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Environmental conditions and individual characteristics influence movement patterns of juvenile *Passerculus sandwichensis* (Savannah sparrow) throughout the post-fledging period

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ABSTRACT

Movements in the post-fledging period, an important first stage of natal dispersal that occurs after juveniles fledge from the nest but before they depart for fall migration, have important implications for survival. However, relatively little is known about movements during this vulnerable period. Here, we used daily radio telemetry data from 137 juvenile *Passerculus sandwichensis* (Savannah Sparrow) between 2022 and 2024 and hierarchical generalized additive models to examine the relationship between movement and age across a 90-day period. We evaluated how movement—distance from the nest and between consecutive daily locations—was influenced by age post-fledging, sex, brood number, year, age at fledging, local nest density, nestling mass, and weather variables. Both the distance of fledglings from their natal nest and the distance moved between days increased with age post-fledging, most steeply when fledglings became independent, then remained steady for the remainder of the post-fledging period. Movement varied among individuals: some fledglings remained near the nest for extended periods, and others traveled long distances soon after fledging. Offspring from second broods traveled greater distances than those from first broods. Nest density also influenced movement, with fledglings from high-density areas traveling farther from their nests but, on average, less far between days. Movement patterns were also influenced by year and sex, and weakly influenced by mass and daily precipitation. Our results demonstrate how movement patterns can change between the early post-fledging period and the relatively understudied late post-fledging period.

Keywords: dispersal, juveniles, migratory bird, movement, *Passerculus sandwichensis*, post-fledging, radio telemetry, Savannah Sparrow

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LAY SUMMARY

- Over 3 years, we radio-tracked 137 juvenile *Passerculus sandwichensis* (Savannah Sparrow) during the first 3 months after fledging to examine factors that influenced distance traveled from their natal nest and distance between daily locations.
- Juveniles dispersed farther from their nests after the age of independence from parental care, then remained at stable distances until migration.
- Movement patterns varied among individuals: some fledglings remained near the nest for the entire post-fledging period, while others traveled much farther.
- Second-brood juveniles traveled farther from the nest and, when older, farther between days than first-brood juveniles. Fledglings from areas of high nest density traveled farther from their nests overall, but smaller distances between days.
- Distance from the nest was also influenced by year and sex, and daily distance traveled was weakly influenced by mass and precipitation.
- Our results detail how fledgling movement patterns can differ between the early and late stages of the post-fledging period.

Las condiciones ambientales y las características individuales influyen en los patrones de movimiento de juveniles de *Passerculus sandwichensis* durante el período post-emplumamiento

RESUMEN

Los movimientos durante el período post-emplumamiento, una etapa inicial clave de la dispersión natal que ocurre después de que los juveniles abandonan el nido, pero antes de migrar en otoño, tienen importantes implicancias para la supervivencia. Sin embargo, se sabe relativamente

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poco sobre los movimientos durante este período vulnerable. En este estudio, utilizamos datos diarios de radio telemetría de 137 juveniles de *Passerculus sandwichensis* entre 2022 y 2024, y modelos aditivos generalizados jerárquicos para examinar la relación entre movimiento y edad a lo largo de un período de 90 días. Evaluamos cómo el movimiento—distancia desde el nido y entre ubicaciones diarias consecutivas—estaba influenciado por la edad post-emplumamiento, el sexo, el número de polluelos, el año, la edad al emplumar, la densidad local de nidos, la masa del polluelo y variables climáticas. Tanto la distancia de los volantones respecto a su nido natal como la distancia recorrida entre días aumentaron con la edad post-emplumamiento, de forma más pronunciada cuando los volantones se independizaron, y luego se mantuvieron estables durante el resto del período. El movimiento varió entre individuos: algunos volantones permanecieron cerca del nido durante períodos prolongados y otros recorrieron largas distancias poco después de emplumar. Los juveniles provenientes de segundas nidadas recorrieron distancias mayores que aquellos de primeras nidadas. La densidad de nidos también influyó en el movimiento: los volantones de áreas con alta densidad se alejaron más de sus nidos, pero en promedio recorrieron distancias diarias menores. Los patrones de movimiento también estuvieron influenciados por el año y el sexo, y débilmente por la masa corporal y la precipitación diaria. Nuestros resultados demuestran cómo los patrones de movimiento pueden cambiar entre el período inicial de post-emplumamiento y el relativamente poco estudiado período tardío de post-emplumamiento.

