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Avian Behavior, Ecology, and Evolution

Why do juvenile Wood Thrushes make long-distance pre-migratory movements across a fragmented landscape?

¿Por qué los juveniles de *Hylocichla mustelina* realizan movimientos pre-migratorios de larga distancia a través de un paisaje fragmentado?

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ABSTRACT. The pre-migratory period for naïve juvenile migratory songbirds is a critical stage in development as they disperse from their natal territories and prepare for their inaugural fall migration. Little is known about this period because of the difficulty in tracking individuals once they make longer dispersal movements. We used the Motus Wildlife Tracking System combined with long life (~400 d) radio-tags to track 119 independent juvenile Wood Thrushes to fall migration departure and to detect their return the subsequent spring. For comparison, we also tracked 60 adults from breeding territories in the same years and study area. We found that 78% of juveniles made long-distance (> 5 km) pre-migratory movements (PMM) at night, mainly 2 h before sunrise, and in random orientations. We found no support for the habitat optimization hypothesis because adults rarely (8.3%) made PMM, and juveniles from small forest fragments did not disperse at an earlier age or make more extensive PMM than those from large fragments. The prospecting for future breeding territories hypothesis seems unlikely because PMM occurred primarily in the 2 wk prior to the onset of fall migration, when social cues of territory quality are less available, and juveniles that returned in spring did not breed closer to their previous fall locations than to their natal site. The extent of PMM also did not predict flight performance (departure date, pace, orientation) as birds crossed a large water barrier on their first migration movement. Our results best support the homing target hypothesis because, of the juveniles that returned the subsequent spring, a large proportion (81%) was detected in the study area rather than elsewhere by the extensive Motus network. Long-distance PMM by juveniles may be common in other forest songbirds and could have implications for landscape-scale habitat conservation.

RESUMEN. El periodo pre-migratorio de los juveniles ingenuos de las aves canoras migratorias es una etapa crítica en su desarrollo, ya que se dispersan desde sus territorios natales y se preparan para su migración otoñal inaugural. Poco se sabe sobre este periodo debido a la dificultad de rastrear a los individuos una vez que realizan movimientos de dispersión más largos. Usamos el sistema Motus Wildlife Tracking combinado con radiomarcadores de larga duración (~400 d) para seguir a 119 juveniles independientes de *Hylocichla mustelina* hasta la salida de la migración otoñal y detectar su regreso en la primavera siguiente. A modo de comparación, también seguimos a 60 adultos de territorios de cría en los mismos años y área de estudio. Encontramos que el 78% de los juveniles realizaban movimientos pre-migratorios (MPM) de larga distancia (> 5 km) por la noche, principalmente 2 h antes del amanecer, y en orientaciones aleatorias. No encontramos apoyo para la hipótesis de optimización del hábitat porque los adultos raramente (8.3%) realizaron MPM, y los juveniles de pequeños fragmentos de bosque no se dispersaron a una edad más temprana ni realizaron MPM más extensos que los de grandes fragmentos. La hipótesis de la prospección de futuros territorios de cría parece poco probable porque los MPM se produjeron principalmente en las 2 semanas previas al inicio de la migración otoñal, cuando las señales sociales de la calidad del territorio están menos disponibles, y los juveniles que regresaron en primavera no se reprodujeron más cerca de sus anteriores ubicaciones otoñales que de su lugar natal. La extensión del MPM tampoco predijo el rendimiento del vuelo (fecha de salida, ritmo, orientación) cuando las aves cruzaron una gran barrera de agua en su primer movimiento migratorio. Nuestros resultados apoyan mejor la hipótesis del objetivo de búsqueda porque, de los juveniles que regresaron en la primavera siguiente, una gran proporción (81%) fue detectada en el área de estudio y no en otro lugar por la extensa red Motus. Los MPM a larga distancia por parte de juveniles puede ser común en otras aves canoras forestales y podría tener implicaciones para la conservación del hábitat a escala de paisaje.

Key Words: *juvenile dispersal; migration; Motus; pre-migratory movement; Wood Thrush*

INTRODUCTION

The autumn pre-migration period for juvenile migratory birds is a critical time in their development because they have become independent of their parents and may disperse from their natal territory prior to fall migration (Mitchell et al. 2010). During this pre-migration stage, naïve but independent juveniles must find adequate food, not only for daily survival, but also to support a preformative feather molt and fattening in preparation for autumn migration (Mitchell et al. 2010) while being alert for predators (Anders et al. 1997, Kershner et al. 2004). Juveniles could remain in or near their parent's breeding territory until migration or could explore the surrounding habitat. However, little is known about pre-migration behavior of juvenile migratory songbirds, or how this behavior affects survival, fall migration timing, and future breeding habitat selection and reproductive success (Patchett et al. 2022). This gap in knowledge is due to the difficulty in radio-tracking individual juveniles after they leave the natal territory (Vitz and Rodewald 2010, Cox and Kesler 2012) and move out of range of manual detection.

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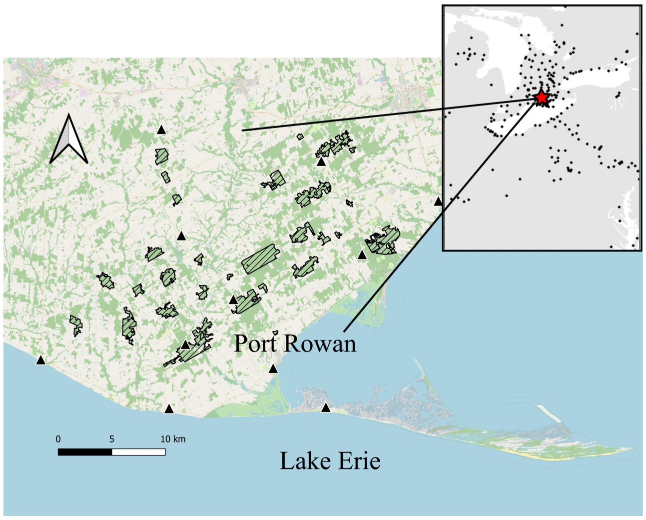
The costs and benefits of pre-migration movements of juveniles are not well understood. Juvenile birds have no knowledge of the surrounding landscape until they begin to disperse from their parents' breeding territory (Brown and Taylor 2015). Venturing out into new areas may place higher energy demands on young birds (Weathers and Sullivan 1989) and expose them to a higher risk of predation (Yoder et al. 2004). In highly fragmented landscapes, crossing open gaps between fragments could increase predation risk, in which case dispersal may be constrained by the connectivity of the remaining forest patches and the surrounding land use (Bélisle et al. 2001, Ricketts 2001, Vitz and Rodewald 2010). However, there are likely short-term and long-term benefits that can be gained from pre-migration dispersal movements by juveniles (Anders et al. 1997), and there are many hypotheses for the adaptive function of these movements (Mitchell et al. 2010). Dispersal movements into habitat with abundant food and shelter from predators (habitat optimization hypothesis; Anders et al. 1997, Kershner et al. 2004) may improve body condition by increasing energy stores and flight muscle, thereby increasing chances of survival during migration (Mitchell et al. 2011). By exploring the regional landscape, juveniles may be scouting for future high-quality breeding territories, which could place them at a competitive advantage upon return the following spring (territory selection hypothesis; Nocera et al. 2006, Mitchell et al. 2010, Samplonius and Both 2017, Patchett et al. 2022). Juveniles may make pre-migratory movements (PMM) near the natal region to form a navigational target that will help them relocate the region when they return in spring (homing target hypothesis; Mitchell et al. 2010). Finally, Mukhin et al. (2005) suggest that nocturnal pre-migratory flights from the natal site function to develop a stellar compass in naïve birds, which is critical for navigation during nocturnal migration in songbirds.

The combination of the Motus Wildlife Tracking System (reviewed by Taylor et al. 2017) with the miniaturization of radio-tags can now be used to monitor movements of juveniles over large distances. Motus allows researchers to track wildlife movements remotely over local, regional, and continental spatial scales via a huge network of receiver towers. Motus also provides a new opportunity with which to study long-distance pre-migration movements in juveniles. A groundbreaking study conducted by Brown and Taylor (2015) used a Motus telemetry array to document pre-migration dispersal movements of independent juveniles and adult Blackpoll Warblers (*Setophaga striata*) captured in late summer at a breeding site on an island in the eastern Gulf of Maine. The adults immediately crossed the Gulf of Maine and moved southwest along the New England, USA coastline in a direction consistent with preparation for a cross-Atlantic, long-distance fall migration. The juveniles, however, made long-distance PMM in more random directions, resulting in an average net displacement of 91 km from the breeding site. Brown and Taylor (2015) suggest that juvenile warblers may have been prospecting for future breeding territories or learning landscape features for navigational purposes. Evans et al. (2020) used Motus in southwestern Ontario, Canada to show that Barn Swallows (*Hirundo rustica*) tagged as nestlings dispersed an average of 118 km from their natal colony prior to the onset of fall migration. Generally, the extent (e.g., proportion of juveniles that exhibit PMM, duration of PMM, dispersal distance) to which juvenile migratory songbirds disperse prior to fall migration is not known.

