.; Table 7) with two or three 9-element Yagi antennas (Laird Connectivity) at all major breeding areas in the northern Lower Peninsula of Michigan from April or May until all birds departed in October (Figure 2). Antennas had a maximum detection range of approximately 15-20 km (Taylor 2017) when birds were flying above the forest canopy and 0.5 km – 3 km when they were within habitat patches (NWC unpublished data).

Radio-tagging Adults and Nestlings

From late May and until early July, we captured adult males using mist nets and conspecific playback. When captured, we aged birds following Pyle (1997) and took standard morphological measurements (wing cord, mass, tarsus, and bill length.) We then applied unique color-band combinations and a uniquely numbered USGS aluminum band to each individual. Finally, we attached a 0.35-g pulse-coded radio-tag (model NTQBW-2, Lotek Wireless Inc.)

using a modified leg-loop harness (Rappole and Tipton 1991, Cooper et al. 2018, Cooper and Marra 2020) made of 1 mm elastic stringing (Bead Landing^{TM}). Tags weighed on average 2.4 ± 0.17% (SD) of body mass (range: 2–3%). Antenna lengths of radio tags were 18.2 cm for both adults and juveniles in 2022, and 14.0 cm in 2023. Pulse lengths (adults: 18.1 s, juveniles: 22.3 s) and associated battery life (181 d and 206 d) were chosen to ensure all birds could be detected upon departure on fall migration in September or October. For descriptions of tag retention and failure, see Appendix A.

While following radio-tagged adults, we searched for and found as many nests as possible. Once found, nests were monitored every 1-4 days following (Cooper et al. 2019). Once nestlings were 6-8 d old, we randomly selected 1-3 (2022) or 1-2 (2023) nestlings to outfit with a radio-tag. If a particular nestling selected appeared too small for a tag, we randomly selected a different nestling. We banded and radio-tagged nestlings using the same methods as in adults. During banding we measured tarsus length and mass and acquired a blood sample from each tagged nestling via brachial venipuncture. To confirm fledging we used handheld telemetry to verify fledgling survival on the first day a nest was found empty.

Resighting Individuals

Hand-held and vehicle-mounted telemetry were used to confirm weekly survival (Lotek SRX800 or SRX1200 attached to a 3- or 5-element Yagi antenna, Lotek Wireless Inc.). Maximum detection range with the 3-element antennas was 2 km, but typically much less (< 500 m), while maximum detection range with the 5-element antenna mounted on a vehicle was up to 4 km. We started searching for individuals in the location of their previous observation and, if necessary, expanded the search area until the individual was located or deemed to have moved from the detectable area. In the post-breeding period, when adults were harder to observe, we occasionally approximated location based on variations in signal strength. If a radio-tagged fledgling could not be relocated within its period of parental dependence (defined below), it was presumed to have been depredated.

Timing of Transition to Post-breeding Periods

Consistent with Walkinshaw (1983), we found (via observations of fledglings and adults) that juveniles became independent after 26 days. By this day, all individuals observed were in their basic plumage, able to move and forage independently, had relocated from their natal area (generally had moved >500m from their nest [unpublished data]), and received little to no supplemental feeding from either parent. For juveniles and successfully nesting adults, we defined the start of the post-breeding periods as 26 days after young fledged from the nest. Kirtland's Warblers often attempt to renest after failure (Walkinshaw 1983), but for those adults that did not attempt to renest after failure, we defined the beginning of the post-breeding period as the day of nest failure. For all individuals the end of the post-breeding was defined as the date they began fall migration (see details in data analysis). The duration of the post-breeding period was calculated for 66 adults but could not be calculated for 30 adults who either died ($n = 10$), were not detected upon departure ($n = 2$), or for which their breeding timing could not be established ($n = 18$). The length of the post-breeding period was calculated for 28 juveniles that survived until migration. Several studies have found very similar first arrival dates for male Kirtland's Warbler of May 12 and 13 (Rockwell et al. 2012, Petrucha et al. 2013, Cooper et al. 2017). Given these dates, we defined the beginning of the post-breeding period as May 12 for adult males in our study. The breeding and post-breeding period for all adults was defined by the mean week of transition between the breeding and post-breeding periods based on observations of individuals.

Data Analyses

To examine detection data from our automated telemetry stations and stations in the Motus network (Taylor et al. 2017), we downloaded data using the “motus” package (Birds Canada 2024) in Program R (R Core Team 2024). Following Cooper et al. (2023a, b), we visually analyzed detection histories to determine departure date on fall migration. We used detection data to build daily encounter histories for each individual. Only consecutive runs of 3 or more detections were considered to represent real detections (Taylor 2017).

To model adult and juvenile survival, we used a robust design approach, while accounting for imperfect detection and temporary emigration using weeks as primary periods, each containing 8 secondary periods for detection (Cooch and White 2002). Secondary periods consisted of 7 daily detections recorded by our automatic telemetry stations as well as one weekly field observations via hand-held or vehicle-mounted telemetry. For adults, we included 21 primary occasions, as well as a 22nd primary occasion to include subsequent detection data from Motus stations outside of the breeding grounds. For juveniles, we aligned encounter histories such that the first occasion represented the fledge week, consequently we considered 17 primary occasions with an 18th occasion included for the migratory period in the same fashion as for adults. We used this non-staggered approach for juveniles to decouple the known effects of age on survival (e.g., Jones et al. 2017, Jones and Ward 2020) with temporal patterns throughout the season.

We fit survival models in Program MARK (White and Burnham 1999) using the Huggins' structure (Huggins 1989, Huggins 1991). Models estimated four separate parameters, apparent weekly survival (φ), probability of detection (p), the probability of emigration out of the study system (γ''), and the probability of remaining outside of the study system given prior emigration (γ'). We examined survival of adults and juveniles separately and considered candidate models for each of the 4 parameters above in a stepwise process (Table 8 and Table 9). We ranked candidate models using Akaike's Information Criterion adjusted for small sample size (Burnham and Anderson 2002). We first considered different structures for detection, while holding survival and emigration parameters constant. Candidate models included constant, temporal variation (e.g., estimates varying weekly, by groups of weeks, or as a linear weekly trend), and combinations of effects of week and year. We next considered candidate models for the emigration parameters while holding survival constant and using the best-fit structure for detection from the prior step. Candidate models for emigration parameters included constant, temporal variation, and combinations of effects of week and year. Temporal patterns for detection and emigration parameters were strongly supported (see Results), but some of the week-specific estimates were poorly estimated due to sparse data. In these cases, we constrained the best-fit models by combining some weeks (Table 8, Table 9). We then used the best-fitting model from this step to consider candidate models for apparent survival, similarly, fitting constant, weekly variation, year effects, and weekly variation with additive or interactive year effects. We also considered a temporal covariate attempting to separate the breeding and post-breeding periods. This simulated the breeding and post-breeding period being estimated as separate groups based on the mean week (week 9 of study, third week of July) observed for adults to transition between the breeding to post-breeding period. To examine the most supported predictors of adult survival, we ranked temporal variation models against additional covariate models while holding (φ) constant (see below).

To examine the effects of age-related variation in survival for juveniles, we fitted age specific models (e.g., survival differing between the first week vs. 2+ constant, first 2 weeks vs. 3+ weeks being constant) in addition to other temporal covariates.

For adults, non-temporal covariates included in survival models were body condition (scaled mass index following Peig and Green [2009]), age (second-year or after second-year), habitat age (the year a stand was planted), nest success (successful or unsuccessful), breeding period status (i.e., if an individual was in its breeding period or post-breeding period), average weekly temperature and cumulative precipitation recorded from the weather station at the Grayling Air Field (accessed from: *https://mesonet.agron.iastate.edu/request/download.phtml*), and whether or not the individual relocated from its territory during the post-breeding period (see Appendix B for details on relocation). We considered the same covariates for apparent survival of juveniles, with additional covariates including fledge date, brood size, and sex (sex obtained via methods in Kahn 1998 and Ellegren 1996) and weekly low temperatures. For specifics of covariate data see Table 10. For missing covariate data, mean values were used. We excluded 6 adults and 25 juveniles from the study due to either being depredated prior to fledgling, or tag-related or outlier mortality. Outlier mortality consisted of five adult birds died in early June of 2022 after storms. We choose to remove these individuals from the analysis because the death of 5 individuals on the same day was an outlier event that greatly impacted the survival estimate. For additional details on individuals excluded from the analysis, and other models considered see Appendix A. Means were reported ± 1 SE unless otherwise noted. We used Student's or Welch's t-test when considering if there were differences in cumulative survival or other groups. We used weekly survival estimates to calculate cumulative survival, with standard errors and corresponding confidence intervals calculated using the delta method (Powell 2007). We examined how fledging timing affected variation in the duration of fledgling independence periods using linear models.

Results

We banded and radio-tagged 102 adults (2022 *n* = 52, 2023 *n* = 50) and 118 nestlings (2022 *n* = 60, 2023 *n* = 58), and monitored 119 (2022: *n* = 58, 2023: *n* = 61) nests that had at least reached the point where one egg was laid. Of 96 adult males included in the analyses, 6 (6.2%) died during the breeding period, 4 (4.1%) died during the post-breeding period, 84 (87.5%) survived until departure on fall migration, and 2 (2.0%) fates were unknown. Of the 94 nestlings included in our analysis, genetic sexing indicated that we radio-tagged 52 (55.3%) male nestlings and 42 (44.7%) female nestlings. Of the 94 nestlings, 28 (29.8%) survived until migration departure, 54 (57.4%) died during their dependence period, 2 (2.1%) died after reaching parental independence, and 10 individuals (10.6%) reached parental independence but were not confirmed to migrate. Using telemetry, we were able to resight most individuals on a weekly basis and confirmed the fates of 177 of 189 (93.6%) tagged birds.

Adult Survival

Only one model received more support than the constant model for adult survival (AICc Weight = 0.17) [Table 1]) This model suggested that survival differed between years and increased across the 20-week study period (Figure 3, for estimates see Table 2, for stepwise model selection see Appendix A Table 8, Figure 6). Across both years, apparent survival (hereafter survival) for the entire 20-week study period (i.e., breeding and post-breeding periods) was 0.85 ± 0.031. Weekly survival was lowest in the first week of the study and improved each week thereafter (Table 3). We did not begin our study at the start of the breeding period (~ May 12th), and therefore lack survival data prior to May 25. However, by calculating mean weekly survival for the duration of the breeding period in which we have data (the initial 9 weeks of our study based on mean transition week into the post-breeding period observed for adults), we estimated survival for the first two weeks of the breeding period before the study began to be 0.98 ± 0.008, each week. Post-breeding survival (0.96 ± .0102, 95% CI = 0.94 to .98 was estimated higher than survival during the breeding period (0.86 ± 0.026, 95% CI = 0.81 to 0.91). However, weekly survival estimates did not significantly differ by week (post-breeding weekly survival = 0.99 ± .003, 95% CI = 0.90 to 1.0, breeding period survival = 0.98 ± 0.009, 95% CI = 0.96 to 1.01).

Juvenile Survival

Two models had support (Delta AICc <2) for juvenile survival (Table 3). The best supported model (AICc weight = 0.40) suggested survival was lowest in the initial week after fledging and then increased each week after the first week (Figure 4, for estimates see Table 4, for stepwise model selection results Table 8, Figure 7). This top model also included the effect of cumulative weekly precipitation with greater amounts of precipitation leading to lower survival estimates. However, it should be noted that estimating survival with or without precipitation only changed the survival estimate by 0.06% in the first week, and much less every subsequent week. The second model with support (AICc weight = .18 [Table 3]), was the same as the model above but lacking the effects of precipitation. The best supported model estimated initial survival at

0.62 ± 0.026 but increasing each week to <0.99 ± 0.004 after six weeks and for the remaining study period (Table 4) Total survival of the 16-week study period for juveniles was 0.39 ± 0.026.