Palabras clave: ave migratoria, dispersión, juveniles, movimiento, *Passerculus sandwichensis*, post-emplumamiento, radio telemetría

INTRODUCTION

Natal dispersal, the movement of an animal from its natal site to its first breeding site, allows individuals to locate optimal habitat and breeding territories, reduce risk of inbreeding, and avoid competition for mates and other resources (Greenwood and Harvey 1982, Dobson and Jones 1985, Johnson and Gaines 1990, Sutherland et al. 2000, Clobert et al. 2001, Olsson and Shine 2003, Wey et al. 2015). The initial phase of natal dispersal, in which juveniles transition from parental care to independence but before they settle at a breeding site, has received little attention. Juvenile movement patterns may affect survival (Green and Cockburn 2001, Vitz and Rodewald 2011, Cox et al. 2014), the ability to find and occupy suitable habitat and breeding territories (Nocera et al. 2005, Matthysen et al. 2010, Patchett et al. 2022), and, in birds, to encounter vocal tutors for learning song (Mennill et al. 2018). Movement patterns in this period, when inexperienced juveniles are particularly vulnerable to predation and starvation, can have strong effects on first-year survival and future fitness (Mitchell et al. 2010, Styles et al. 2021).

In migratory birds, juveniles begin to move away from the natal site during the post-fledging period, the time between fledging from the nest and departure for fall migration. This period can be considered the first stage of natal dispersal, punctuated by migration and the overwintering period, before individuals return to the breeding grounds and select their first nesting sites (King and Belthoff 2001, Barbraud et al. 2003, Matthysen et al. 2010). A variety of pressures influence the movement patterns of juvenile migratory birds in the post-fledging period. Juveniles must locate foraging areas that balance predator avoidance (Sullivan 1989, Anders et al. 1997) against the need to obtain food resources for metabolic maintenance, molt, and migratory fattening (Morton et al. 1991, Mitchell et al. 2010). At the same time, juveniles may be prospecting for future breeding territories or mates (Patchett et al. 2022), exploring the landscape to familiarize themselves with local landmarks to assist with upcoming migration (Morton et al. 1991), engaging in social behavior like flocking (Vega Rivera et al. 1998), encountering vocal tutors that will play a vital role in determining the songs they sing as adults (Mennill et al. 2018), or making directed pre-migratory movements (e.g., beginning to move southward for fall migration; Mitchell et al. 2010). However, due to the cryptic coloration and behavior of fledglings, movements and spatial use patterns during the post-fledging period are often difficult to monitor and remain unknown for many species (Mitchell et al. 2010, Ausprey and Rodewald 2013).

Across species, age is an important driver of post-fledging movement patterns and, in particular, the distances moved by fledglings away from their natal nests and between daily locations (Anders et al. 1998, Kershner et al. 2004, White and Faaborg 2008, Small et al. 2015, Jenkins et al. 2016, Jones et al. 2017). When fledglings first leave the nest, they have limited mobility and may be unable to fly (Sullivan 1989, Berkeley et al. 2007, Martin et al. 2018, Jones and Ward 2020). As fledglings develop and their mobility increases, their daily movement rate and distance from the nest increase steadily (Fisher and Davis 2011, Vormwald et al. 2011, Small et al. 2015, Jenkins et al. 2016, Jones et al. 2017, Fiss et al. 2020). After reaching independence from parental care, fledglings may disperse away from their natal territories and settle into a post-fledging home range, where they remain for the overwintering period (if resident) or until departing for fall migration (if migratory; Vega Rivera et al. 1998, White and Faaborg 2008, Styles et al. 2021). The actual range of post-fledging dispersal distances varies widely depending on the species and its life history traits (Morton et al. 1991, Anders et al. 1998, Fiss et al. 2020). In the limited studies that have tracked songbirds during this period, it appears that for the first 1–4 weeks post-fledging, distance from the nest increases linearly (Yackel Adams et al. 2001, Jenkins et al. 2016, Jones et al. 2017, Raybuck et al. 2020). Past the age of independence (2–4 weeks post-fledging in most songbirds), distance from the nest may stop increasing as fledglings settle into new home ranges, and the variation in distance across individuals is larger (White and Faaborg 2008, Styles et al. 2021). Similarly, distance traveled between daily locations increases with age for the first 1–3 weeks in most songbirds as fledglings disperse from their natal territories (Kershner et al. 2004, Fisher and Davis 2011, Jenkins et al. 2016, Raybuck et al. 2020), then levels out or may even decrease after fledglings form new post-fledging home ranges (Styles et al. 2021). However, the relatively short duration of most studies of post-fledging movement in songbirds (4 weeks after fledging or less, often due to technological limitations like radio transmitter battery life) means that any patterns occurring later in the post-fledging period, and any differences between the dependent and independent periods, remain understudied.