Wood Thrush (*Hylocichla mustelina*) fledglings that survive to independence disperse from their natal territory on average 32 days post-fledging to sites approximately 1.5 km away (Vega Rivera et al. 1998). However, it is not known whether they subsequently engage in longer distance movements prior to migration, and if so, how they benefit from doing so. To test for the occurrence of and hypotheses for the benefits of long-distance PMM in juveniles, we equipped nestling Wood Thrushes with radio-tags that had a 1-yr battery life. Our study area, Norfolk County, Ontario, had a high density of Motus towers that could detect regional movements as well as onset of fall migration and spring return (Fig. 1A,B). Our first objective was to test whether the nestling environment predicts juvenile Wood Thrush long-distance PMM. We determined the proportion of juveniles that were detected at Motus towers long distances (> 5 km) from the natal site prior to fall migration and tested if fledge date, sex, or natal fragment size predicted age at dispersal. We also tested whether these variables were significant predictors for each of three measures of extent of PMM: (1) duration of pre-migration dispersal period > 5 km from natal fragment, (2) number of different Motus towers at which detections > 5 km occurred, and (3) furthest detection distance (e.g., net displacement) from the natal forest prior to onset of migration.

Fig. 1. (A) Map of study sites in Norfolk County on the north shore of Lake Erie, near Port Rowan, Ontario, Canada (42.7131° N, 80.5372° E). Twenty-nine study sites (black hatched boxes) ranging from 11 to 500 ha were used over the course of the three field seasons (2016, 2017, 2018). Pre-migratory movements were detected by all local Motus Wildlife Network towers (black triangles). (B) Inset map shows study area in the broader context of the active Motus tower network (black dots) in 2018.



Our second objective was to test four hypotheses for the benefit of PMM. The habitat optimization hypothesis predicts that adults and juveniles will have similar PMM (Brown and Taylor 2015) and that juveniles from small forest fragments (assumed to be lower quality habitat; see Burke and Nol 2000, Hannon et al. 2009, Falk et al. 2011) will have earlier and/or greater PMM. The territory selection hypothesis predicts that males (which are more territorial) should search more intensively for future territories than should females (Patchett et al. 2022), the landscape movements should be nearly randomly oriented relative to the natal site (Mitchell et al. 2010), and juveniles should exhibit far more extensive movements than adults that have already held breeding territories (Brown and Taylor 2015). If juveniles are successfully locating future breeding sites, then we predicted that the distance between the previous fall detection and the subsequent breeding site should be significantly smaller than the distance between the natal site and the breeding site (Patchett et al. 2022). The homing target hypothesis predicts that a high proportion of juveniles will return to the region and that their PMM should be random in direction, to increase the size of the homing target, and more frequent than those of adults. The final hypothesis proposes that the extent of PMM improves first migration flight performance. Pre-migratory landscape movements could provide juveniles with experience that improves performance during their first migratory flight, especially if movements are nocturnal (e.g., through development of the stellar compass; Mukhin et al. 2005). Individuals that have dispersed far from their natal site and/or have made more frequent landscape movements may depart on fall migration earlier, travel at a faster pace on their first flight, or be more likely to fly south across the large (50 km) water-barrier of Lake Erie that lies immediately south of the study area.

METHODS

Study area

The study took place from 2016 to 2019 in forest fragments in Norfolk County on the north shore of Lake Erie in Ontario, Canada. Study sites ($N = 29$ fragments) were selected to represent a gradient of forest size, ranging from 11 to 500 ha (Fig. 1A,B; Appendix 12). Study sites were on both public (Nature Conservancy of Canada; Ministry of Northern Development, Mines, Natural Resources and Forestry; Long Point Conservation Authority) and privately owned lands. Norfolk County is part of the Long Point Conservation Authority jurisdiction, which is 21% forested, with predominant land uses being crop agriculture (Long Point Region Conservation Authority 2019). This region was chosen because of the high-density coverage of the Motus automated telemetry system (Fig. 1B).

Nest monitoring and radio-tagging

Beginning mid-May of each year, forest fragments were searched for Wood Thrush nests by locating singing males on territories and subsequently observing nests or nesting behavior. Nest contents were checked every 4 to 6 days using a pole with an attached cellphone set to video mode. On day 10 after hatching, nestlings were banded with uniquely numbered aluminum bands (U.S. Fish and Wildlife Service/Canadian Wildlife Service) and a unique color band combination, and measurements of tarsus length to 0.1 mm, wing chord to 1 mm, and mass to 1 g were taken using an electronic scale. The largest nestling (by mass) in the nest had a blood sample (25 uL) drawn for genetic sexing (HealthGene Corporation) and was equipped with a uniquely coded radio transmitter (Lotek NTQB-6; 1.5–1.7 g, ~1-yr battery life, 12.7-s burst rate) using a figure-eight leg loop harness (Rappole and Tipton 1991). Three slightly different tag models were deployed due to manufacturing limitations throughout the 3-yr study; however, tags remained ~5% of the total body weight of 10-day-old nestlings. Only one nestling was tagged at 131 of the 160 nests; two nestlings were tagged at 29 (18%) nests. Of the 189 tagged nestlings (2016: $N = 47$, 2017: $N = 66$, 2018: $n = 76$), there was an even sex ratio of males to females (95:94). Adult Wood Thrushes in a parallel study were also measured and radio-tagged in the same field sampling period and forest fragments (Boyd et al. 2023).

Manual, automated, and aerial radio-tracking

Manual radio-tracking was done approximately every 4 days post-tagging by returning to the last known location of the fledgling. Each tracking event documented the status of the bird by determining if it was alive (tag was moving) or dead (tag not moving); tags were recovered when possible. If birds were not relocated upon return to the last known location, a 1-h search was conducted throughout the forest fragment.

Automated tracking using the tower array of the Motus Wildlife Tracking System (Taylor et al. 2017) allowed us to detect tagged juveniles during the pre-migration period, during migration departure, and upon their return the following spring. The high density of automated towers within the study area and surrounding regions in all directions (Fig. 1) allowed for possible detection of juveniles that survived migration but did not return to their natal site. Each tag detection recorded the unique tag number for the individual bird, signal strength for each antenna, and date and time of each detection. Motus tower detections of forest-dwelling birds mainly occur once a radio-tagged bird comes out of the forest and flies across an open area (Crewe et al. 2019) or flies above the forest canopy. Motus is designed to detect landscape-level movements and, unlike manual or aerial tracking, it does not allow one to determine the actual location of a bird (i.e., whether it is at vs. near its natal site).

Aerial telemetry was conducted to locate juveniles that returned to the general study area each spring as a supplement to Motus automated detection and to locate breeding sites. A Cessna 172 was equipped with a strut-mounted H-type antenna and SRX 600 Lotek receiver. One systematic search of the study area was conducted each year during the breeding season, requiring approximately 5 h of flight time (18 July 2017, 2 June 2018, and 15 May 2019). When a detection was made, the search pattern was a series of smaller circles to pinpoint the bird's location and record a Global Positioning System point.

Motus data filtering

Motus tower data records were accessed using the Motus R package and cleaned following guidelines provided in the Motus R manual (Crewe et al. 2020). The Motus filter was applied to flag detections that had a run length < 3 to minimize false positive records, but these records were incorporated on occasion when there were additional supporting detections such as filling a time gap between towers with positive detections (< 5 instances). Subsequently, we manually reviewed all detections (individual hits received by each tower) that the Motus filter had flagged as true positives and removed any that had pulse rates that differed from 12.7 s, occurred in unlikely locations (e.g., outside the breeding range), or were well outside migration routes that have been identified for Wood Thrushes in previous geolocator studies (Stutchbury et al. 2009). For each tagged juvenile, detections were ordered by date, time of day, and each Motus tower, providing a full chronological profile of movement activity after the bird was no longer detected using manual radio-telemetry at its natal territory natal site. There was a total of 788,565 individual detections (hits) made by Motus towers during pre-migration, fall, and spring periods, with false detections making approximately 21% of the total.