Duration of the post-breeding period

Across both years, the mean fledge date was July 1 ± 1.17 d and the mean adult departure date was October 2 ± 0.8 d and neither estimate differed between years (*t* = -1.17, *df* = 76.19, *p* = 0.24). The mean duration of the post-breeding period for the 66 adults was 71.3 ± 2.2 d (range 32-110 d). Adults that successfully fledged young from their nest had a shorter post-breeding period (64.7 ± 1.9 d, *n* = 50, range = 32-84 d) than adults whose nests failed prior to fledging (91.9 days ± 3.3 d; *n*=16, range = 70-110 d*; t* = 7.401, *df* = 26.857, *p* <0.001). The mean week of transition from the breeding to post-breeding period was week 9 (the third week in July) in our 20-week study. Interestingly, the mean number of days after the termination of nesting until migration was similar between successful (90.7 ± 1.9 d) and unsuccessful breeders (91.9 ± 3.1 d; *t* = 0.336*, df* = 26.857*, p* = 0.739)

Given the assumption of the breeding period beginning on May 12, the mean duration of the period was 73.2 d (± 2.2 d), and shorter for failed breeders 51.7 d (± 3.24 d; range 38-74 d), than for successful breeders (80.3 ± 1.9 d, range = 63-107 d); (*t* = -7.563, *df = 26.541, p* <0.001). However, the duration of the breeding and post-breeding periods was not significantly different (*t* = -0.5839, *df* = 129.91, *p* = 0.5603), with 47% (*n=31*) of individuals having post-breeding period durations equal to or longer than their breeding period.

The mean duration of the post-breeding period for juveniles that survived until fall migration (*n* = 28) was 50.8 ± 1.64 d. We found a negative correlation in the duration of the independence period and fledge date (*r* = -0.4, *t (26)* = -2.22, *p* = 0.03; Figure 5), such that individuals with later fledged dates had shorter post-breeding periods prior to departure on fall migration. For juveniles, for both 2022 and 2023, the mean date of departure on fall migration was September 18 (± 2.17 d).

Discussion

What is typically defined homogenously as 'the breeding period' is comprised of both a breeding and post-breeding period. Though the duration of either period is dependent on the reproductive success of an individual, either can comprise most of the time spent by an individual between spring and fall migration. Based on mean arrival dates, the duration of the post-breeding period was equal to or longer than the breeding period for 47% of the adults we observed in our study. We provide the first post-breeding period survival estimates for the Kirtland's Warbler and one of the few post-breeding survival estimates derived directly from observations of the post-breeding period of individuals.

The most supported model for adult survival suggested that survival increased throughout the 20-week study period. Interestingly, the model that included period (breeding and post-breeding) was not supported. This suggests that while survival increases over time, the increase in survival was not directly related to whether an individual was in the breeding or post-breeding period. Individuals in our study transitioned to the post-breeding period at different times (weeks 4 to 14), while the overall average was week 9. We know there are fundamental differences in activities and habitat use upon transitioning from the breeding to the post-breeding period, thus, it is likely that part of the reason why survival increases over time is due to changes in the behavior of adults and/or their primary predators. So, while the breeding vs. post-breeding model received little support it is important to recognize that changes in adult behavior over time might be reflected in the most supported model suggesting survival increases over the 20-week period.

Adult survival estimates did not differ between the breeding and post-breeding periods and were similar to previous estimates (Rockwell et al. 2017) for the breeding period for Kirtland's Warblers. Rockwell's estimates were calculated from breeding period survival and extrapolated for a four-month summer period (defined as May 1 – August 31; 17 weeks 3 days) at 96.3% monthly or 86.2% cumulative survival for the entirety of the four-month period (but did not distinguish the breeding from post-breeding periods in the estimates). Adjusting Rockwell's estimate (83.03%) to match the duration of our study provides a similar estimate (85.27%). Additionally, average monthly survival (95.8%) derived from the entirety of our 20-week study period was similar to Rockwell's monthly estimate.

Our juvenile survival estimates were in the range of other estimates (see Olah et al. 2023). Most post-fledging survival studies generally only include estimates for the first few weeks, however, Cox et al. 2014 calculated average post-fledging survival for 20- and 50 days post-fledging across species and noted survival remained relatively constant after day 20. However, the range in survival reported included lower estimates of 23% after 20 days for another *Setophaga sp*. but also provided an average cumulative survival rate about 15% higher than our estimates for juvenile Kirtland's Warblers (39%) during our study period (16 weeks for juveniles). Our estimates after ~21 (43.1%) and ~50 (39.1%) days were similar, but somewhat lower compared to average survival rates for passerines in similar durations post-fledging. These estimates for post-fledgling survival are within the range of estimates reported for other warblers: 29% after 25 days for Golden-winged Warblers (*Vermivora chrysopter*a) (Lehman 2017), 65% after 28 days for Golden-Cheeked Warblers (*Setophaga chrysoparia*) (Trumbo

2021), 67% for Worm-eating Warblers (*Helmitheros vermivorum*) after 31 days and 65% for Ovenbirds (*Seiurus aurocapilla*) after 51 days (Vitz and Rowland 2011). We also found no support that survival of juveniles declines after they become independent.

The breeding period for migratory passerines is thought to have high survival reaching 96 to nearly 100% (Sillett and Holmes 2002, Wieruckat et al. 2016, Paxton et al. 2017, Rockwell et al. 2017). However, studies often fail to distinguish post-breeding from breeding survival, often lumping estimates together into a 3 to 4-month stationary period followed by a survival estimate for a migration period. This is potentially problematic as it not only reduces the resolution of period-specific survival, but by combining post-breeding survival estimates with breeding or with migratory survival, estimates may artificially inflate or reduce survival rates for either period. For example, if post-breeding or pre-migratory survival rates are high (90-99%) but are combined with a typically lower one-month migratory survival rate, the apparent survival rate of migrating birds may be overestimated, leading to conclusions such as diminished conservation priority in identifying and improving stopover sites for key species in decline. By identifying durations of the post-breeding period and specific migratory timing provides an opportunity for more accurate survival estimates through multiple periods of the annual cycle.

Implications

For the Kirtland's Warbler, habitat use in the breeding and post-breeding periods may differ (Appendix B), and therefore habitat-use strategies and how they affect survival rates warrant further examination. Future studies should assess breeding and post-breeding habitat preferences, especially for adults and juveniles who leave their breeding and natal territories in the post-breeding period. Particularly, habitat-use research during the post-breeding period should focus on understanding the potential effects of the quality and accessibility of the habitat, and any potential carry-over effects into the migratory or other periods of the annual cycle. Additional future research should be directed to quantifying trends in the movements of juvenile birds in the independence period and how fledging timing may affect the distance and breadth of the area juveniles explore prior to migratory departure. Potential findings could reveal exploratory trends informing future recruitment and possible range expansion. Exploration by juveniles in the natal independence period could differ by sex and ultimately cause uneven recruitment between sexes, slowing colonization in other areas. Previous research has shown that male Kirtland's Warblers are usually the first recruited to unoccupied sites (Anich and Ward 2017).

Our survival estimates were similar to other estimates for Kirtland's Warblers, but it should be noted that if the 5 adults that died due to the apparent effects of a storm had not been excluded, the survival estimate would have been greatly reduced and the effect of a time trend (increased survival over the course of the season) would have been more pronounced. More details are available in Appendix A, but this storm event did not appear to be particularly severe for the season or location. From a management perspective, it would be difficult to mitigate the impact of storms, though the majority of other adults appeared to have been depredated by raptors based on the distance tags retrieved from individual territories. As adults that moved to a new location after breeding tended to go to older stands, it may be beneficial to select denser vegetation to avoid predation, especially while molting. While more research is needed it may be that adult Kirtland's Warblers select denser habitats in the post-breeding period to avoid raptor predation as hypothesized for wood thrushes (Vega Rivera et al. 1998a). Weather was also included in the top model explaining the survival of juveniles, and greater precipitation predicted slightly lower survival. There are several studies of birds that have shown that recently fledged young are vulnerable to hypothermia due to either the lack or cost of thermoregulating (e.g., Giovanni et al. 2009). While we often think about cold as the primary cause of death due to poor thermoregulation, in several species it is precipitation that leads to young birds becoming wet and being unable to thermoregulate (e.g., Schöll and Hille 2020).

The Kirtland’s Warbler is a recovering species whose population has been increasing over the last couple of decades. To continue this upward trajectory, it is imperative to understand the factors that impact seasonally specific-survival. Continued management and monitoring of Kirtland’s Warbler is important to maintain this recovery and inform future successful conservation and management strategies.

FIGURES AND TABLES

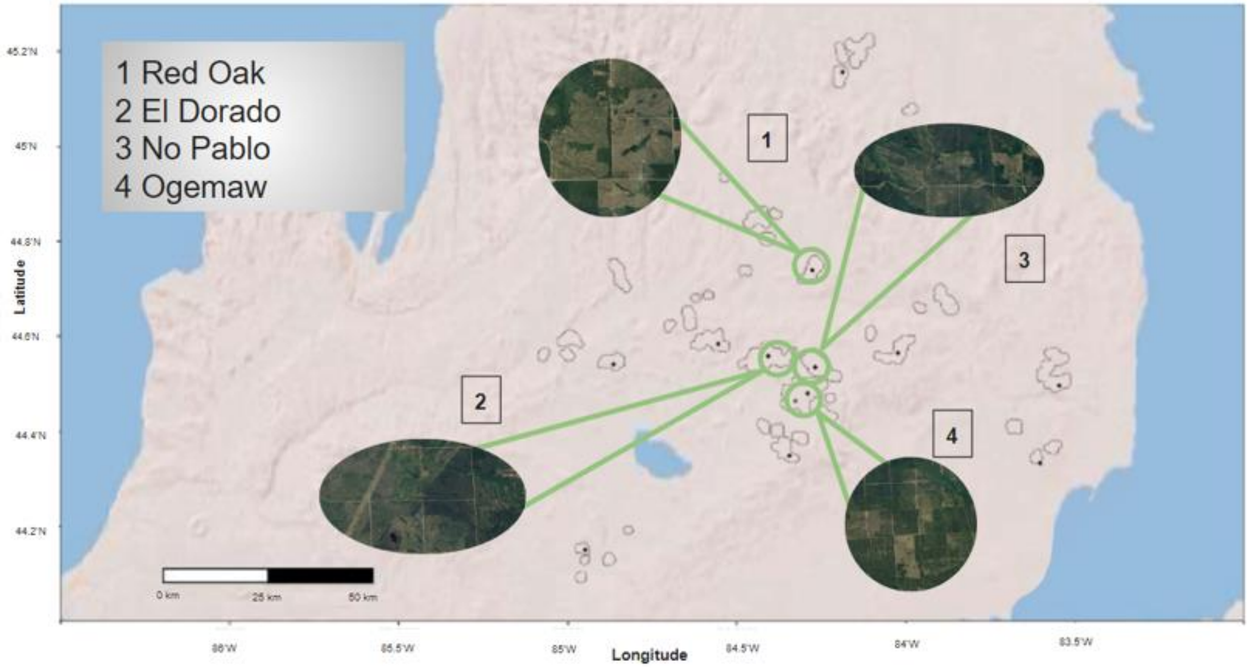

Figure 1. The four study sites in northern Lower Michigan. Green circles denote the wider area and black polygons denote habitat managed for Kirtland’s Warblers. Black dots are locations of automated telemetry stations.