In addition to age, other intrinsic characteristics may influence post-fledging movements. First, in species that can fledge young from multiple broods in a single breeding season, breeding adults may cease parental care or force first-brood fledglings out of the territory to begin raising another brood. Thus, fledglings from earlier broods may leave the natal territory sooner, relative to their hatching time, and go farther than fledglings from subsequent broods. Seasonal changes, including variation in food availability or predation risk, can also influence movement rates because young and/or their parents must search farther when resources are limited (Jenkins et al. 2016). In both cases, movement patterns would be predicted to differ between earlier-fledging first brood and later-fledging second brood young. Second, body mass or condition may influence movement rates because larger fledglings in better condition have more energetic reserves and a greater ability to meet the physiological requirements of movement and thus travel farther (Nilsson and Smith 1985, Barbraud et al. 2003, Grüebler and Naef-Daenzer 2008; but see Jenkins et al. 2016). Third, individuals that are older and more developed at the time of fledging may be able to travel farther from the nest more quickly. Wing development, in particular, contributes to improved flight ability among fledglings (Jones et al. 2017), and across species, those with longer nestling periods have greater flight ability at fledging (Martin et al. 2018, Jones and Ward 2020). Finally, sex may influence movement patterns. Female birds often have longer natal dispersal distances than males (Greenwood and Harvey 1982), and female fledglings may begin to move farther from the nest than males after independence from parental care (Jenkins et al. 2017). However, because of the difficulty of sexing fledglings of most species by visual or morphometric methods, it is unknown whether this pattern generally holds for the post-fledging period.

Environmental conditions are also likely to influence the movement patterns of fledglings. Local weather conditions may influence movement either directly, with inclement weather limiting the activity of birds, or indirectly, through effects on food availability and body condition of fledglings. Additionally, fledgling movement may be driven by the search for optimal habitat; fledglings often prefer denser vegetation and understory that provides more protection from predators (Jenkins et al. 2016, Jones et al. 2017). Population density may also influence fledgling movement patterns: fledglings from areas of high density may travel farther from their natal areas to reduce intraspecific competition, or, alternatively, high density could indicate high-quality habitat, such that fledglings would remain in high-density areas (Ausprey and Rodewald 2013). Moreover, given that exposure to adult songs during the post-natal period can be important for vocal learning by fledglings (Marler 1970, Wheelwright et al. 2008, Mennill et al. 2018), the location and behavior of adult vocal tutors may influence fledgling movement patterns if young birds are attracted to areas with a high density of adults to diversify the acoustic signals they experience.

Here, we use daily radio telemetry data collected over three years to quantify the behavior of *Passerculus sandwichensis* (Savannah Sparrow) fledglings to examine post-fledging movement patterns across a 90-day period. We used 2 metrics of movement: (1) distance from the natal nest and (2) distance between consecutive daily locations, and we evaluated how movement was influenced by factors including age post-fledging, sex, brood number, year, age at fledging, local nest density, mass, and daily weather. We used generalized additive models (GAMs) to flexibly model the nonlinear relationship between fledgling age and distance from the nest or distance between daily locations. This is one of the few studies to investigate factors influencing post-fledging movement patterns late into the post-fledging period and to investigate the effects of brood number, localized population density, and daily weather on movement.