Classification of pre-migratory vs. migration departure detections

Prior to the onset of migration, radio-tagged independent juveniles that had survived the fledgling period were detected by Motus towers in the study area. PMM were classed for all movements > 5 km from the natal forest fragment prior to the first migratory Motus tower detection (N = 425 movement detections for 93 individuals). To confirm that such PMM were not migration departures, we analyzed the date and time of day to test whether they differed from known migratory flights. Most PMM were nocturnal, but unlike migration departure flights, they occurred during a 2-h period before sunrise (Rayleigh test, Z = 0.383, P < 0.001; Appendix 10A and C) rather than near sunset. PMM also did not have an orientation bias in any cardinal direction (Rayleigh test, Z = 0.108, P = 0.46; Appendix 10B and D), unlike the southerly movements associated with migration flights. Thus, we assumed that these movements within the study area were pre-migratory in nature. See Appendix 1 for full methodology for classifying pre-migratory vs. migratory movements.

Predictors of pre-migratory movements by juveniles

For each individual (N = 93), age at which long-distance PMM was first detected was calculated as the days elapsed between fledge date (set as the date 2 days post-tagging of nestling at 10 days of age) and the first Motus tower detection > 5 km from the natal site. We used three different measures of the extent to which individuals moved through the local landscape prior to departing on migration. The first was the duration of this PMM period, calculated from the date of the first detection > 5 km from the natal site to the last detection prior to the night of departure on fall migration. The second measure was the number of different Motus towers where PMM detections occurred, regardless of how far apart the towers were. The third was the straight-line distance from the natal site to the furthest tower where a pre-migratory detection occurred.

Pace, direction, and distance of first migratory flight of juveniles

There were 20 birds both with known first migration flights (e.g., detected on the same night on the north and south side of Lake Erie) and that had been detected making PMM. Because songbirds such as the Wood Thrush cannot land on water, the time elapsed between detections likely reflects their actual pace of flight (i.e., actual ground speed). Motus tower detections provide data for a tagged bird as flying linearly because the bird is detected in succession by individual towers, but its actual flight path is unknown. Further, because each Motus tower has a different detection range and antenna orientation, there is uncertainty in calculating the ground speed of a flying bird. To reduce this error in calculating the pace of migration, we used the time of peak signal for each consecutive Motus tower detection to estimate the amount of time elapsed between detections (Bégin-Marchand et al. 2021). We used the straight-line distance between tower detections and divided it by the total time elapsed. Direction of flight used the bearing from the last Motus tower detection on the north side of Lake Erie to the first tower detection on the south side of the lake. Distance between these two tower locations was used as the distance travelled during the first flight.

Analytical methods

Generalized linear models in the "stats" package (R Core Team 2020) were used with gamma distribution and log link because the age of dispersal, duration of PMM, and dispersal distance predictor variables were right skewed. Models for number of towers used a Poisson distribution. First migratory flight generalized linear models were fitted with gamma distribution and log link to determine if the pre-migratory movement measures (duration of PMM, dispersal distance, and number of Motus tower detections) could predict the timing of departure, pace, direction, and distance travelled during the first fall migratory flight. Fledge date, sex, and year were also included in the model sets.

We used the dredge function from the "MuMIn" package (Bartoń 2020) to run all combinations of additive models. Models were ranked using Akaike information criterion (AIC) values adjusted for small sample size (AICc; Burnham and Anderson 2002), and the top models with ΔAICc < 2 were considered equivalent to the best model. No model averaging was conducted when only one model was ΔAICc < 2, but model estimates are reported. Model residuals were examined using the "DHARMa" package (Hartig 2022), and variation inflation factors were checked for all parameters using the "car" package. All continuous predictor variables were scaled and centered.

RESULTS

Most juvenile Wood Thrushes (93 of 119) were detected making long-distance (> 5 km) PMM, and the duration of this pre-migration period ranged widely among individuals (median = 8 d, range = 1 to 68 d). Using the same methods to define PMM for a parallel study using Motus tracking of adult Wood Thrushes in the same study sites and years (Boyd et al. 2023), we found that only 5 of 60 adults exhibited PMM and that those movements occurred over a 1–3 d duration immediately prior to individuals beginning fall migration.

Predictors of age at first dispersal and extent of pre-migration dispersal movements

Detections of first dispersal movements usually occurred at night (84 of 93; 90%), with 48% occurring during the period 2 h before sunrise (Fig. 2A). Age at first detection > 5 km from the natal fragment was highly variable, even for birds fledged at a similar time of year. For instance, birds that fledged in June were first detected > 5 km from the natal site ranging from 24 to 93 days post-fledging. For individuals that fledged later the season, there was less variation, and individuals typically dispersed at a younger post-fledging age. Fledge date was a strong predictor of age at first long-distance detection from the natal woodlot (model estimate ± standard error: −0.174 ± 0.030, P < 0.001; Table 1, Fig. 2B). Those that fledged in June were 20 days older, on average, when first detected > 5 km from their natal woodlot than individuals that fledged in July or August. Males dispersed at a later age than females from the natal site, although sex was not a significant predictor (0.019 ± 0.043, P = 0.66), and neither was natal forest fragment size (0.004 ± 0.016, P = 0.79; Table 1; Appendix 2).

Fig. 2. (A) Time of day of first dispersal movement as detected > 5 km from the natal forest site for juvenile Wood Thrushes (*N* = 93). Most first-dispersal movements occurred at night (397 of 425; 93%), with ~48% occurring during the 2 h before sunrise. (B) Juvenile Wood Thrush fledge date and sex as predictors of age (days since fledging) at first detection > 5 km from the natal forest fragment (*N* = 93). Filled circles with dashed line = females, open triangles with solid line = males, grey shading = 95% confidence intervals around the trend line (Table 1; Appendix 2).

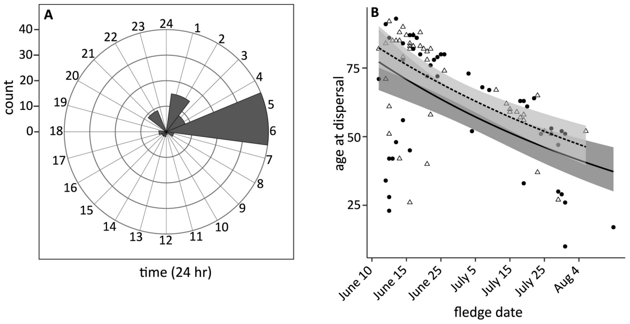


Table 1. Age at first Motus detection > 5 km from the natal forest fragment for juvenile Wood Thrushes (*N* = 93). Generalized linear models included additive predictors of fledge date, natal forest fragment size, sex, and year. Model variable beta coefficient estimates, adjusted standard error (SE), 95% confidence limits (CL), and statistical significance (*P*) for models with < 2 ΔAICc (Akaike information criterion corrected for small sample size) are reported. *P*-values < 0.05 are shown in bold font. See Appendix 2 for model AIC results.

Predictor	Estimate (β) ± SE	95% CL	*P*
Intercept	3.939 ± 0.058	3.823, 4.054	**< 0.001**
Fledge date	−0.174 ± 0.030	−0.232, −0.116	**< 0.001**
Year (2017)	0.308 ± 0.077	0.157, 0.459	**< 0.001**
Year (2018)	0.222 ± 0.073	0.078, 0.365	**0.003**
Sex	0.019 ± 0.043	−0.048, 0.181	0.66
Natal fragment size	0.004 ± 0.016	−0.038, 0.079	0.79

Both earlier fledge date and younger age at first long-distance dispersal led to earlier first detection of PMM and thus increased the period of PMM that occurred before onset of fall migration (Table 2, Fig. 3A,B). Although males had a 1-wk longer PMM dispersal period than females, sex was not a significant predictor of pre-migration dispersal (Table 2, Fig. 3A; Appendix 3).

Individuals were detected at up to 11 different towers (median = 4, range = 1 to 11) as they moved around the landscape prior to onset of migration. Fledge date was not significant, but juveniles that first dispersed at an older age were detected by more towers (0.156 ± 0.063, *P* = 0.01, Table 3), suggesting that these birds were more active in exploring the regional landscape. Sex (0.008 ± 0.049, *P* = 0.87) and natal fragment size (0.045 ± 0.059, *P* = 0.45) were not strong predictors of the number of towers where individuals were detected (Table 2; Appendixes 4 and 11).