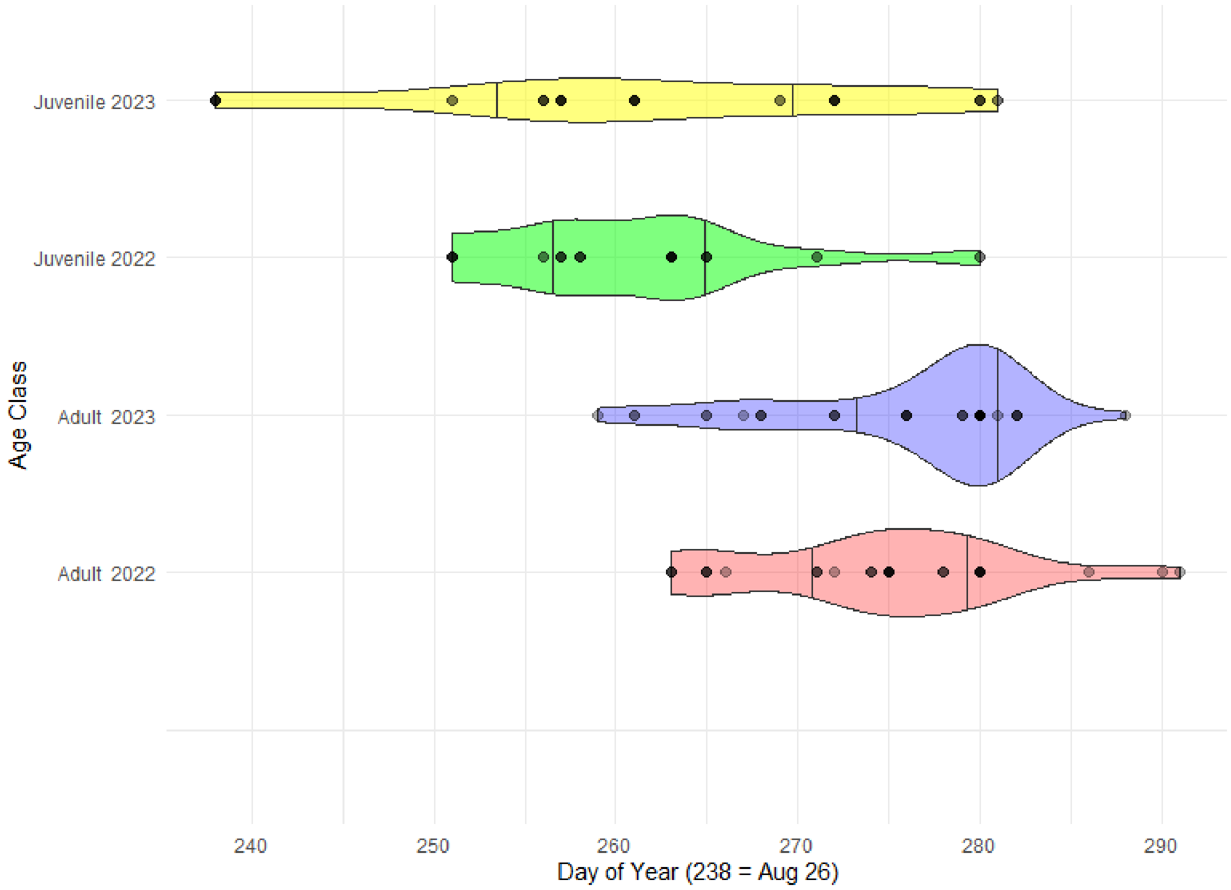

Figure 2. Fall departure timing for adults and juveniles as determined from our array of automated telemetry stations. The depth of shading of each point as well as the width of the graph represent the proportional number of individuals departing on a particular evening. In both years juveniles tended to depart earlier (mean departure date = September 18) than adults (mean departure date = October 2).

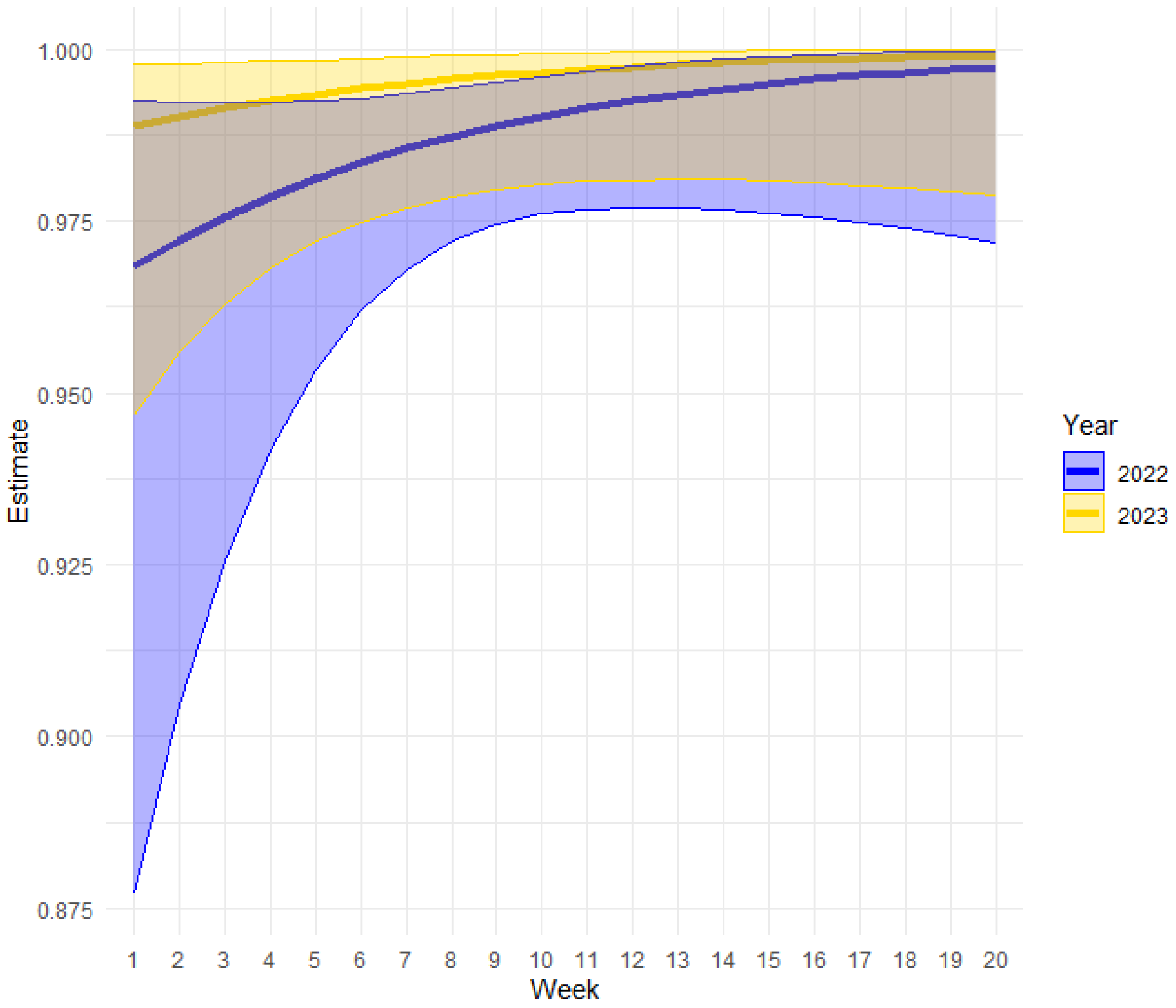

Figure 3. Weekly survival estimates for adult Kirtland's Warblers in 2022 and 2023 across the 20-week study period (which included both the breeding and post-breeding periods).

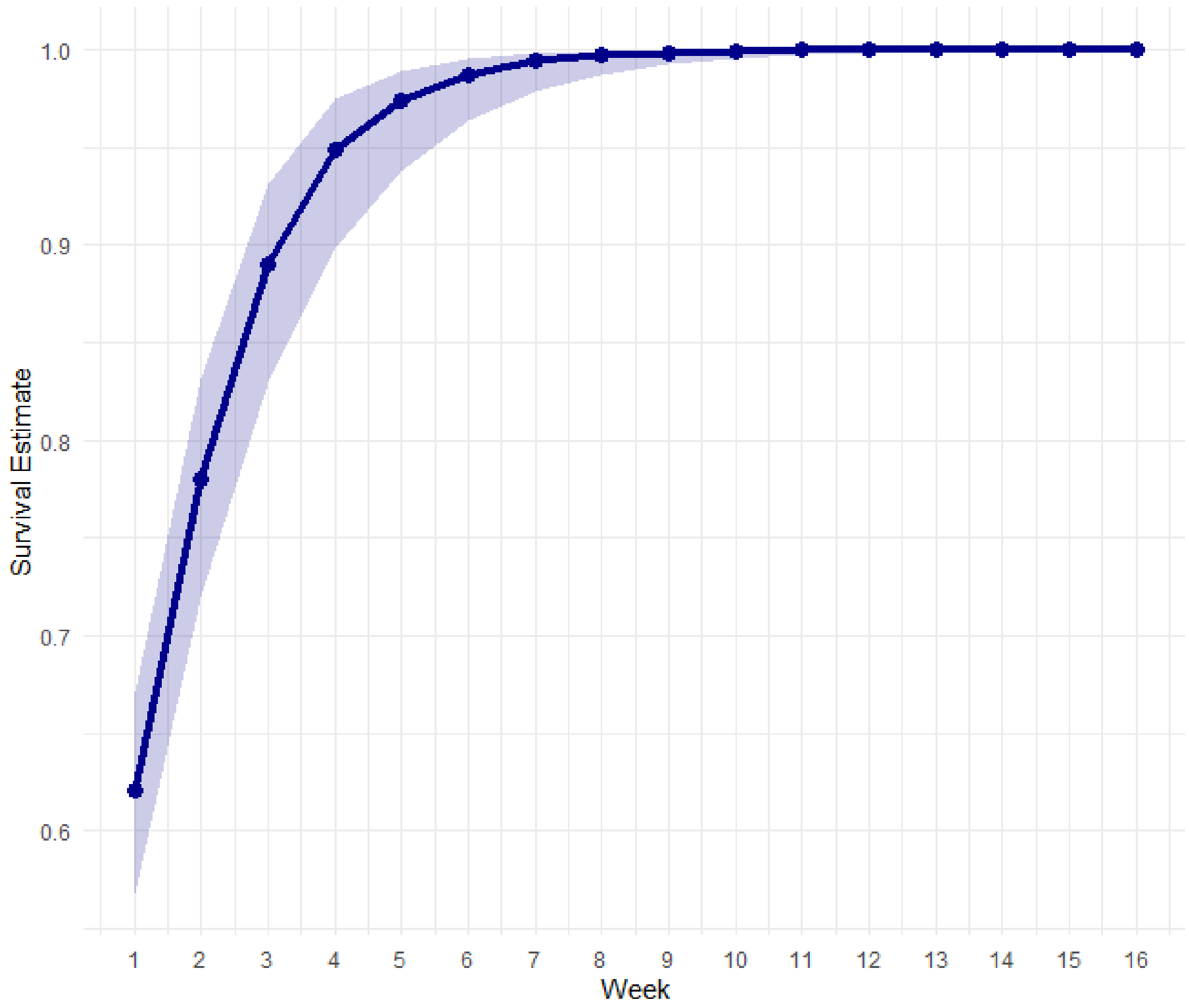

Figure 4. Weekly survival estimates for juvenile Kirtland's Warblers for the 16-week juvenile study period in Michigan. Weeks 1-16 represent the age of a juvenile in respects to its fledge week. Confidence intervals are shaded.