METHODS

Study System and Field Methods

Passerculus sandwichensis is a migratory songbird that breeds in grasslands and open habitats across North America and winters in the southern United States, Mexico, and parts of Central America (Wheelwright and Rising 2020). Our study population breeds on Kent Island, NB, Canada (44.582°N, 66.755°W), an approximately 80-ha island in the Bay of Fundy. The current study, using data over 3 seasons (2022–2024), adds to a long-term study that began in 1987 on the breeding biology of this population (Woodworth et al. 2017).

Each year, between late May and late July, we observed birds within a ~10-ha study area in the center of the island. We mapped territories, searched for and monitored all nests, color-banded all adults and nestlings, and resighted banded individuals. Nests were primarily found during egg laying or incubation and were monitored every other day to determine the number of nestlings and fledglings, hatching and fledging dates, and nest fates. In this population, females usually lay 4–5 eggs per clutch and may successfully fledge up to two broods per year (Woodworth et al. 2017). Females may begin laying a second clutch while still caring for first-brood fledglings. Here, we refer to any nest attempts prior to fledging one brood, including replacement clutches, as “first broods” and any nest attempts after fledging one brood as “second broods.” About one-third of females each year attempt a second brood (mean: 29%, range: 14–58%; Woodworth et al. 2017). Females incubate eggs for 12 days, on average, and young fledge from the nest after 8–12 days. The parents typically divide the brood after fledging and each care for 1–3 young (Wheelwright et al. 2003). Parental care generally continues until 23 days post-hatching (but up to 35 days), about 13 days post-fledging, when fledglings rapidly develop foraging skills (Wheelwright and Templeton 2003, Wheelwright et al. 2003). Fledglings typically remain on Kent Island until late September to early October, when they begin migration (Mitchell et al. 2012, Woodworth et al. 2016).

We banded and weighed all nestlings on the seventh day after hatching, approximately 2–4 days before the typical date of fledging, to prevent premature fledging. At this time, we also collected a blood sample via brachial venipuncture for genetic sex determination. Blood was collected with microhematocrit capillary tubes and stored on filter paper.

Nest Density Estimates

To estimate local density around a nest, we calculated the number of nests within a 50-m radius of the focal nest that were simultaneously active (following Woodworth et al. 2017). For focal nests and neighboring nests that fledged young, the active period was defined as the period from the laying of the first egg to 14-day post-fledging, approximately the age at which fledglings become independent from parental care (Wheelwright and Templeton 2003). Because females begin the 12-day incubation period after laying their penultimate egg, we calculated the laying date of the first egg as the hatch day minus 12 days minus one less than the clutch size (Burant et al. 2022). For neighboring nests that did not fledge young, due to abandonment or predation, the active period was defined as the period from the laying of the first egg to the date on which the nest failed. For these nests, we estimated the hatch date as the date the nest was found plus the mean difference between found and hatch dates for all nests in the same year, then used this estimated hatch date to calculate the first egg laying date as described above.

Radio Telemetry

From 2022 to 2024, we attached radio transmitters (Lotek NTQB2-5-1 MOTUS Tag, frequency 166.38 MHz, 7-s burst rate, battery life ~111 days) to 1 or 2 nestlings per nest on the day they were measured and banded. We attached tags using a leg loop harness (Rappole and Tipton 1991) made with elastic thread to allow for future growth of the individual. Nestlings were selected for transmitter attachment at random, after excluding individuals that weighed <14 g so that the tag and harness mass (0.51 g total; 0.43 g tag + 0.08 g harness) would be <3.6% of the nestling's body mass. To reduce the probability of entanglement in vegetation, tag antennas were 14–15 cm long, shorter than the standard 17 cm. Nestlings with transmitters were marked with a unique combination of one USGS/CWS metal band and three plastic color bands for field identification, while nestlings without transmitters received one USGS/CWS metal band and one plastic color band on the opposite leg. One hundred fourteen birds were tagged as nestlings: 38 nestlings in 2022, 26 nestlings in 2023, and 50 nestlings in 2024. In 2022 and 2023, we also captured 23 known-age fledglings, which had been banded as nestlings, in mist nests and attached radio transmitters (average age at capture: 26-day post-fledging, range: 4–71 days): 8 birds in 2022 and 15 birds in 2023. As the expected date of fledging approached, around 9 days post-hatch, we confirmed each day whether the nestlings had left the nest either visually or via radio telemetry. The first day out of the nest was considered the fledge day and the beginning of the post-fledging period, and was used to calculate age at fledging (in days) of each individual.