Table 2. Model results for duration of pre-migratory dispersal period (number of days from first detection to last pre-migratory detection) as measured by detections > 5 km from the natal forest fragment for juvenile Wood Thrushes, total number of different Motus towers at which juvenile Wood Thrushes were detected during pre-migration dispersal movements, and maximum distance from natal site detected during pre-migratory movements for juvenile Wood Thrushes (*N* = 93). Generalized linear mixed models included additive predictors of age at dispersal, natal forest fragment size, fledge date, sex, and year. Model variable beta coefficient estimates, adjusted standard error (SE), 95% confidence limits (CL), and statistical significance (*P*) for models with < 2 ΔAICc (Akaike information criterion corrected for small sample size) are reported. *P*-values < 0.05 are shown in bold font. See Appendixes 3–5 for model AIC results.

Model	Predictor	Estimate (β) ± SE	95% CL	*P*
Duration of pre-migratory dispersal	Intercept	2.208 ± 0.102	1.991, 2.420	**< 0.001**
	Age at dispersal	−0.780 ± 0.090	−0.976, −0.626	**< 0.001**
	Fledge date	−0.650 ± 0.088	−0.822, −0.477	**< 0.001**
	Sex (male)	0.103 ± 0.153	−0.070, 0.523	0.55
	Natal fragment size	−0.011 ± 0.040	−0.202, 0.096	0.78
Total number of Motus towers	Intercept	0.813 ± 0.150	0.499, 1.097	**< 0.001**
	Age at dispersal	0.148 ± 0.064	0.013, 0.2776	**0.02**
	Natal fragment size	0.021 ± 0.042	−0.040, 0.166	0.62
	Sex (male)	−0.009 ± 0.050	−0.256, 0.168	0.85
	Year (2017)	0.468 ± 0.185	0.122, 0.870	**0.01**
	Year (2018)	0.927 ± 0.165	0.616, 1.273	**< 0.001**
Maximum distance detected	Intercept	2.772 ± 0.109	2.556, 2.992	**< 0.001**
	Age at dispersal	0.015 ± 0.039	−0.067, 0.180	0.71
	Natal fragment size	0.050 ± 0.057	−0.022, 0.189	0.38
	Sex (male)	0.007 ± 0.042	−0.176, 0.256	0.86
	Year (2017)	0.326 ± 0.146	0.031, 0.614	**0.03**
	Year (2018)	0.448 ± 0.136	0.174, 0.714	**0.001**

Fig. 3. Duration of pre-migratory movement period for juvenile Wood Thrushes (*N* = 93) as measured from the first Motus tower detection > 5 km from the natal forest fragment to the last detection that occurred prior to fall departure with (A) age at first detection > 5 km from natal site, and (B) fledge date. Filled circles with dashed line = females, open triangles with solid line = males, grey shading = 95% confidence intervals around the trend line. Fledge date (−0.649 ± 0.088, *P* < 0.001) and age at dispersal date (−0.801 ± 0.090, *P* < 0.001) were both significant predictors in the model (Table 2; Appendix 3).

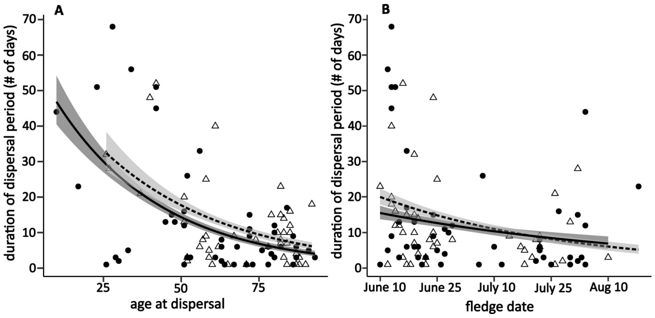


Table 3. Distance and direction of detections from final fall Motus tower detection to breeding site and for natal site to spring breeding site for juvenile Wood Thrushes ($N = 9$). Distance of final fall tower to final spring tower is also given (see Appendix 13).

	Fall tower to breeding site		Natal site to breeding site		Fall tower to spring tower
Tag	Distance (km)	Bearing (°)	Distance (km)	Bearing (°)	Distance (km)
1	16.1	37.0	1.2	208.0	18.3
2	6.9	282.4	0.8	307.5	0.0
3	6.6	284.0	0.6	330.1	25.1
4	7.4	68.3	4.2	126.5	6.1
5	13.2	41.7	3.7	253.1	13.3
6	10.5	48.5	4.8	72.0	9.4
7	8.2	176.9	8.9	161.0	9.4
8	11.7	356.1	1.1	119.2	15.1
9	15.3	10.7	11.4	358.7	13.5
Mean distance	10.7		4.1		12.2
Standard deviation	3.6		3.8		7.2

On average, the maximum distance detected away from the natal site (e.g., net displacement) was 21.8 km (standard deviation [SD] ± 1.25), with 21 of 93 individuals detected > 30 km away. One individual was detected 85 km west of the natal site but returned to the study area prior to onset of fall migration. Natal forest fragment size was not a significant predictor of maximum distance detected from the natal site (0.050 ± 0.057, $P = 0.38$; Table 2; Appendixes 5 and 12), and neither was age at first dispersal (0.015 ± 0.039, $P = 0.71$).

Are second-year individuals that return in spring detected in the same region as their pre-migratory movements as juveniles?

We confirmed the spring return for 31 second-year birds, including 25 that were detected within the study area. One was detected through aerial tracking 7 km from the natal site, and 24 were detected at Motus towers that were within ~12 km on average (SD ± 24.5 km) of their natal nest site. The other six individuals were detected in the spring only outside of the study area (mean 61.9 ± 28.0 km from their natal site) by the Motus tower network.

We determined the breeding sites for nine second-year birds that had been detected within the study area in spring. The final fall pre-migratory dispersal detection location of individuals did not correspond closely with either Motus spring detections or the breeding location of second-year individuals (Table 3; Appendix 13). The last spring tower detection averaged 12.2 ± 7.2 km from the fall tower, and the first breeding location was 10.7 ± 3.6 km from the last fall dispersal detection. By comparison, breeding locations were on average only 4.1 km from their natal site (SD ± 3.8, range = 0.6 to 11.1 km) and, contrary to our prediction, were significantly closer to the natal site than the last fall Motus tower detection (paired t-test $t_8 = 4.3$, $P = 0.001$). Two individuals returned to breed in their natal forest fragment (with territories < 1 km from the natal nest site) and seven of nine individuals bred < 5 km from their natal site.

Does the extent of pre-migratory movements predict fall departure date or first migratory flight performance?

Nestling fledge date and number of towers that juveniles were detected at during PMM were significant predictors of departure date. Individuals departed on fall migration, on average, 1 wk earlier if they fledged the nest during early June compared to birds that fledged at least 6 wk later in the season (model estimate ± standard error: 0.017 ± 0.004, $P < 0.001$). Contrary to our prediction, birds that were detected by more towers during the pre-migratory dispersal period departed later on fall migration (0.014 ± 0.0037, $P = 0.04$; Table 4; Fig. 4A,B). The duration of the pre-migratory dispersal period was not a significant predictor of departure date (0.001 ± 0.003, $P = 0.67$), and neither was maximum distance travelled from the natal nest (−0.003 ± 0.006, $P = 0.62$; Fig. 4C,D; Appendix 6).

The orientation of the first migratory flights for juvenile Wood Thrushes (range 129° to 241°) was not correlated with the different PMM variables or fledge date, and these models were not < 2 AICc from the null model (Table 4; Fig. 5A–D; Appendix 7). The average pace of the first migratory flight (mean = 44.9 km/h, SD ± 18.7 km/h, range = 19.4 to 77.5 km/h) was also not correlated with fledge date or extent of PMM (Table 4; Fig. 6A–D; Appendix 8). Juveniles were detected a mean distance of 74.3 km from their last detection on the north side of Lake Erie commencing migration (SD ± 22.2 km, range = 42.7 to 149.2 km) to the first detection on the south shore of Lake Erie during their first migratory flight. None of the modeled predictors were better than the intercept model with < 2 AICc (Fig. 7A,D; Appendix 9).