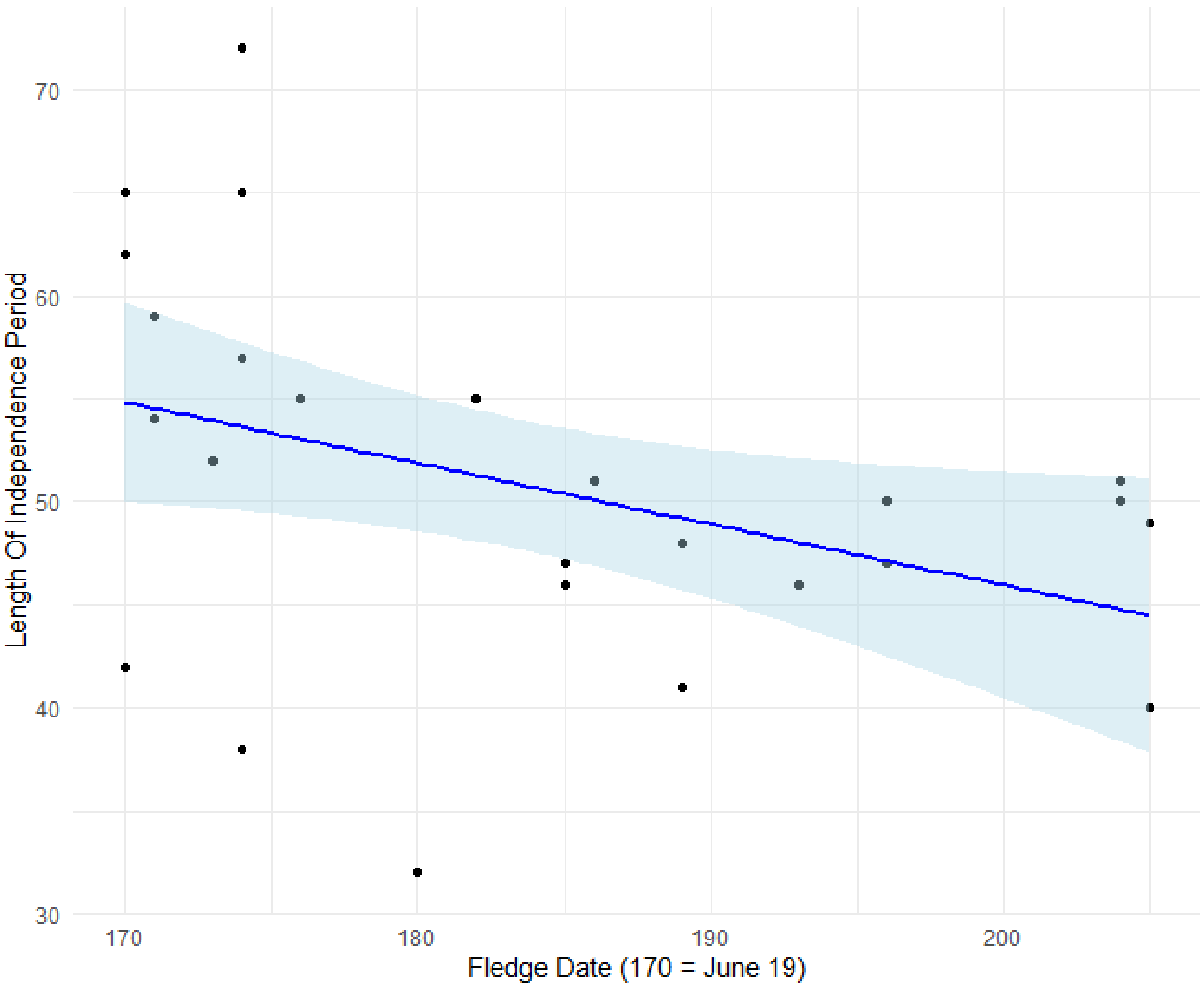

Figure 5. Duration of the post-breeding period for juvenile Kirtland's Warblers in response to fledge date for 28 juveniles. The negative trend (*r* = -0.4, *t (26)* = -2.22, *p* = 0.03) suggests that individuals fledging earlier in the season have longer independence periods prior to migration.

Table 1. Candidate models in order of support for adult survival. The table includes the model's name, AICc, Delta AICc, AICc weights, model likelihood, and deviance. Model_1 is the base top selected in the primary analysis to determine the correct detectability, emigration, and immigration covariates (Table 8). Model_1 includes a week in the immigration and emigration model, and an interactive effect of the method used to detect the adults (hand-tracking vs automated telemetry), week, and year were used in the detectability model. Paired covariates include: average weekly temperature (temperature), breeding status (individual in its breeding or post-breeding period), age of the individual (second-year or after second-year), breeding success (successful or unsuccessful breeder), body condition (scaled mass index), habitat age (age of stand in which an individual was resighted in a given week), move (if an individual relocated in the post-breeding period), week-trend is a linear trend per week over the course of the season, and precipitation (weekly cumulative precipitation).

Model	**AICc**	**Delta AICc**	**AICc Weights**	**Model Likelihood**	**Deviance**
Model_1, φ(week-trend + year)	**12649.410**	**0**	**0.168**	**1**	**12461.340**
Model_1, φ(constant)	**12649.630**	**0.221**	**0.150**	**0.896**	**12465.650**
Model_1, φ(year)	**12650.180**	**0.766**	**0.114**	**0.682**	**12464.150**
Model_1, φ(temperature)	**12650.810**	**1.401**	**0.083**	**0.497**	**12464.780**
Model_1, φ(breeding status)	**12651.050**	**1.640**	**0.074**	**0.441**	**12465.020**
Model_1, φ(9/11 week + breeding vs post-breeding)	**12651.050**	**1.641**	**0.074**	**0.440**	**12465.020**
Model_1, φ(age)	**12651.440**	**2.023**	**0.061**	**0.364**	**12465.400**
Model_1, φ(breeding success)	**12651.600**	**2.184**	**0.056**	**0.336**	**12465.570**
Model_1, φ(body condition)	**12651.640**	**2.229**	**0.055**	**0.328**	**12465.610**
Model_1, φ(habitat age)	**12651.650**	**2.237**	**0.055**	**0.327**	**12465.620**
Model_1, φ(move)	**12651.660**	**2.248**	**0.055**	**0.325**	**12465.630**
Model_1, φ(precipitation)	**12651.670**	**2.262**	**0.054**	**0.323**	**12465.640**
Model_1, φ(week)	**12669.360**	**19.949**	**0.000**	**0.000**	**12444.400**
Model_1, φ(week*year)	**12697.560**	**48.146**	**0.000**	**<.001**	**12431.430**
Model_ 1, φ(week-trend)	**12895.040**	**245.624**	**0.000**	**<.001**	**12711.050**

Table 2. Weekly adult survival estimates and 95% confidence intervals for 2022 and 2023. Each row corresponds to weekly estimates, standard errors (SE), and lower and upper bounds of the confidence intervals. Week 1 begins May 25.

Year	Week	Estimate	SE	Lower	Upper	Year	Week	Estimate	SE	Lower	Upper
2022	1	0.968	0.023	0.877	0.992	2023	1	0.989	0.009	0.947	0.998
2022	2	0.972	0.018	0.904	0.992	2023	2	0.990	0.008	0.956	0.998
2022	3	0.976	0.014	0.926	0.992	2023	3	0.991	0.006	0.963	0.998
2022	4	0.979	0.011	0.942	0.992	2023	4	0.993	0.006	0.968	0.998
2022	5	0.981	0.009	0.953	0.993	2023	5	0.993	0.005	0.972	0.998
2022	6	0.984	0.007	0.962	0.993	2023	6	0.994	0.004	0.975	0.999
2022	7	0.986	0.006	0.968	0.994	2023	7	0.995	0.004	0.977	0.999
2022	8	0.987	0.005	0.972	0.994	2023	8	0.996	0.004	0.979	0.999
2022	9	0.989	0.005	0.975	0.995	2023	9	0.996	0.003	0.980	0.999
2022	10	0.990	0.005	0.976	0.996	2023	10	0.997	0.003	0.980	0.999
2022	11	0.991	0.004	0.977	0.997	2023	11	0.997	0.003	0.981	<0.999
2022	12	0.993	0.004	0.977	0.998	2023	12	0.997	0.003	0.981	<0.999
2022	13	0.993	0.004	0.977	0.998	2023	13	0.998	0.002	0.981	<0.999
2022	14	0.994	0.004	0.977	0.999	2023	14	0.998	0.002	0.981	<0.999
2022	15	0.995	0.004	0.976	0.999	2023	15	0.998	0.002	0.981	<0.999
2022	16	0.996	0.004	0.976	0.999	2023	16	0.998	0.002	0.981	<0.999
2022	17	0.996	0.004	0.975	0.999	2023	17	0.999	0.002	0.980	<0.999
2022	18	0.997	0.004	0.974	<0.999	2023	18	0.999	0.002	0.980	<0.999
2022	19	0.997	0.003	0.973	<0.999	2023	19	0.999	0.002	0.979	<0.999
2022	20	0.997	0.003	0.972	<0.999	2023	20	0.999	0.001	0.979	<0.999

Table 3. Candidate models in order of support for juvenile survival. The table includes the model's name, AICc, Delta AICc, AICc weights, model likelihood, and deviance. Model_1 is the base top model selected in the primary analysis to determine the correct detectability, emigration, and immigration parameters, and for age-specific trends in weekly survival. (Table 9). Paired covariates include weekly low temperature (temperature), sex (the sex of an individual) body condition (scaled mass index), habitat age (age of stand in which an individual was resighted in a given week), fledge date (the day of the year an individual fledged), brood size (number of nestlings in a nest on fledge day), week-trend is the linear trend over the course of the season, and precipitation (weekly cumulative precipitation).

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Deviance
Model1phi(precipitation)	5089.060	0	0.400	1	4955.424
Model1	5090.674	1.614	0.179	0.446	4959.150
Model1phi(sex)	5091.772	2.712	0.103	0.258	4958.136
Model1phi(brood size)	5092.595	3.535	0.068	0.171	4958.959
Model1phi(fledge date)	5092.737	3.677	0.064	0.159	4959.101
Model1phi(habitat age)	5092.783	3.723	0.062	0.155	4959.148
Model1phi(temperature)	5092.785	3.725	0.062	0.155	4959.150
Model1phi(body condition)	5092.785	3.725	0.062	0.155	4959.150

Table 4: The juvenile survival estimates and 95% confidence intervals for each post-fledging sampling period in 2022 and 2023. Each row corresponds to survival estimates of age in weeks post-fledging, with standard errors (SE), and lower and upper bounds of the confidence intervals.

Year	Week	Estimate	SE	Lower	Upper
2022, 2023	1	0.621	0.026	0.568	0.671
2022, 2023	2	0.781	0.028	0.720	0.831
2022, 2023	3	0.890	0.026	0.829	0.931
2022, 2023	4	0.949	0.018	0.899	0.975
2022, 2023	5	0.974	0.012	0.938	0.989
2022, 2023	6	0.987	0.007	0.963	0.996
2022, 2023	7	0.994	0.004	0.979	0.998
2022, 2023	8	0.997	0.002	0.987	0.999
2022, 2023	9	0.999	0.001	0.993	<0.999
2022, 2023	10	0.999	0.001	0.996	<0.999
2022, 2023	11	<0.999	< 0.001	0.998	<0.999
2022, 2023	12	<0.999	< 0.001	0.999	<0.999
2022, 2023	13	<0.999	< 0.001	0.999	<0.999
2022, 2023	14	<0.999	< 0.001	<0.999	<0.999
2022, 2023	15	<0.999	< 0.001	<0.999	<0.999
2022, 2023	16	<0.999	< 0.001	<0.999	<0.999

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CHAPTER 3: SUMMARY

This study investigated the survival and habitat use of juvenile and adult Kirtland's Warblers during two periods of the annual cycle. Our findings provide new insights into the ecology of the post-breeding and parental independence periods. The post-breeding period (mean duration 71 d) was longer than the breeding period for nearly half the adults (mean duration 73 days) based on a May 12 mean arrival date. Additionally, the post-breeding period was longer than the breeding period observed for all juveniles. For adults, survival rates varied across both years and periods, but with cumulative survival similar to previous estimates. For juveniles, survival was low immediately after fledging but quickly increased.