We obtained locations of fledglings once per day, with the exception of days with inclement weather (e.g., heavy rainfall or high wind) or on rare occasions when we were off-island. We used a 2- or 3-element Yagi antenna and a Lotek SRX-600 or SRX-800 receiver to find each fledgling, then visually confirmed the location of the bird. For each tracking occasion, we recorded a GPS point where the bird was first seen (because the bird was often not visually located until it flushed) and the fate of the bird (alive or dead). Tracking continued until (1) the transmitter battery died ($n = 1$); (2) the tag fell off ($n = 19$); (3) the bird died, determined either by finding the dead fledgling or a tag with evidence of predation (bones and/or plucked feathers around tag) or by assuming the fledgling was dead if the signal disappeared within the first week post-fledging, too early for the bird to have dispersed out of tracking range ($n = 72$); or (4) the end of the study period (September 10 in 2022, September 7 in 2023, September 5 in 2024, $n = 45$).

Genetic Sex Determination

We used molecular techniques for sex determination of nestlings (Supplementary Material Appendix 1 for a more detailed description of molecular methods). We extracted DNA from dried blood on filter paper using a Qiagen QIAmp DNA Mini Kit (Qiagen, Hilden, Germany). We then conducted polymerase chain reaction using the CHD1 primers following Çakmak et al. (2017) to amplify portions of the CHD gene that differ in length on the Z and W sex chromosomes. To visualize the results, we photographed gels under UV light, and sex was manually scored by the presence of 2 bands (female, ZW) or 1 band (male, ZZ).

Weather Data

We obtained daily mean temperature (°C) and daily precipitation (mm) data for 2022–2024 from the Environment and Climate Change Canada weather station on Grand Manan Island ("Grand Manan SAR CS," 44.712°N, 66.802°W; Environment and Climate Change Canada 2024), ~15 km away from Kent Island.

Statistical Analysis

All analyses were conducted using the R statistical environment (v. 4.4.0; R Core Team 2024). For each location point, we calculated the distance of the fledgling from the natal nest (hereafter "distance from nest") and the distance from the location on the previous day ("daily distance") using the *st_distance* function from the *sf* package (v. 1.0.16; Pebesma and Bivand 2023). On occasions when a fledgling did not have a location point on the previous day, we did not calculate a daily distance. As a result, our dataset for daily distance had fewer observations ($n = 1{,}202$) than our dataset for distance from nest ($n = 1{,}903$).

We used hierarchical generalized additive models to model the nonlinear relationship between the age of fledglings and (1) their distances from their natal nest each day or (2) their distance from their location the previous day, while also considering effects of additional predictors. Each hierarchical generalized additive model specified a gamma distribution and log link and was fit using the *gam* function from the *mgcv* package (v. 1.9.1, Wood 2011). Model fit was assessed using diagnostics provided by functions in the packages DHARMa (v. 0.4.6, Hartig 2022) and mgcViz (v. 0.1.11, Fasiolo et al. 2020) and the function *gam.check* from the *mgcv* package. Each model had a global smooth term for the relationship between distance from nest and age common to all individuals and an "individual-level" smooth term, akin to a random effect, to allow for variation in the shape of the distance-age curve by individual but shrunk toward the global average smooth (Pedersen et al. 2019, see "GS" model). The "wiggliness," or smoothing parameter, of the individual-level smooth was not allowed to vary between individuals (Pedersen et al. 2019).

Models for distance from nest included smooth terms for age post-fledging and fixed effects of sex, brood number (categorical: first or second brood), year (categorical: 2022, 2023, or 2024), nestling mass, age at fledging, and local nest density around the natal nest. Models for daily distance included the same terms, except for age at fledging, and also included total daily precipitation and mean daily temperature. We assessed collinearity between predictors by inspecting correlation matrix plots of each continuous predictor versus all others and by fitting the model as a generalized linear mixed model with a Gamma distribution and log link and calculating variance inflation factors using the R package *misty* (v. 0.6.2, Yanagida 2024). Variance inflation factors were <1.3 for all predictors in both the distance from nest and daily distance models. All numeric predictors except age post-fledging were grand mean-centered so that each model intercept represents the distance from the nest at the mean of these variables. Age post-fledging was not centered, so that the model intercept would be at zero days post-fledging, which was the starting point for all individuals. We used deviation coding for the parametric effects of categorical variables.