DISCUSSION

To our knowledge, this is the first study of a migratory songbird to tag nestlings and subsequently track their long-distance (> 5 km) PMM, fall departure date, first migratory flight performance, and return in spring. Prior studies of PMM in forest migratory songbirds, including the Wood Thrush, found that first dispersal from the natal area began 3–5 wk after fledging, and birds moved 1–2 km away (Vega Rivera et al. 1998, Vitz and Rodewald 2010). In our study, we do not know when juveniles first left their natal area or the extent to which they made short-distance movements. However, we demonstrate that long-distance exploration of the landscape occurs for a high proportion (78%) of juveniles prior to onset of fall migration. These PMM occurred at night, mainly during 2 h before sunrise, and the random orientation indicates that these were not simply small-scale migration movements, which would be southerly in orientation. Most juveniles began these PMM 2–3 mo after fledging, which suggests that juveniles do not travel far from their natal territory as soon as they are fully independent or capable. Instead, pre-migration dispersal occurred primarily during the 2 wk before departure on fall migration. Long-distance movements through a fragmented landscape, which require gap-crossing between forest patches, are assumed to increase risk of predation (Yoder et al. 2004, Vitz and Rodewald 2010); however, 89% of fledglings survived the pre-migration period (Hayes et al. 2024). For the second-year birds that returned the following spring, 80.6% were detected making these larger distance movements compared to birds that were not detected making PMM (19.4%). By the time long-distance PMM occur, juvenile Wood Thrushes may have acquired sufficient experience and flight skills to detect and evade aerial predators.

Table 4. Fall migration departure date, orientation, and pace of first migratory flight models for juvenile Wood Thrushes (*N* = 20) with Akaike information criterion corrected for small sample size (AICc) < 2. Generalized linear models included additive predictors of three pre-migratory movements: duration of pre-migratory dispersal period, maximum distance travelled from natal site, and total number of unique Motus tower detections. Fledge date and sex were also added to the models. Model variable beta coefficient estimates, adjusted standard error (SE), 95% confidence limits (CL), and statistical significance (*P*) for models with < 2 ΔAICc are reported. *P*-values < 0.05 are shown in bold font. See Appendixes 6–8 for model AIC results.

Model	Predictor	Estimate (β) ± SE	95% CL	*P*
Fall migration departure date	Intercept	5.563 ± 0.004	5.556, 5.571	**< 0.001**
	Fledge date	0.017 ± 0.004	0.008, 0.026	**< 0.001**
	Number of towers	0.014 ± 0.007	0.0009, 0.027	**0.04**
	Maximum distance	−0.003 ± 0.006	−0.003, 0.017	0.62
	Duration	0.001 ± 0.003	−0.003, 0.017	0.67
Orientation of first migratory flight	Intercept	5.10 ± 0.034	5.031, 5.175	**< 0.001**
	Fledge date	0.029 ± 0.037	−0.015, 0.124	0.43
	Number of towers	−0.005 ± 0.018	−0.110, 0.048	0.78
	Maximum distance	−0.009 ± 0.023	−0.111, 0.041	0.71
	Duration	−0.004 ± 0.016	−0.103, 0.048	0.81
Pace of first migratory flight	Intercept	3.763 ± 0.083	3.593, 3.944	**< 0.001**
	Fledge date	0.193 ± 0.126	0.019, 0.435	0.12
	Number of towers	−0.032 ± 0.076	−0.371, 0.140	0.67
	Maximum distance	−0.050 ± 0.088	−0.348, 0.059	0.57
	Duration	−0.116 ± 0.119	−0.394, 0.005	0.33

Fig. 4. Fall migratory departure date of juvenile Wood Thrushes (*N* = 20) modeled with (A) fledge date (*P* < 0.001) and with three pre-migratory movement measures of (B) total number of different Motus towers at which juveniles were detected > 5 km from the natal site (*P* = 0.04), (C) maximum distance detected from the natal site (*P* = 0.62), and (D) duration of pre-migration dispersal period (*P* = 0.67). Top weighted models included fledge date with the total number of different Motus tower detections (Table 4; Appendix 6).

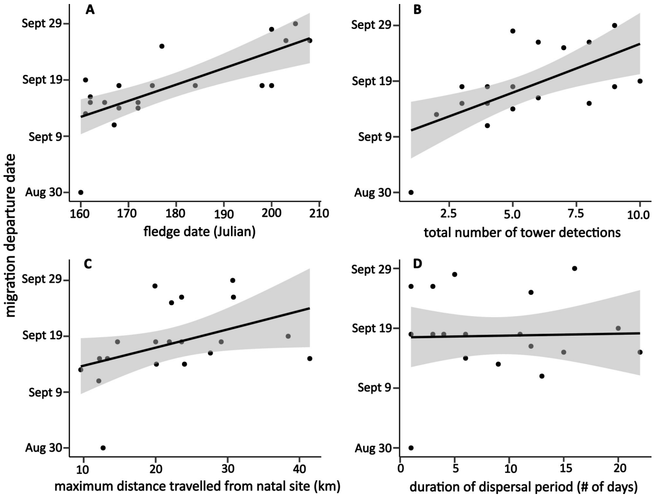
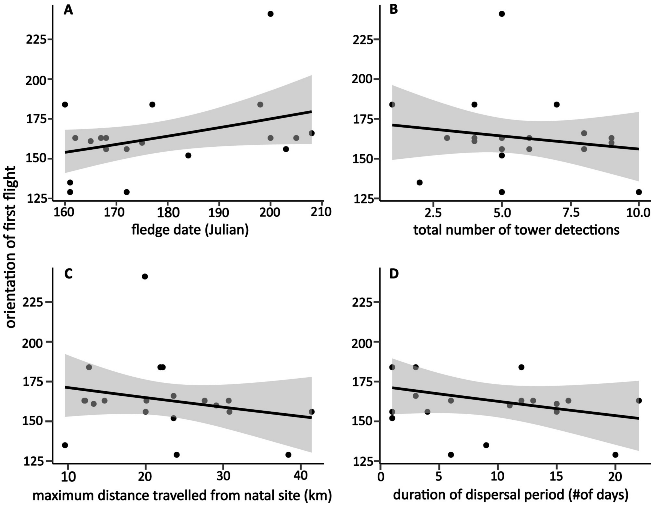


Fig. 5. First migratory flight orientation of juvenile Wood Thrushes (*N* = 20) modeled with (A) fledge date (*P* = 0.43) and with three pre-migratory movement measures of (B) total number of Motus towers at which juveniles were detected (*P* = 0.78), (C) maximum distance travelled from natal site (*P* = 0.71) and (D) duration of pre-migration dispersal period (*P* = 0.81). None of the models with predictors were > 2 AICc (Akaike information criterion corrected for small sample size) different from the null model (Table 4; Appendix 7).



Benefits of pre-migration movement

We found mixed evidence for different hypotheses for the benefits of PMM (Table 5). Contrary to predictions of the habitat optimization hypothesis, the extent of PMM (> 5 km from the natal site) was not similar for juvenile and adult Wood Thrushes (Table 5). Furthermore, juveniles from small forest fragments did not disperse at an earlier age or have more extensive PMM, which would be expected if small forest fragments are low-quality habitat. However, in a parallel study (Hayes et al. 2024), we found that small forest fragments were surprisingly good breeding sites because nesting success, fledgling survival, and juvenile survival were not lower than for large forest fragments. A more direct test

Fig. 6. Pace of the first migratory flight by juvenile Wood Thrushes (*N* = 20) modeled with (A) fledge date (*P* = 0.12) and with three pre-migratory movement measures of (B) total number of Motus towers at which juveniles were detected (*P* = 0.67), (C) maximum distance travelled from natal site (*P* = 0.57), and (D) duration of pre-migration dispersal period (*P* = 0.33). See Table 4; Appendix 8.

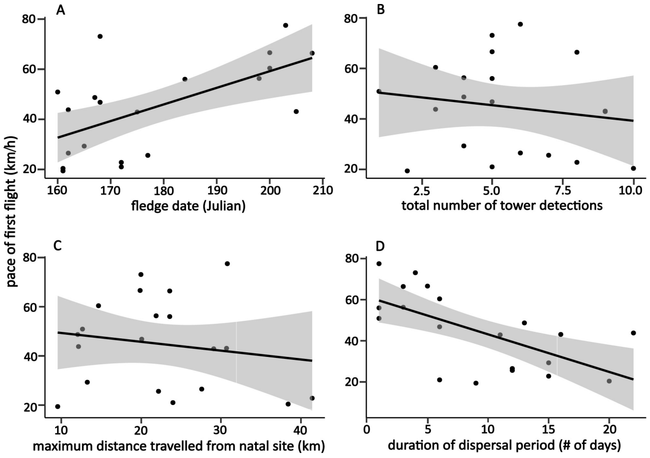


Fig. 7. Distance between first and last detections of first migratory flight for juvenile Wood Thrushes (*N* = 20) with predictors of (A) fledge date and pre-migratory movements, (B) total number of Motus towers at which juveniles were detected, (C) maximum distance travelled from the natal site, and (D) duration of the pre-migration dispersal period. None of the modeled parameters were good predictors of the distance travelled during the first flight and were all > 2 AICc (Akaike information criterion corrected for small sample size) different from the intercept model (Appendix 9).