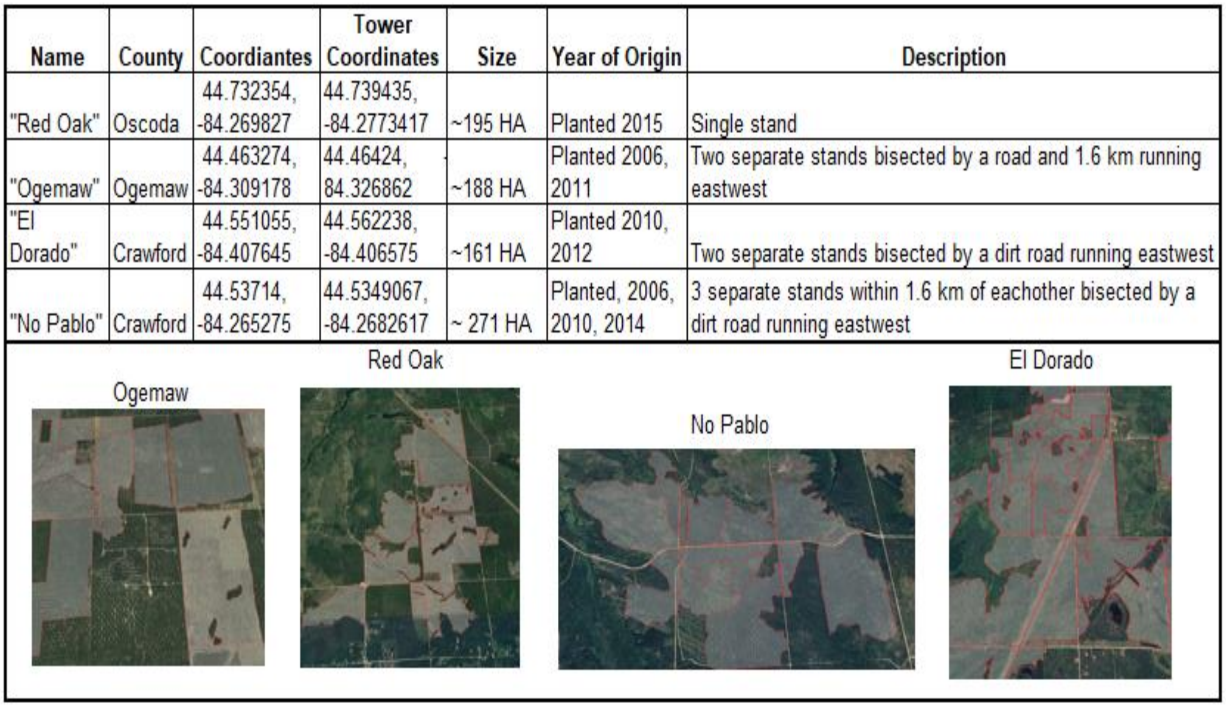
Additionally, we documented relocations of adults from their territories (Appendix B) after the cessation of breeding activities. These individuals relocated generally into older stands of trees, usually occupying this area until migratory departure. Young birds that left their natal area remained in the broader habitat matrix in norther Lower Michigan prior to migration. Although we lack sufficient data to examine the specifics of habitat use, we highlight the extensive movement of individuals after leaving their natal areas, possibly in an exploratory phase to gain information for future breeding. The limited data we did have for juvenile habitat use outside of the natal area also suggested that juveniles occupied planted tree stands older than the stands they fledged from. Understanding the spatial scale and movement patterns of juveniles can provide insights into their broader habitat needs.

Moreover, insights into the durations and distinct ecological requirements of the breeding periods could inform more effective conservation of migratory birds, particularly for species like the Kirtland's Warbler with obligate specific habitat needs. Conservation initiatives should incorporate the protection of habitats on spatial scales that support both breeding and post-breeding requirements. This may include maintaining a mosaic of habitat types that cater to the different needs of both periods. Populations of migratory birds should be studied from their arrival on the breeding grounds until migratory departure to gain a more complete comprehension of the duration of these periods and to aid in more accurate period-specific survival estimates.

In conclusion, though survival for adult Kirtland's Warblers across the breeding and post-breeding are not statistically different, the age of planted jack pines stands which were occupied in the post-breeding period did differ for adults that moved from their breeding territories. As with other post-fledging studies, juvenile survival was initially low, but increased in subsequent weeks, with most individuals spending weeks to months outside of their natal areas prior to migration. We found that the post-breeding period constitutes a significant portion of the annual cycle for both juvenile and adult Kirtland's Warblers. Managers should incorporate information from both periods when modeling survival or forming strategies for creating and maintaining habitat. Further research is needed to explore the intricate dynamics of the post-breeding period across broad spatial scales and migratory bird species.

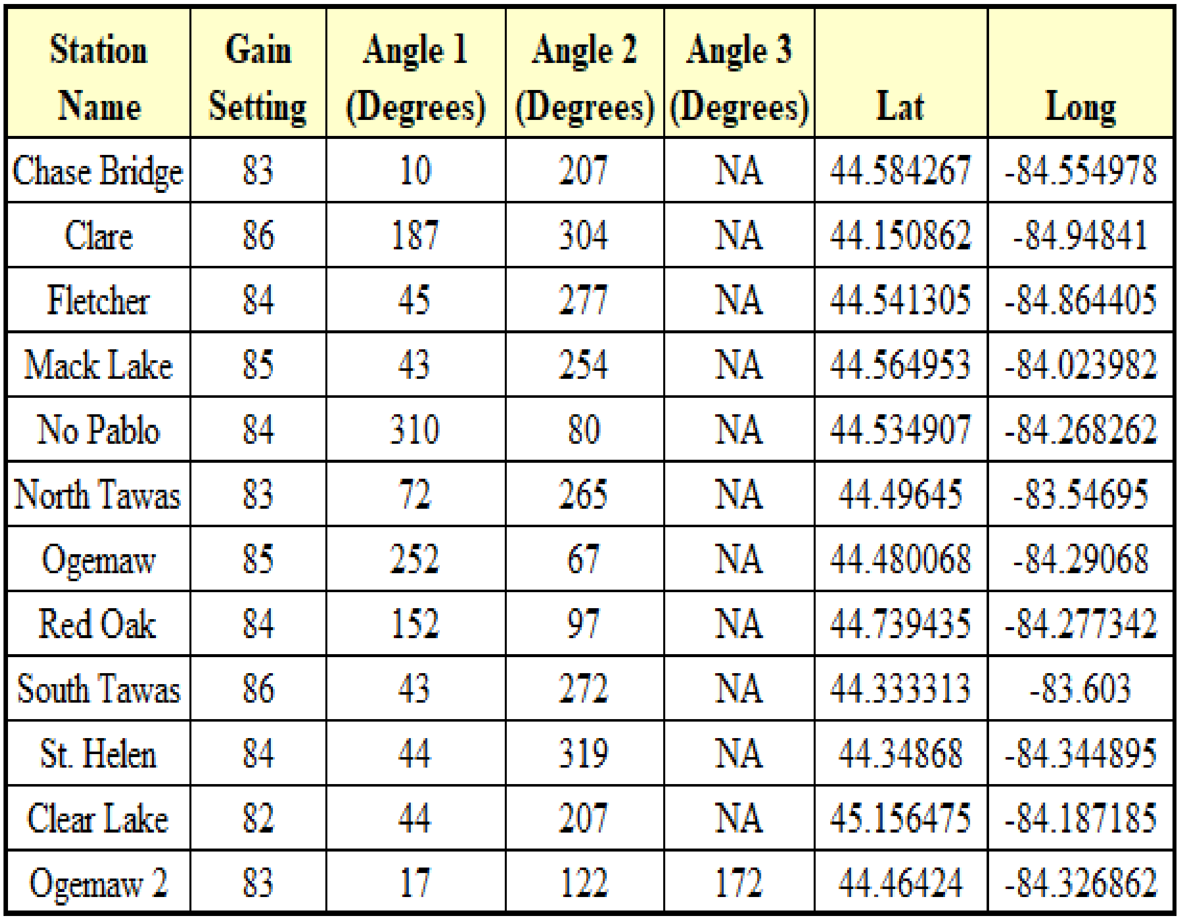
APPENDIX A SUPPORTING MATERIALS TO CHAPTER 2

Table 6. This table provides detailed information on our four study sites in Michigan. It includes the name of the site, county, telemetry station coordinates, the size of the study area, the year of planting, and a brief description of each site.



Name	County	Coordiantes	Tower Coordinates	Size	Year of Origin	Description
"Red Oak"	Oscoda	44.732354, -84.269827	44.739435, -84.2773417	~195 HA	Planted 2015	Single stand
"Ogemaw"	Ogemaw	44.463274, -84.309178	44.46424, - 84.326862	~188 HA	Planted 2006, 2011	Two separate stands bisected by a road and 1.6 km running eastwest
"El Dorado"	Crawford	44.551055, -84.407645	44.562238, -84.406575	~161 HA	Planted 2010, 2012	Two separate stands bisected by a dirt road running eastwest
"No Pablo"	Crawford	44.53714, -84.265275	44.5349067, -84.2682617	~ 271 HA	Planted, 2006, 2010, 2014	3 separate stands within 1.6 km of eachother bisected by a dirt road running eastwest

Table 7. The location and specification of the 13 automated telemetry stations across northern Lower Michigan. It includes the station name, gain setting, directional angles of the antennas, and the latitude and longitude coordinates for each station.



Station Name	Gain Setting	Angle 1 (Degrees)	Angle 2 (Degrees)	Angle 3 (Degrees)	Lat	Long
Chase Bridge	83	10	207	NA	44.584267	-84.554978
Clare	86	187	304	NA	44.150862	-84.94841
Fletcher	84	45	277	NA	44.541305	-84.864405
Mack Lake	85	43	254	NA	44.564953	-84.023982
No Pablo	84	310	80	NA	44.534907	-84.268262
North Tawas	83	72	265	NA	44.49645	-83.54695
Ogemaw	85	252	67	NA	44.480068	-84.29068
Red Oak	84	152	97	NA	44.739435	-84.277342
South Tawas	86	43	272	NA	44.333313	-83.603
St. Helen	84	44	319	NA	44.34868	-84.344895
Clear Lake	82	44	207	NA	45.156475	-84.187185
Ogemaw 2	83	17	122	172	44.46424	-84.326862

Birds not included in survival estimates.

Thirty-one individuals were removed from the data set prior to the analysis (6 adults, 25 juveniles). Five adults were removed due to a weather-related mortality in early June of 2022, which produced unrealistic breeding season survival estimates (see below). The remaining were removed either for mortality caused by antenna entanglement (n=2), excluded as nestlings being depredated prior to fledging (n=2), for evidence of transmitters being removed from nestlings by parents while in the nest (n=7), or by transmitter application causing pre-mature fledging and subsequent mortality in nestlings (n= 15).

Weather-related mortality.

On the night of June 4, 2022, a weather system passed over northern Lower Michigan. Weather data accessed from the nearest weather station in Grayling, Michigan (https://mesonet.agron.iastate.edu/request/download.phtml) recorded an overnight temperature drop of 20 degrees Celsius, reaching 1 degree C. Minimal rain and wind were recorded; however, this station is approximately 27-41 KM east of our study areas, and weather in this area typically travels from east to west, possibly resulting a disparity in precipitation being recorded between the two areas. Though we lack high-resolution weather data localized specifically to our study areas, observations from our field housing noted heavy rain, wind, and temperatures falling just below freezing (personal observation), which were not captured by this weather station.

A combination of field observations and automated telemetry data confirmed that four of the five individuals were alive on the 5th but appeared to have died that night or in the morning of the 6th. This storm, or carryover effects caused by it, appeared to have caused the mortality of 5 adults either during the night of the storm or the following morning. All five specimens were recovered intact with no signs of depredation during the subsequent days. Four of the 5 birds were confirmed alive before the storm by station detections. Each had been caught and their transmitter affixed the week prior, had exhibited no signs of stress, and had been observed alive for multiple days before this storm.

The bodies were collected and sent to MDNR and tested negative for avian flu, showing no other evidence diagnostic of alternative causes of mortality, forcing us to conclude that the weather event was the cause of mortality for these individuals. These weather conditions are not unusual for this time of year in this part of Michigan, making these mortalities somewhat anomalous. Besides this weather event, all other adult mortality ($n = 10$) during our study showed obvious signs of depredation, most likely caused by an avian predator due to the distance from the territory where the tags were recovered or other direct evidence.