For both distance from the nest and daily distance, we first fit a full model that included global and individual-level smoothers for age post-fledging; a main effect for each fixed effect predictor, implemented as linear effects for categorical predictors and as smoothers for continuous predictors; and all 2-way interactions of age post-fledging with other fixed effect predictor variables (for model formulas, see Supplementary Material Appendix 2; for model results, see Supplementary Material Tables S1 and S3). We used factor-smooth interactions for interactions involving categorical predictors and 2D tensor product smooths for interactions involving continuous predictors. We used a sum-to-zero basis for factor-smooth interactions (basis "sz" in mgcv) and tensor product interactions (function *ti* in *mgcv*). The full model was fit using the double-penalty approach to remove smooth components from the model that were not supported (Marra and Wood 2011). When using the double-penalty approach, smooth terms that are not supported by the model have their effective degrees of freedom (EDF) shrunken to near 0 (Marra and Wood 2011). The EDF indicates the complexity or "wiggliness" of a smooth term, with lower values indicating a less wiggly term (Pedersen et al. 2019).

To reduce model complexity and improve interpretability—because linear terms are more straightforward to interpret than smooth terms—we then fit a reduced model in which smooth interactions with EDF near 0 in the full model were removed. The reduced model for distance from nest omitted the interactions of age post-fledging with sex, brood number, mass, age at fledging, and nest density (for model formula, Supplementary Material Appendix 2; for model results, Supplementary Material Table S2). The reduced model for daily distance omitted the interactions of age post-fledging with year, sex, temperature, and precipitation (for model formula, see Supplementary Material Appendix 2; for model results, see Supplementary Material Table S4). In a subsequent reduction, we replaced the smooth with a linear effect for each continuous predictor that had an EDF near 0 in the reduced models. Our final model for distance from nest included global and individual-level smooths for age post-fledging; parametric effects for brood number, year, sex, mass, age at fledging, and nest density; and a factor-smooth interaction of year and age post-fledging (formula in Supplementary Material Appendix 2). Our final model for daily distance included global and individual-level smooths for age post-fledging; parametric effects for brood number, year, sex, temperature, and precipitation; a factor-smooth interaction of brood number and age post-fledging; and smooth terms for weight and nest density and their interactions with age (formula in Supplementary Material Appendix 2).

RESULTS

We obtained 810 locations for 46 individuals in 2022, 448 locations for 41 individuals in 2023, and 645 locations for 50 individuals in 2024 (n = 1,903 total locations, 137 total individuals; Supplementary Material Figure S1). The median number of locations per individual was 13.5 in 2022 (range: 2–61 locations), 7 in 2023 (range: 2–37 locations), and 8.5 in 2024 (range: 2–45 locations). The median age at which tracking ceased, for individuals tagged as nestlings, was 16.5 days in 2022 (range: 1–87 days), 6 days in 2023 (range: 1–50 days), and 10.5 days in 2024 (range: 1–76 days). The ratio of males to females tracked was close to 1 (66 females, 71 males). Local nest density around the natal nest of fledglings ranged from 0 to 12 birds ha^{-1} (mean ± SD: 5.2 ± 3.0).

Fledglings left the nest between 8 and 12 days after hatching (mean ± SE: 10.2 ± 0.1 days, n = 137). For the first 0–3 days after fledging, fledglings were unable to fly and, when approached by observers, they froze and remained concealed by vegetation or sometimes ran away. Beginning around day 3–4 post-fledging, fledglings made short flights of 5–15 m when flushed by observers. By day 5–7 post-fledging, fledglings were capable of longer, sustained flights of 15–20 m or more. Between days 13 and 15, when fledglings typically become independent from parental care (Wheelwright et al. 2003), many left their natal territories. Beginning in early August, most of the surviving fledglings joined small flocks of around 10–25 juveniles that roamed around the study area and other open areas of the island.