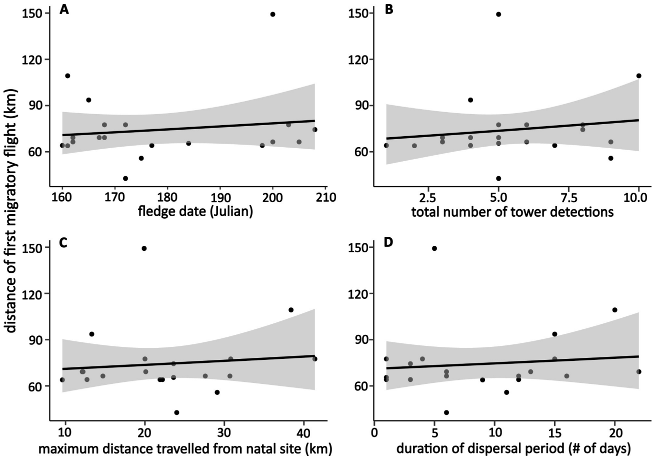


Table 5. Summary of outcomes for each prediction of the four hypotheses for the benefit of pre-migratory movements (PMM) in juvenile Wood Thrushes.

Hypothesis	Prediction	Support for hypothesis
Habitat optimization	Juvenile PMM = adult PMM	No
	Juvenile PMM greater in small than large natal fragments	No
Territory selection	Male PMM > female PMM	No
	Juvenile PMM > adult PMM	Yes
	Random orientation of PMM	Yes
	Spring return to last PMM location	No
Homing target	Juvenile PMM > adult PMM	Yes
	Random orientation of PMM	Yes
	High return rate to region	Yes
Flight performance	Nocturnal PMM	Yes
	Extent of PMM improves performance	No

of the habitat optimization hypothesis would require measurement of habitat quality and juvenile body condition at the dispersal sites at the time they were visited by juveniles, but this is not possible for Motus detections, which do not pinpoint bird locations. Vega Rivera et al. (1998) used manual and aerial telemetry to monitor dispersal of juvenile Wood Thrushes and suggested that post-fledging dispersal is driven by the location of fruiting shrubs and trees as a food source. Although fruit supply may explain short-distance movements (1–2 km), it does not explain why juveniles would need to travel > 5 km in search of fruit-rich habitat, which is abundant in forest edges, nor why adults did not do so.

We found mixed support for the territory selection hypothesis (Table 5). Juvenile PMM were far more extensive than those of adults and were random in orientation, but this is also predicted by the homing target hypothesis. Males had a longer period of PMM (~1 wk longer than females), but other measures of extent of PMM did not differ between the sexes. Males are expected to be under stronger selection than females to prospect for future territories so that they can compete for a good-quality breeding territory soon after spring arrival. In the Cyprus Wheatear (*Oenanthe cypriaca*), males visited prospective breeding territories during pre-migration dispersal movements and were detected the subsequent spring on breeding territories closer to their fall dispersal site rather than their natal areas, but this was not the case for females (Patchett et al. 2022). However, in our study, juvenile Wood Thrushes recruited to breeding territories that were closer to their natal site than their fall pre-migration dispersal site.

If long-distance PMM in juveniles functions to locate future high-quality territories, then these movements should be timed to coincide when cues of breeding habitat quality are optimal (Johnson 1989). Public information can provide cues about breeding habitat quality (access to mates, food abundance, territory quality, and shelter from predators; Pärt et al. 2011, Kivelã et al. 2014). Betts et al. (2008) found that juveniles returned to the treatment sites (poor quality habitats) where they used call playback of male Black-throated Blue Warbler (*Setophaga caerulescens*) song and begging calls of young during the post-breeding season the year prior. In our study, long-distance PMM for most juveniles occurred during the 2 wk prior to fall migration, in late August or early September, which may be too late in the season to use social cues to assess breeding habitat quality.

Our results provide strongest support for the homing target hypothesis because long-distance PMM were common in juveniles but not adults, were random in orientation, and a relatively large proportion of juveniles returned the subsequent spring. The majority of juveniles (81%, 25 of 31 individuals) detected in spring were within the study area. While the study area was chosen because of the high density of Motus towers, there were 34–41 other towers (depending on year) within 100 km of the study area that could have detected returning juveniles but did not (Fig. 1B). Technology to track all surviving juveniles to their breeding sites would be needed to test if extensive PMM in fall improves the likelihood of returning to breed near natal sites.

Mukhin et al. (2005) found that Eurasian Reed Warblers (*Acrocephalus scirpaceus*) made short, nocturnal flights for 1–2 wk prior to fall migration by leaving, and repeatedly returning to, their natal site. They suggested that these flights could function to establish a navigational home target for the subsequent spring, but also to develop a more accurate stellar compass for the first migration. If the pre-migratory dispersal observed in juvenile Wood Thrushes functions in part to prime the navigation system, or possibly to improve physiological flight ability, we expected that more extensive PMM would advance the fall departure date and improve performance on an individual's very first migration flight (which we measured as birds crossed the Lake Erie water barrier). Pre-migration dispersal flights were nocturnal, but we found no evidence that birds with more limited PMM were less able to orient southward or had shorter or slower flights. Furthermore, individuals that were detected by more Motus towers prior to migration departed later on migration, not earlier. It is unclear what frequency and duration of movements or what displacement from the natal site are needed to best establish the stellar compass in first-time migrants. Unlike Eurasian Reed Warbler juveniles that migrate only 3 wk after becoming independent from their parents, independent Wood Thrush juveniles typically have 2 mo before onset of migration (Hayes et al. 2024), and therefore, PMM may not be needed to prepare for this first flight.

CONCLUSION

We have shown that Motus tracking technology can be used to quantify the prevalence of long-distance PMM by juvenile songbirds and to test if these PMM are related to fledging conditions, timing of fall migration, and return the subsequent spring. Future studies could explore how and why PMM vary among populations or closely related species to further test hypotheses for the costs and benefits of these movements. For instance, PMM could be less extensive in highly fragmented landscapes if naïve birds face a higher risk of predation while gap-crossing. The benefits of PMM for territory acquisition are expected to be more important in species with strongly male-biased sex ratios or limited breeding habitat, where there is greater competition for breeding territories.

For Wood Thrushes and other forest songbirds, it is unclear how PMM far from the natal site inform conservation policy. First, we would need to know the consequences to individuals of having PMM that are constrained by costs of predation (e.g., gap crossing) or limited habitat availability. Aerial tracking could be used to locate and quantify habitat characteristics of sites used by juveniles during PMM to determine if these differ from, or are less common than, habitats occupied by breeding adults. We found that the extent of pre-migratory dispersal was not related to survival or return the subsequent spring. However, there may be sublethal effects on body condition during pre-migration, stopover duration during fall migration, and arrival at the wintering grounds, all of which are currently difficult to measure for juveniles.

Author Contributions:

B. J. M. Stutchbury conceived the idea, design, and experiment. S. M. Hayes and B. P. Boyd collected the data. S. M. Hayes analyzed the data. S. M. Hayes and B. J. M. Stutchbury wrote the paper.

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Data Availability:

Data and code for this study are available at https://doi.org/10.17605/OSF.IO/ENPX6.