Unconfirmed fates

In 2022, 2 adults and 6 juvenile birds were never confirmed to have departed on migration or have tags recovered from depredation or mortality. In 2023, 4 juveniles (but no adults) were also unconfirmed to have either migrated or died on the breeding grounds. Individuals of unknown fates either 1) experienced transmitter failure and thus were rendered undetectable, 2) their transmitter fell off in an undetectable location, 3) individuals were depredated and the transmitter was destroyed or moved to an undetectable location, 4) or migrated without being detected. Ten juveniles survived to parental independence but were not confirmed to have migrated. At least one of these tags failed during the post-independence period as confirmed by a resight. Additionally, some of these juveniles were last detected at our southernmost station in late September, with one individual being resighted in early October approximately 8 kilometers south of its natal territory, making it plausible that at least some juveniles migrated undetected. Further indications of possible undetected migration in juveniles is demonstrated by only 22 of 28 (78.57%) juveniles whose departure was confirmed from our telemetry array were also confirmed by Motus telemetry stations outside of our array (21.43% being a similar proportion of juveniles unconfirmed to have migrated among those who survived to parental independence). During the natal dependence period, several juvenile tags became undetectable. Consequently, any juvenile birds that became undetectable on or before 26 days per the parental dependence period, were presumed to have died, regardless of if the tag could not be relocated or mortality confirmed.

Other models considered

Adult models were originally run containing 5 adults that appeared to have died due to a weather even in early June of 2022. Including these individuals in the model produced unrealistic survival estimates (52%), and because this event is assumed to be rare, having only happened once during the duration of our study, those individuals were excluded from the final model.

Additionally, four adults could not be confirmed as breeding/territory holding birds. We ran the same models both including and excluding these four individuals, but these considerations did not significantly affect the survival estimates. (.2% difference in cumulative survival estimate across both years), so we included them in the analyses.

Additionally, two survival models were run for juvenile birds. One included only nestlings with direct observations of confirmed fledging and the other included an additional thirteen individuals that experienced mortality between the time their transmitter was affixed and the first fledging survival check (thus successful fledging could not be separated with absolute certainty from the possibility of transmitter-induced mortality). The difference in survival estimates was similar (3% lower) for the data excluding these 13 individuals than for the estimate including these individuals. We choose the lower and more conservative of the two estimates for survival.

Table 8. Candidate models in order of support for adult survival. We used a multiple-model approach to determine the top models for detectability (p), emigration (γ"), and immigration (γ'). We did this first by determining the top model for detectability and incorporating that best-supported model to determine the best-supported model for the subsequent step for both emigration and immigration. We then used the best-supported models for those subsequent steps to evaluate the covariates of survival for adults. The table includes the model’s name, AICc, Delta AICc, AICc weights, model likelihood, and deviance. Method refers to using both hand-tracking and automated telemetry to search for tagged juveniles, week is a week of the study, the week-constrained bin describes weeks that were combined for better estimation, week_trend is a linear change over the course of the season, year is the year of the study (2022, 2023), and “.” is constant survival. Also note the bolded model was the model determined to be the most appropriate, as for emigration and immigration we needed to constrain the weekly estimates in order for the model to produce better estimates (denoted as week-constrained in table). For emigration, we grouped weeks 1-16 together, estimated weeks 17 and 18 separately, then grouped weeks 19-20 together. For immigration we grouped weeks 1-7 with weeks 11-13 and 16-18 together, estimated weeks 8, 9, 10, 14, and 15 separately, then grouped together weeks 19-20.

A. Detectability					
Model	**AICc**	**Delta AICc**	**AICc Weights**	**# of Parameters**	**Deviance**
φ(.), γ’’(.), γ’(.), p(method*week*year)	12305.830	0	1	87	19344.170
φ(.), γ’’(.)γ’, (.), p(hand-tracking*week)	13442.130	1136.30	0	25	20606.130
φ(.), γ’’(.)γ’(.), p(hand-tracking*week*year)	13449.690	1143.86	0	46	20571.330
φ(.), γ’’(.), γ’(.), p(method*week_trend)	13512.330	1206.50	0	8	20710.460
φ(.), γ’’(.), γ’(.), p(method)	13551.440	1245.61	0	6	20753.590
φ(.), γ’’(.), γ’(.), p(.)	13921.170	1615.34	0	5	21125.320

B. Emigration and Immigration					
Model	**AICc**	**Delta AICc**	**AICc Weights**	**# of Parameters**	**Deviance**
φ(.), γ’’(week), γ’(week), p(method*week*year)	12529.87	0	1	121	19498.510
φ(.), γ’’(week*year), γ’(week*year), p(method*week*year)	12584.730	54.8599	0	162	19468.560
φ(.), γ’’(week-constrained), γ’(week-constrained), p(method*week*year)	12649.630	119.7626	0	91	19679.800
φ(.)γ’’(weektrend)γ’(weektrend), p(method*week*year)	12740.230	210.3638	0	84	19784.700
φ(.)γ’’(.)γ’(.), p(method*week*year)	12877.090	347.2211	0	82	19925.630

Table 9. Candidate models in order of support for juvenile survival. We used a multiple-model approach to determine the top models for detectability (p), emigration (γ"), immigration (γ'), and best age structure to use for juveniles. We did this first by determining the top model for detectability and considering that top model to determine the top model for both emigration and immigration. Once we determined the top model for these 3 parameters, this model was used in a survival (φ) to determine the best age structure to use for juveniles. Once we incorporated that top model, the model was used to evaluate the covariates of survival for juveniles. The table includes the model's name, AICc, Delta AICc, AICc weights, model likelihood, and deviance. 'Method' refers to using both hand-tracking and automated telemetry to search for tagged juveniles, week represents the week of the season, the week-constrained bin describes weeks that were combined for better estimation, week_trend is a linear change over the course of the season, year is the year of the study (2022, 2023), and "." is constant survival. Also note the bolded model was the model determined to be the best, as for both detectability and emigration and immigration we needed to constrain the weeks in order for the model to produce robust estimates. For detectability we constrained (denoted as year-constrained in the table) recapture probability by method by estimating weeks 1-12 separately in each year, but combined weeks 13-16 together for both years. Also note the bolded model supported estimates which produced better estimates, as for emigration and immigration constrained the weeks in order for the model to produce better estimates. For emigration, we grouped (denoted as week-constrained in table) weeks 1-9 with weeks 15-16 grouped together, estimated 10, 11, and 12 separately, and grouped weeks 13-14 together. For immigration, we grouped weeks 1-7 together, 8-14 together, then grouped together weeks 15-16.

A. Detectability					
Model	**AICc**	**Delta AICc**	**AICc Weights**	**# of Parameters**	**Deviance**
φ(.) γ"(.) γ'(.) p(method*week*year)	5151.979	0	1	72	6589.974
φ(.) γ"(.) γ'(.) p(method*week-constrained)	5243.741	91.76	<0.001	58	6711.312
φ(.) γ"(.) γ'(.) p(method*week)	5528.231	376.25	<0.001	40	7033.319
φ(.) γ"(.) γ'(.) p(method + week_trend)	5810.349	658.37	<0.001	42	7311.296
φ(.) γ"(.) γ'(.) p(method*week_trend)	5816.045	664.07	<0.001	8	7386.449
φ(.) γ"(.) γ'(.) p(hand-tracking*week)	5860.72	708.74	<0.001	39	7367.875
φ(.) γ"(.) γ'(.) p(method)	5960.509	808.53	<0.001	6	7534.937
φ(.) γ"(.) γ'(.) p(.)	6056.52	904.54	<0.001	5	7632.958

Table 9. (cont.).

B. Emigration and Immigration					
Model	**AICc**	**Delta AICc**	**AICc Weights**	**# of Parameters**	**Deviance**
φ(.), γ''(week), γ'(week), p(method*week-constrained)	5144.359	0	1	89	6545.964
φ(.), γ''(week-constrained), γ'(week-constrained), p(method*week-constrained)	5169.374	25.02	<0.001	64	6624.313
φ(.), γ''(week*year), γ'(week*year), p(method*week*year), p(method*week-constrained)	5183.631	39.27	<0.001	122	6513.063
φ(.), γ''(week_trend), γ'(week_trend), p(method*week*year), p(method*week-constrained)	5240.259	95.90	<0.001	60	6703.626
φ(.), γ''(.), γ'(.), p(method*week*year), p(method*week-constrained)	5243.741	99.38	<0.001	58	6711.312
φ(.), γ''(year), γ'(year), p(method*week*year), p(method*week-constrained)	5244.085	99.73	<0.001	60	6707.453

C. Age Structure					
Model	**AICc**	**Delta AICc**	**AICc Weights**	**# of Parameters**	**Deviance**
φ(week_trend), γ''(week-constrained), γ'(week-constrained), p(method*week-constrained)	5090.674	0	0.442	64	4959.150
φ(week_trend*year), γ''(week-constrained), γ'(week-constrained), p(method*week-constrained)	5090.996	0.32	0.376	66	4955.247
φ(week 1,2-3,4+), γ''(week-constrained), γ'(week-constrained), p(method*week-constrained)	5093.405	2.73	0.113	66	4957.656
φ(week 1,2,3,4+), γ''(week-constrained), γ'(week-constrained), p(method*week-constrained)	5095.359	4.69	0.042	67	4957.495
φ(1,2,3,4,5+), γ''(week-constrained), γ'(week-constrained), p(method*week-constrained)	5096.464	5.79	0.024	68	4956.482
φ(1-2,3,4+), γ''(week-constrained), γ'(week-constrained), p(method*week-constrained)	5101.679	11.01	0.002	66	4965.930
φ(1-3,4+), γ''(week-constrained), γ'(week-constrained), p(method*week-constrained)	5105.308	14.64	<0.001	65	4971.673
φ(1-2,3+), γ''(week-constrained), γ'(week-constrained), p(method*week-constrained)	5107.472	16.80	<0.001	65	4973.837
φ(1,2+), γ''(week-constrained), γ'(week-constrained), p(method*week-constrained)	5108.877	18.20	<0.001	65	4975.241
φ(week), γ''(week-constrained), γ'(week-constrained), p(method*week-constrained)	5111.927	21.25	<0.001	79	4948.539
φ(1-4,5+), γ''(week-constrained), γ'(week-constrained), p(method*week-constrained)	5114.912	24.240	<0.001	65	4981.276
φ(week*year), γ''(week-constrained), γ'(week-constrained), p(method*week-constrained)	5139.314	48.64	<0.001	96	4939.318
φ(year), γ''(week-constrained), γ'(week-constrained), p(method*week-constrained)	5164.262	73.59	<0.001	65	5030.626
φ(.), γ''(week-constrained), γ'(week-constrained), p(method*week-constrained)	5169.374	78.70	<0.001	64	5037.850

Table 10. Additional information of adults and juvenile covariates compared in the analysis. Temperature, precipitation, habitat age, body condition, Brood size, and fledge date are shown. Mean, Standard Deviation, and the range of the covariate are given.

Covariate (Adult)	**Mean**	**SD**	**Min**	**Max**
Mean weekly temperature (C)	17.37	4.14	6.2	22.3
Weekly cumulative precipitation (mm)	41.31	56.4	0.0	304.3
Habitat Age (years)	13.55	3.16	7.0	88.0
Body Condition	13.58	0.54	12.2	14.8
Covariate (Juveniles)	**Mean**	**SD**	**Min**	**Max**
Low weekly temperature (C)	11.82	6.19	-3.6	33.5
Weekly cumulative precipitation (mm)	37.41	42.67	0.0	304.3
Habitat Age (years)	13.16	2.39	9.0	22.9
Body Condition	11.54	1.03	10.02	15.5
Brood Size	4.32	1.04	2.0	6.0
Fledge Date	1-Jul	12.29	16-Jun	1-Aug

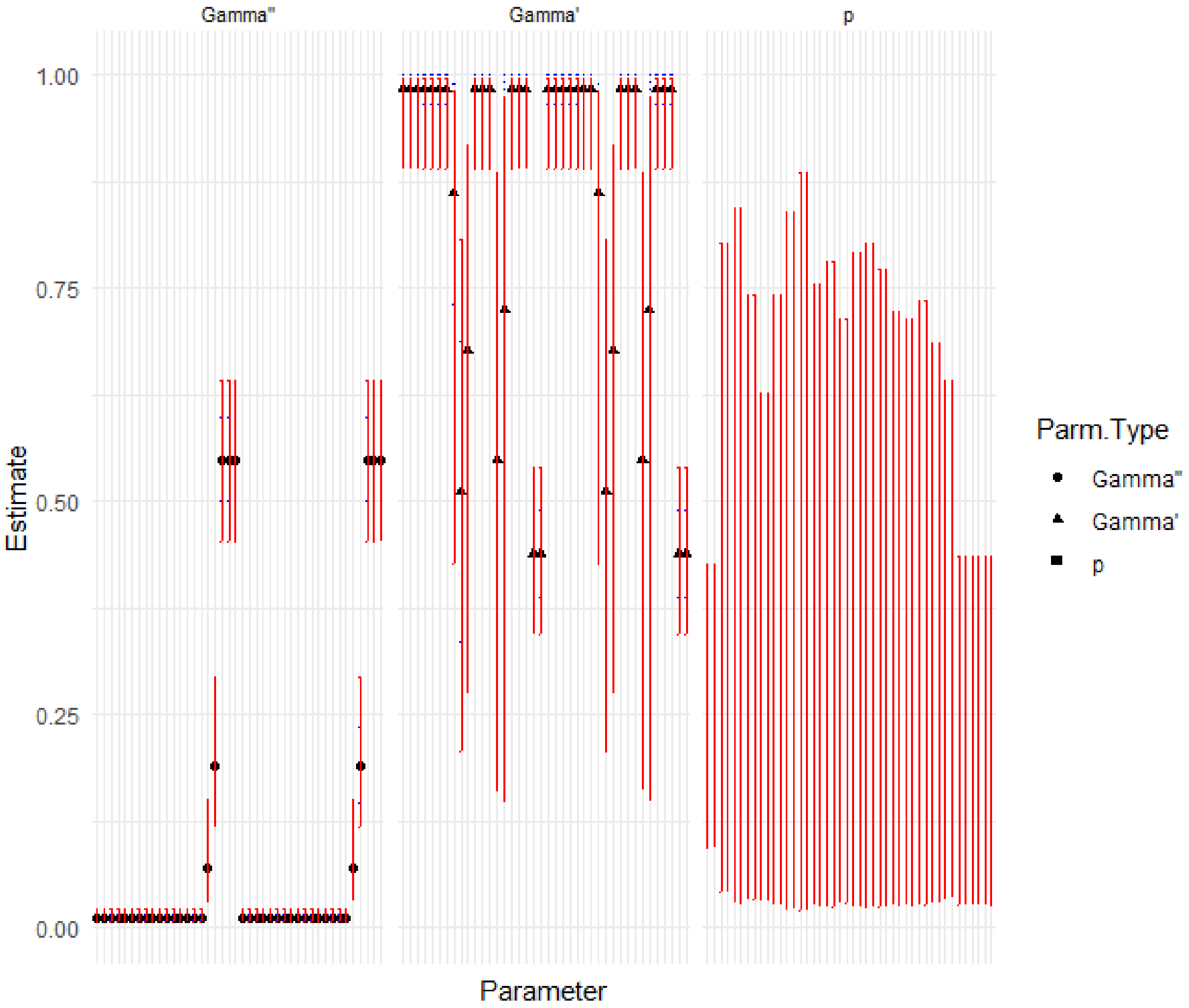


Figure 6. Estimates for adults of the probability of emigration out of the study system gamma'' (γ''), and the probability of remaining outside of the study system given prior emigration gamma' (γ') and of probability of detection (p) for each week of the study. The x-axis is the length of the study for each parameter.

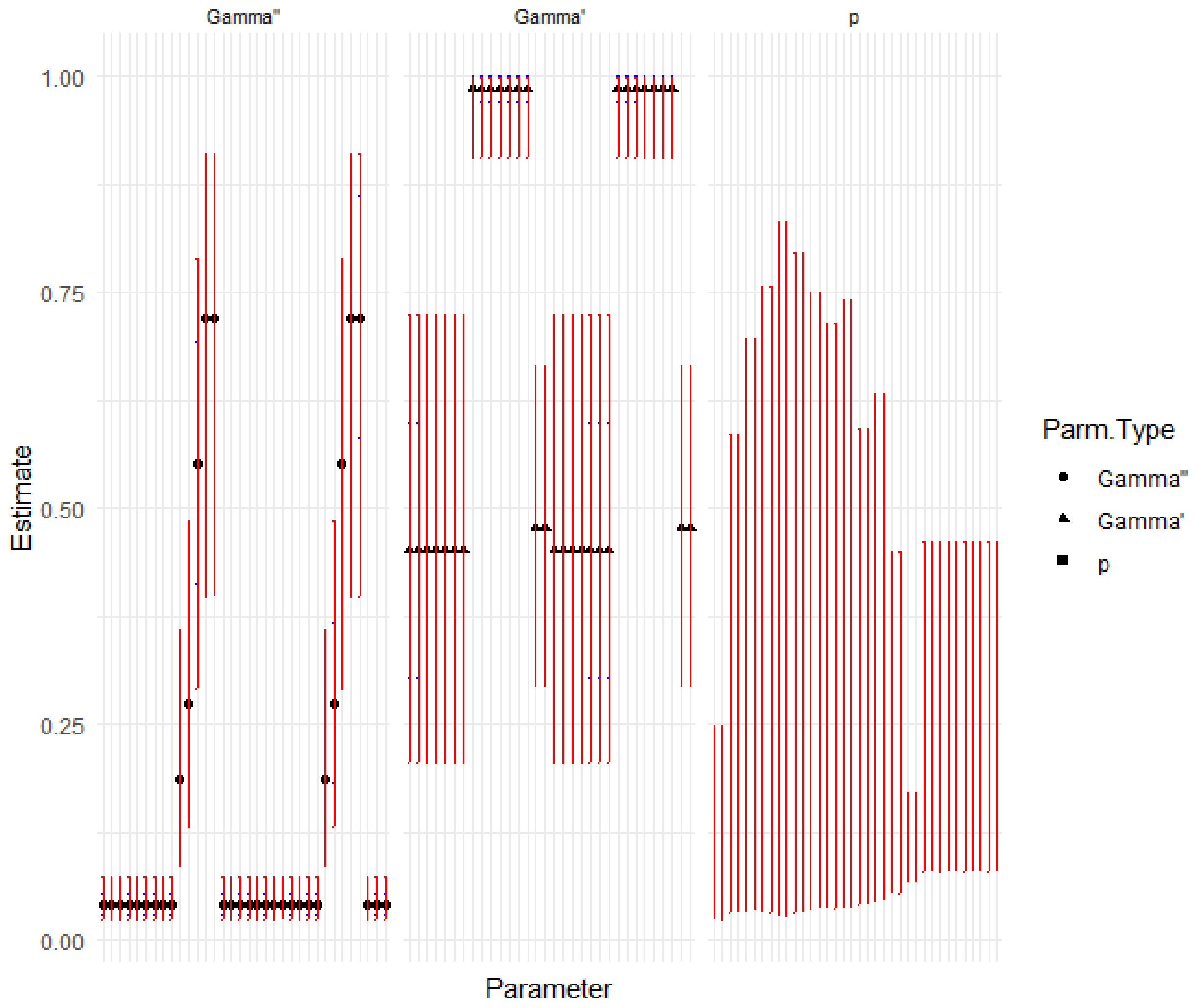


Figure 7. Estimates for juveniles of the probability of emigration out of the study system gamma'' (γ''), and the probability of remaining outside of the study system given prior emigration gamma' (γ') and of probability of detection (p) for each week of the study. The x-axis is the length of the study period for each parameter.

APPENDIX B: HABITAT, MOVEMENT AND RELOCATIONS IN THE POST-BREEDING PERIODS

Purpose of study

To examine habitat use in the post-breeding period, we tracked 85 adult and 34 juvenile warblers in 2022 and 2023. For each individual we determined the date of cessation of parental care (Methods in Chapter 2). Using handheld telemetry, we resighted individuals weekly throughout the breeding and post-breeding periods until they migrated. We examined habitat characteristics and other intrinsic conditions to address if individuals in the post-breeding period:

i. Relocated from their breeding or natal areas and, if so, what distances were these relocations?
ii. What factors predicted whether a bird would relocate?
iii. What habitat characteristics were associated with the new areas for relocated birds?

Methods

For information on methods related to radio-tagging adults and juveniles, the automated telemetry array, resighting individuals, post-breeding timing period, study sites, and departure timing, see Chapter 2: Methods.

Individuals considered for analysis

Any adults that did not live for at least 4 weeks after the termination of an active nest were not considered for the analysis. Additionally, 3 adults who were not confirmed breeders were omitted from the analysis. For juveniles, any individual that did not live for at least 4 weeks post-fledging were omitted from the analysis given a lack of adequate time to reach parental independence and thus the potential to exhibit exploratory behavior. Both adults and juveniles meeting this criterion were considered regardless of whether migration was confirmed.

Covariates Considered

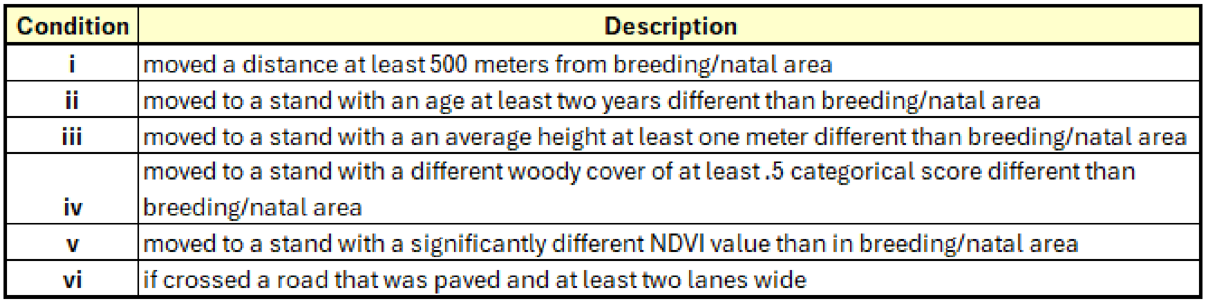
Five habitat characteristics were considered for each managed stand as possible predictive features of the habitat. These were: normalized difference vegetation index (NDVI), estimated average tree height, planted stand age, and stand size (Obtained from Michigan DNR or USFWS) or woody cover. NDVI calculations were made possible from NAIP (National Agriculture Imagery Program) data downloaded from: https://earthexplorer.usgs.gov/. NAIP aerial photography was taken in August or September of 2022 (accessed in March of 2024). This data was used as a proxy for both years within the study period. Because the vegetation in the study area is nearly completely comprised of young coniferous trees, the NDVI score was assumed to have not changed significantly between the breeding and post-breeding periods (a span of just a few months) and was expected to be nearly identical between years. To calculate NDVI scores for individual bird locations, a 10-meter radial area was buffered around each re-sighted individual to plot changes in habitat via NDVI score each week based on an individual's location. Buffering and calculations were done in ArcGIS Pro (*ESRI 2023. ArcGIS Pro Desktop: Release 3.2. Redlands, CA: Environmental Systems Research Institute*) using the buffer tool and the formula: NDVI = (Band 4 – Band 3) / (Band 4 + Band 3). Average tree height was obtained for nearly every occupied stand via visual estimates in 2023, also representing both years. Finally, ground cover was estimated in 2023 representing both years by categorical estimates of average cover excluding planted openings within a stand (1 = 0-20%, 2 = 21-40%, 3 = 41-60% 4

= 61-80%, 5 = 81-100%). Categorical woody cover estimates excluded ground cover from herbaceous substrates.

Defining Relocations

For both adults and juveniles, we considered a bird to have made a relocation upon cessation of the breeding or dependence period and it met any combination of the conditions in Table 11.

Table 11. The conditions in which a radio-tagged Kirtland's Warbler was considered to have relocated upon cessation of breeding or parental dependence. An individual was still considered to have made a relocation even if it later returned to or near its breeding or natal area as long as it was not resighted within those areas for at least two weeks. If a bird moved multiple times within its respective post-breeding period, the first relocation was representative of the area of relocation.