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Appendix 1 – Classification of Pre-migratory versus Migratory Movement

To distinguish pre-migratory from migration departure flights, we first analyzed the time of day of departure for juveniles undergoing their very first long-distance migratory flight. The location of the study area is on the north shore of Lake Erie so when a bird flew in a southerly direction overnight across the lake (~50 km) we assumed that this must represent the onset of fall migration. There were 25 tagged juveniles that were last detected by a tower within the study area and subsequently detected on the same night at a tower on the south side of Lake Erie along the lakeshore, and within a reasonable time frame (birds flying at ~50 km/hr.). We determined the average departure date and time of day of these 25 unambiguous first migratory flights. We used R package *circular* (Agostinelli and Lund 2018) to analyze if the time of migratory flight departure was non-random, as would be expected for true migratory flights which typically occur just after sunset. As expected, the time of day of these migratory movements was non-random (Rayleigh test, $\overline{R}$= 0.713, $p < 0.001$; Supplementary Material Fig. 1A) and on average within 2 hr. and 14 mins. of local civil sunset (sunset on average departure date was 08:42 p.m.). And as expected, the directional bearing for each first migration flight measured from the individual's last Motus tower detection within the study area to the next Motus tower on the south side of Lake Erie was southerly which was the case ($\overline{R}$= 0.925, $p < 0.001$; Supplementary Material Fig. 1B). Using the range of departure dates and times of day of departure for these 25 individuals, we subsequently assigned migration departure dates for an additional 57 individuals whose departure dates and times of day fell within the range of the unambiguous departures (mean departure date Sept. 19, range: Aug. 25 to Oct. 15; mean departure time 20:48, range: 18:26 to 22:47;). We could not confirm a southerly bearing of departure flights for these 57 individuals because they were not detected by Motus later the same night.

Motus towers cannot pinpoint the location of a bird (or the distance from the bird to the tower) and so smaller distance movements (e.g., ~ 1 km) near the natal site cannot be distinguished from birds that have not dispersed from the natal fragment. The detection range of Motus towers is low (~ 500 m) for radio-tagged songbirds within forest habitat (Crewe et al. 2019) but is far greater (~10 km or more) for birds that are flying in the open (Taylor et al. 2017). The estimated antennae range varies widely among towers due to differences in tower height, antennae type and orientation, and these are shown on the Motus Wildlife Tracking System interactive mapping (https://motus.org/data/receiversMap). There were Motus towers located < 5 km from the natal site, with antennae that were oriented away from the natal fragment but detected juveniles during the pre-migration period. These were included in this analysis because it was assumed that the tagged bird had to move out of the natal forest and into an area that was within range of that tower. There were 4 instances where this occurred, and the birds were added to the analysis and described as birds making > 5 km dispersal movements (i.e., included in $n = 93$).

Appendix 2

Table S2. Top competing models (with ΔAICc <2) for age at first detection > 5 km away from the natal site for juvenile Wood Thrushes (*n* = 93). Generalized linear models included additive predictors of natal forest fragment size, fledge date, sex, and year. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with degrees of freedom (df), log likelihood (LL), and model averaged weight (w_i) given for each model.

Model	**df**	**LL**	**ΔAIC**	$\boldsymbol{w}_{\mathbf{i}}$
~ fledge date + year	5	-401.64	0.00*	0.51
~ fledge date + year + sex	6	-401.09	1.18	0.29
~ fledge date + year + fragment size	6	-401.44	1.89	0.20

*AICc = 813.97

Appendix 3

Table S3. Top competing models (with ΔAICc <2) for duration of pre-migratory period > 5 km from the natal forest fragment for juvenile Wood Thrushes (*n* = 93), as estimated from the first detection to the last pre-migratory detection. Generalized linear models included additive predictors of natal forest fragment size, fledge date, sex, and year. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with degrees of freedom (df), log likelihood (LL), and model averaged weight (w_i) given for each model.

Model	**df**	**LL**	**ΔAIC**	w_i
~ age at dispersal + fledge date	4	-296.64	0.00*	0.34
~ age at dispersal + fledge date + sex	5	-295.67	0.29	0.30
~ age at dispersal + fledge date + natal fragment size	5	-296.38	1.70	0.15

*AICc = 601.7

Appendix 4

Table S4. Top competing models (with ∆AICc <2) for total number of Motus tower detections during pre-migratory period away from the natal forest fragment for juvenile Wood Thrushes (*n* = 93). Generalized linear models included additive predictors of natal forest fragment size, fledge date, sex, and year. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with degrees of freedom (df), log likelihood (LL), and model averaged weight (w_i) given for each model.

Model	**df**	**LL**	**∆AIC**	w_i
~ age at dispersal + year	4	-189.98	0.00*	0.26
~ age at dispersal + year +natal fragment size	5	-189.23	1.13	0.18
~ age at dispersal + fragment size + sex	5	-189.85	1.99	0.09

*AICc = 388.41

Appendix 5

Table S5. Top competing models (with ΔAICc <2) for farthest distance travelled during pre-migratory period away from the natal forest fragment for juvenile Wood Thrushes (*n* = 93). Generalized linear models included additive predictors of natal forest fragment size, fledge date, sex, and year. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with degrees of freedom (df), log likelihood (LL), and model averaged weight (w_i) given for each model.

Model	**df**	**LL**	**ΔAIC**	w_i
~ year + fragment size	5	-339.38	0.00*	0.33
~ year	4	-341.13	0.47	0.26
~ year + fragment size + age at dispersal	6	-339.39	1.51	0.16
~ year + age at dispersal	5	-340.73	1.89	0.13
~ year + fragment size + sex	6	-339.61	1.95	0.12

*AICc = 690.26

Appendix 6

Table S6. Top competing models (with ∆AICc <2) for fall migration departure date of juvenile Wood Thrushes (*n* = 20). Generalized linear models included additive predictors of three pre-migratory movements; duration of pre-migration dispersal period (Dur), maximum distance travelled from natal site (MaxDist), and total number of unique Motus tower detections (#Towers). Fledge date (FD) and sex were also added to the models. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with degrees of freedom (df), log likelihood (LL), and model averaged weight (w_i) given for each model.

Model	**df**	**LL**	**∆AIC**	w_i
~ FD + #Towers	4	-53.88	0.00*	0.47
~ FD + #Towers + MaxDist	5	-52.54	0.93	0.29
~ FD + #Towers + Dur	5	-52.73	1.32	0.24

*AICc = 118.4

Appendix 7

Table S7. Top competing models (with ΔAICc<2) for first flight orientation models for juvenile Wood Thrushes (*n* = 20). Generalized linear models included additive predictors of three pre-migratory movements; duration of pre-migratory dispersal period (Dur), maximum distance travelled from natal site (MaxDist), and total number of unique Motus tower detections (#Towers). Fledge date (FD) and sex were also added to the models. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with degrees of freedom (df), log likelihood (LL), and model averaged weight (w_i) given for each model.

Model	**df**	**LL**	**ΔAIC**	w_i
~ FD	3	-89.01	0.00*	0.26
~ 1	2	-90.43	0.04	0.25
~ FD + MaxDist	4	-88.03	1.20	0.14
~ FD + #Towers	4	-88.12	1.39	0.13
~ Dur	3	-89.82	1.62	0.12
~ MaxDist	3	-89.99	1.96	0.10

*AICc = 185.5

Appendix 8

Table S8. Top competing models (with ΔAICc<2) for first flight pace models for juvenile Wood Thrushes (*n* = 20). Generalized linear mixed effect models included additive predictors of three pre-migratory movements; duration of pre-migratory dispersal period (Dur), maximum distance travelled from natal site (MaxDist), and total number of unique Motus tower detections (#Towers). Fledge date (FD) and sex were also added to the models with year included as a random effect. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with degrees of freedom (df), log likelihood (LL), and model averaged weight (w_i) given for each model.

Model	**df**	**LL**	**ΔAIC**	w_i
~ Dur + FD	4	-79.91	0.00*	0.22
~ Dur + FD + MaxDist	5	-78.27	0.35	0.18
~ Dur	3	-81.86	0.75	0.15
~ FD + MaxDist	4	-80.31	0.81	0.14
~ FD + #Towers	4	-80.38	0.94	0.14
~ FD	3	-82.39	1.80	0.09
~ Dur + FD +#Towers	5	-79.03	1.87	0.08

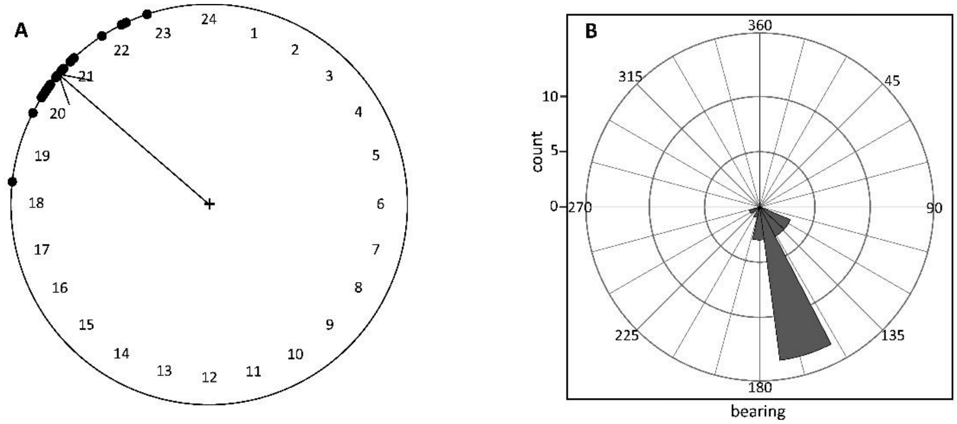
*AICc = 170.5

Appendix 9

Table S9. First flight distance travelled models with <2 ΔAICc for juvenile Wood Thrushes (*n* = 20). General linear models included additive predictors of three pre-migratory movements; duration of pre-migratory dispersal period (Dur), maximum distance travelled from natal site (MaxDist), and total number of unique Motus tower detections (#Towers). Fledge date (FD) and sex were also added to the models. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with degrees of freedom (df), log likelihood (LL), and model weight (w_i) given for each model. Models were not averaged as intercept model only competing model with <2 ΔAICc.

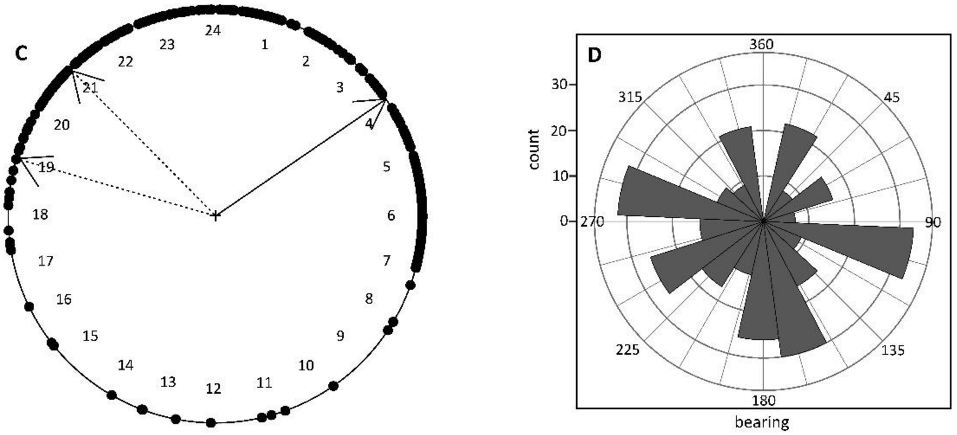
Model	**df**	**LL**	**ΔAIC**	w_i
~ 1	2	-86.93	0.00*	0.32
~ FD	3	-86.64	2.21	0.11
~ #Towers	3	-86.66	2.25	0.10
~ MaxDist	3	-86.79	2.50	0.09
~ Dur	3	-86.79	2.51	0.09

*AICc = 178.6



mean departure time 20:42
range = 18:26 to 22:47, $\bar{R}$= 0.713, $p < 0.001$

mean =171°, $\bar{R}$= 0.925, $p < 0.001$



mean local pre-migratory flight times = 03:42, $\bar{R}$= 0.383, $p < 0.001$

mean =171°, $\bar{R}$= 0.925, $p < 0.001$

Fig. S1. Circular graph depicting time of day (0 to 24 hr. clock) and directional movement for juvenile Wood Thrushes based on Motus tower detections to classify movements as pre-migratory or migratory. Unambiguous first migratory flight (*n* = 25 individuals) classed by: **(A)** Time of day for first flight; and **(B)** Direction of first fall migration flight. Pre-migratory flights (*n* = 93 individuals) classed by: **(C)** Time of day of movements; and **(D)** Direction of movements. Solid arrow indicates the average departure/movement time and dashed arrow indicating average local sunset time (range for sunset given by two broken arrows in Fig. C from July 3 – 9:03 pm to Oct. 1 – 7:04).

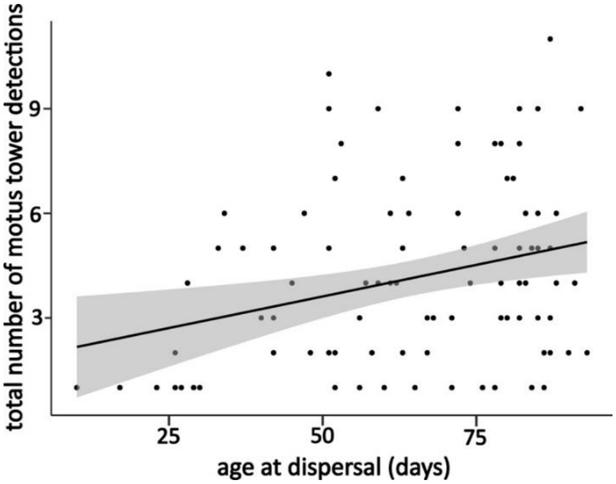


Fig. S2. Total number of unique Motus tower detections for juvenile Wood Thrushes during pre-migratory movements (*n* = 93) with age at first detection > 5 km from the natal site (0.148±0.064, *p*<0.001), and grey shading indicating 95% confidence interval around trend line (Table 2, Supplementary Material Table S4).

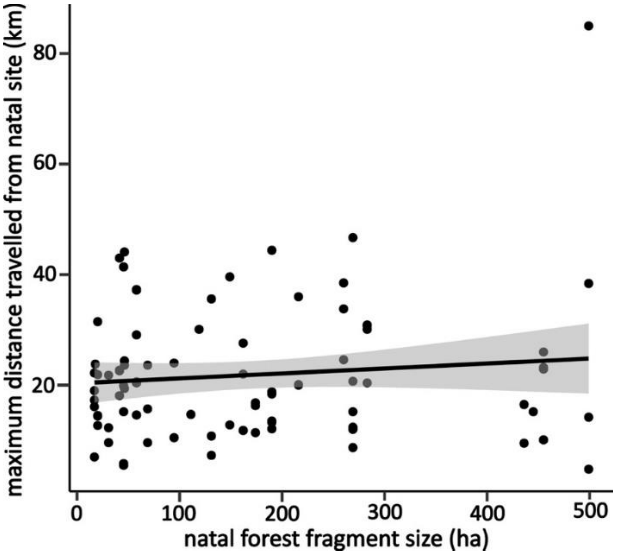


Fig. S3. Maximum distance travelled from natal site as detected by the Motus tower network during pre-migratory landscape movements for juvenile Wood Thrushes (*n* =93) with natal forest fragment size (0.050±0.057, $p = 0.38$). Grey shading indicating 95% confidence interval around trend line. (Table 2, Supplementary Material Table S5).

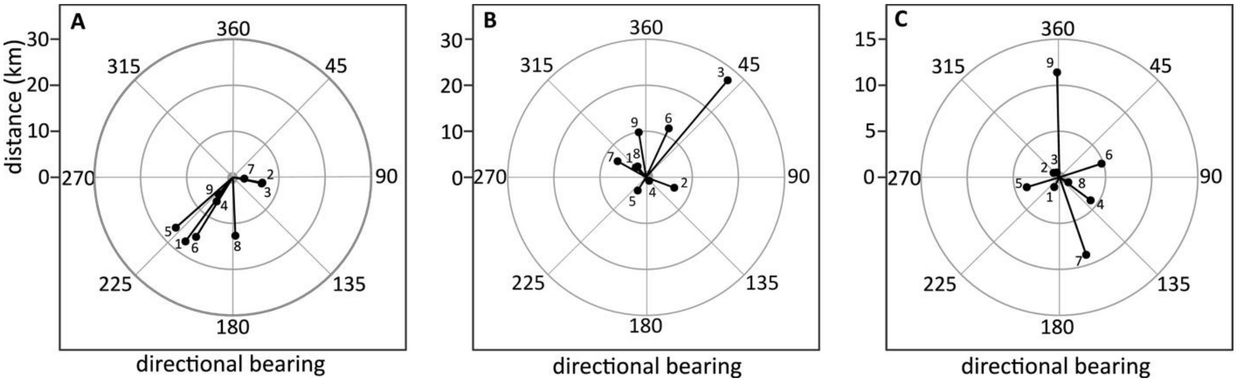


Fig. S4. Direction and distance of Motus detections (A, B) and first breeding site (C) for juvenile Wood Thrushes with known breeding sites the next year in the study area (*n* = 9, labelled 1-9). For each bird, the center point is its natal site and distance is represented by the grey circular lines. Circular plots show the location (relative to each bird's natal site) of **(A)** last dispersal detection prior to onset of fall migration, **(B)** last spring Motus tower detection, and **(C)** location of first breeding site (Table 3).