Condition	Description
i	moved a distance at least 500 meters from breeding/natal area
ii	moved to a stand with an age at least two years different than breeding/natal area
iii	moved to a stand with a an average height at least one meter different than breeding/natal area
iv	moved to a stand with a different woody cover of at least .5 categorical score different than breeding/natal area
v	moved to a stand with a significantly different NDVI value than in breeding/natal area
vi	if crossed a road that was paved and at least two lanes wide

Results

Of the 85 adults for which we had data, 43.5% relocated from their breeding territory in the post-breeding period. Additionally, all juveniles moved from their natal areas, though most moved unknown distances and to unknown locations precluding an understanding of habitat use.

However, despite the paucity of resighting via hand-held telemetry, these broad scale movements of juveniles were confirmed by our array of automated telemetry stations (Haradon, unpublished data).

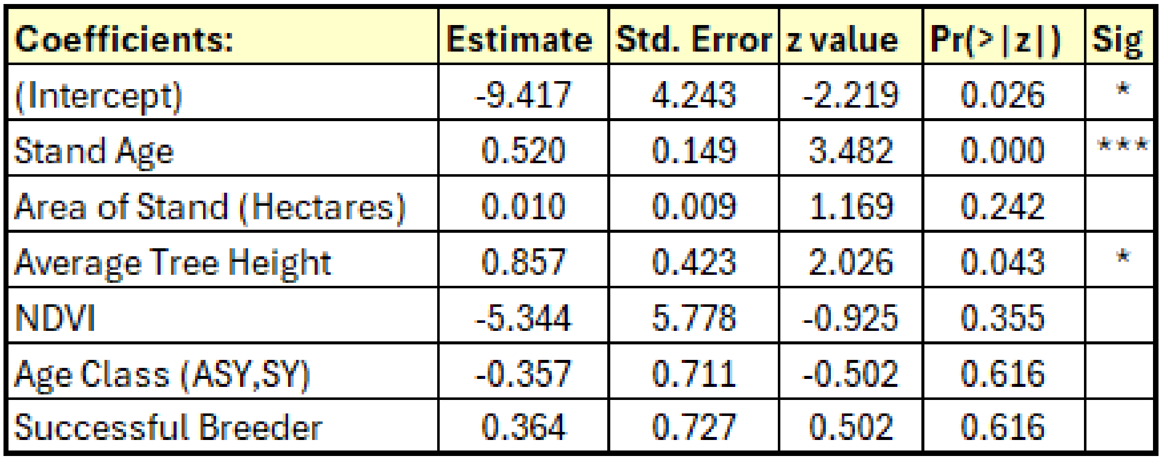
The average relocation distance for adults was 4.9 km (range 0.7 to 22.3 km). For adults that did relocate, habitat age was a significant predictor in both making a relocation, and as a characteristic in the area of relocation, and average tree height was slightly different (Table 12). These stands were on average 8.6 years older than the age of the stand in which an individual held their breeding territory (Figure 8). Stand age and height are likely correlated, though specific management regimes (e.g., planted tree density) and other stand-specific factors may create variability in the relationship between age and tree height. Neither adult age nor nest success were significant predictors of post-breeding relocations.

We aggregated data on the movements of 34 juveniles. Nearly all juveniles appeared to move from their natal areas before departing on migration, though some individuals we lake data to confirm individual movements. Automated radio telemetry stations detected movements between stations prior to the detections indicating migratory departure. These pre-migratory directions in the parental independence period ranged over multiple weeks, and the average number of times an individual was detected between stations was 6.31 (range = 0-51). Distance calculations from individuals resighted via hand tracking telemetry found the maximum distance moved averaged 4.7 km (range 0.3 to 28.1 km), though this is only representing juveniles that could be reliably relocated thus representing a minimum. When juveniles moved, they tended to move to older stand ages, on average moving to a stand that was 17.4 years older than the stand in their natal area (Figure 8). All but one individual was resighted in an older stand after reaching parental independence. Females moved to stands 8.6 years older while males moved to stands that were 25.7 years older. The average max distance moved by females and males was similar (4.8 km and 4.7 km, respectively).

Conclusions

Both adults and juveniles exhibited considerable movement in the post-breeding period (Figure 9). Adults often relocated upon cessation of breeding, moving to older stands. Additionally, nearly every juvenile was directly observed or confirmed via automated telemetry to move from their natal area after reaching parental independence, however, but could be less reliably relocated following these movements. These movements and relocations have previously not been documented for this species and may be indicative of more complex habitat use across the breeding post-breeding periods than what is required during the breeding period alone. Future research should aim to better capture the distances traveled and habitat used by juveniles in their independence period, and in particular how these movements could inform future dispersal. Additionally, efforts should be made to assess post-breeding habitat requirements for both adults and juveniles.

Table 12 Summary of the logistic regression model predicting breeding period conditions of relocation in the post-breeding period Estimates, standard errors, z-values, and p-values for each predictor are shown. Significant predictors are marked with * and *** indicating different levels of significance.



Coefficients:	Estimate	Std. Error	z value	Pr(>|z|)	Sig
(Intercept)	-9.417	4.243	-2.219	0.026	*
Stand Age	0.520	0.149	3.482	0.000	***
Area of Stand (Hectares)	0.010	0.009	1.169	0.242	
Average Tree Height	0.857	0.423	2.026	0.043	*
NDVI	-5.344	5.778	-0.925	0.355	
Age Class (ASY,SY)	-0.357	0.711	-0.502	0.616	
Successful Breeder	0.364	0.727	0.502	0.616	

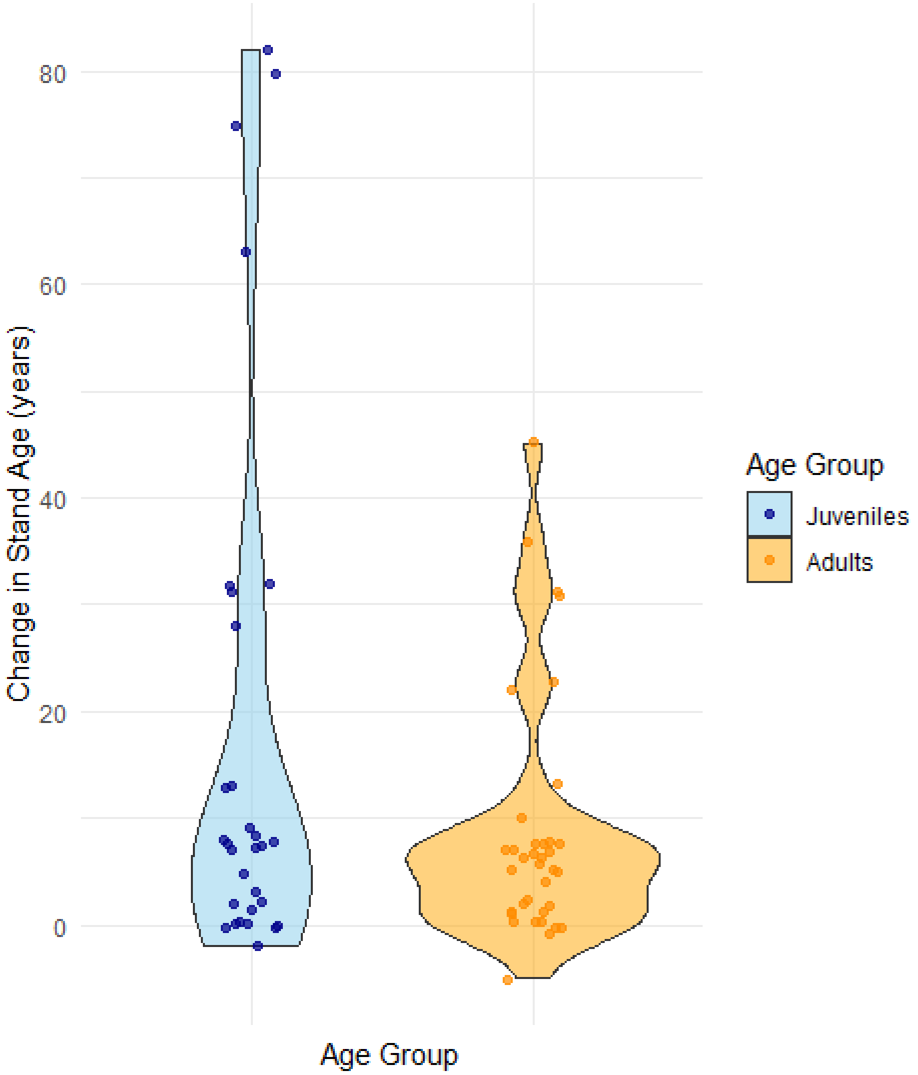


Figure 8. Denotes the difference in stand age in years of adult and juvenile birds in the post-breeding period. The Y-axis shows the difference in age relative to the natal area (juveniles) or nesting area (adults) respectively.

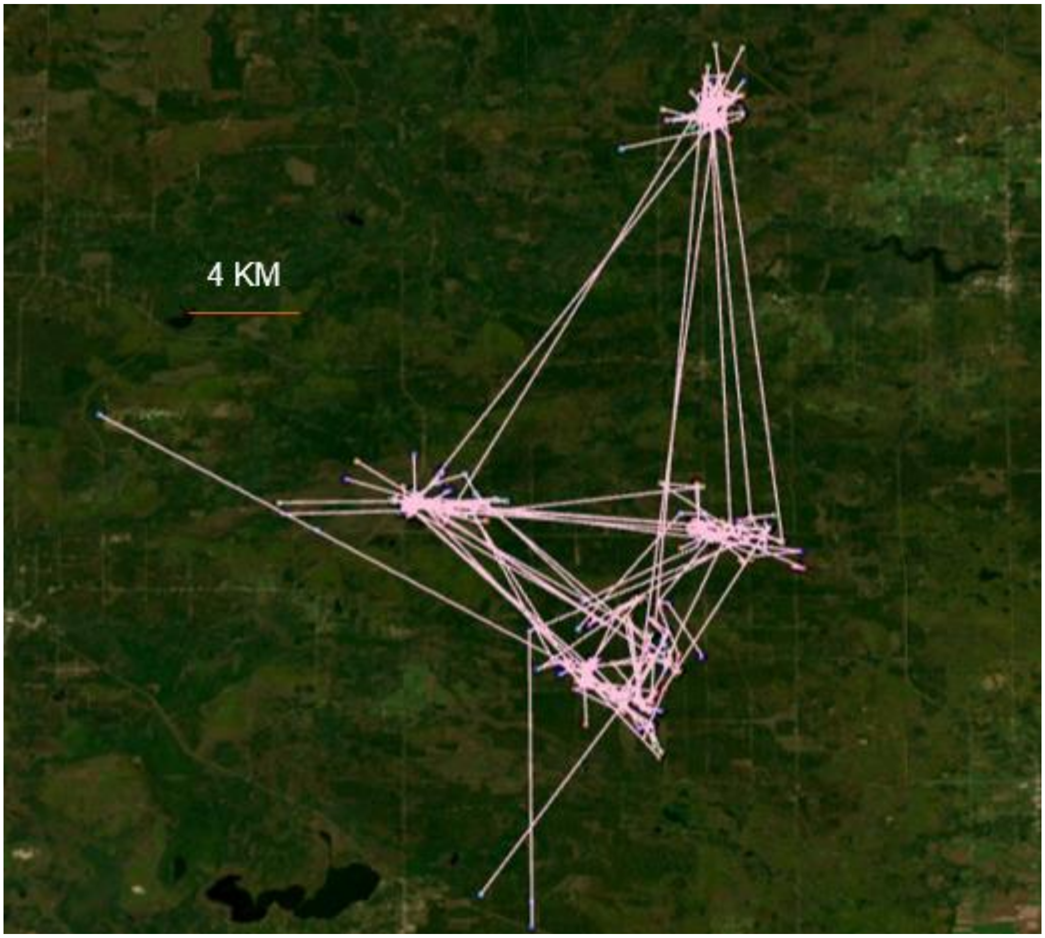


Figure 9. The movement of adults and juveniles in the post-breeding period in either 2022 or 2023. Pink lines track relocations from breeding or natal areas to other areas in the post-breeding period. Colored dots denote individual birds. Points are clustered around our four study sites.