The distance of fledglings from their natal nest increased with age, most steeply around days 15–25 post-fledging—shortly after fledglings become independent (Wheelwright et al. 2003)—then generally remained steady for the rest of the post-fledging period (global smoother: EDF = 6.3, $P < 0.001$; Figure 1A, Table 1). The shape of the relationship between distance from nest and age post-fledging varied widely among individuals: some fledglings remained near their natal territories for the entire study period while others traveled long distances soon after fledging (individual-level smoother: EDF = 231.6, $P < 0.001$; Figures 1A and 2, Table 1; Supplementary Material Figure S2). Brood number also influenced movement from the nest; fledglings from second broods traveled, on average, farther from the nest across all ages than fledglings from first broods ($P = 0.018$; Figure 3A, Table 1). The shape of the relationship between distance from nest and age post-fledging differed between years (year * age smoother: EDF = 2.6, $P < 0.001$; Figure 3B, Table 1); fledglings traveled a similar distance from the nest between years until 15–20 days post-fledging, but after approximately day 20, fledglings in 2023 traveled farther from the nest than fledglings in 2022 or 2024. The overall mean distance from the nest did not differ significantly between years (parametric year effect: $P = 0.283$). In 2023, fledgling survival was lower, and thus, sample sizes of older fledglings were smaller (Figure S4), which substantially increased error in model estimates in the late post-fledging period (Figure 3B). Male fledglings also travelled farther from the nest across all ages than did females ($P = 0.032$, Figure 3C, Table 1). Local nest density had a nonlinear effect on distance from the nest; fledglings from areas with low and middling densities did not differ in their mean distance, but birds from areas of higher densities moved farther from the nest on average (EDF = 1.6, $P < 0.001$, Figure 3D, Table 1). Mass and age at fledging had no significant effect on distance from nest (Table 1).

The distance fledglings moved between consecutive daily locations also increased with age, peaking around day 20–30 and then leveling off (global smoother: EDF = 4.5, $P < 0.001$; Figure 1B, Table 2). Some individuals began to move greater distances between days again late in the post-fledging period, around day 70–80. The relationship between daily distance and age varied between individuals, with some making large movements as they dispersed from natal territories around

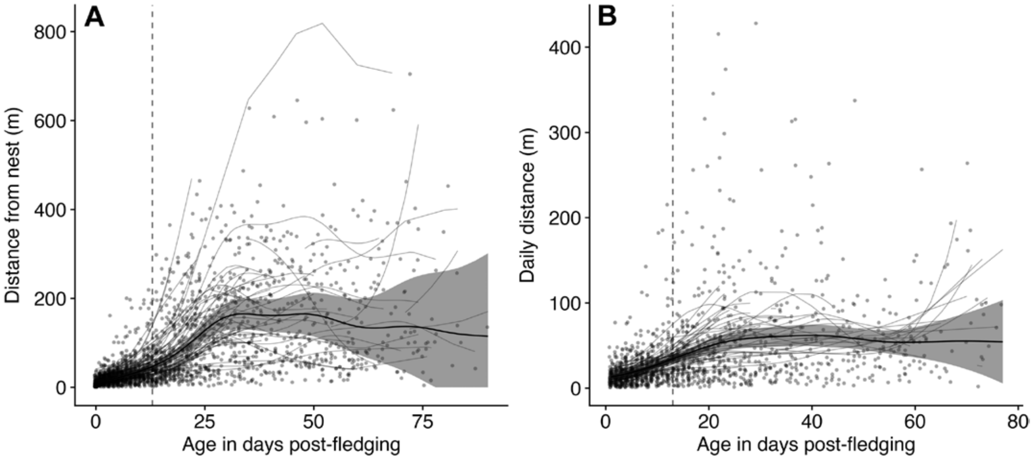

FIGURE 1. The distance (m) of fledgling *P. sandwichensis* on Kent Island, NB, from (**A**) their natal nests ("distance from nest") and (**B**) their previous daily location ("daily distance"). Both distances increased with age post-fledging until approximately day 20–25, then leveled off. Late in the post-fledging period (after day 60), the daily distance moved began to increase again. The black line and shaded 95% CI represent model predictions based on the global smoother from the hierarchical generalized additive models (HGAM); the light gray lines represent model predictions based on individual-level smoothers from the HGAM. Points are the distance from the nest or daily distance versus age for all individual birds. The dashed line at 13-day post-fledging represents the approximate age of independence for *P. sandwichensis* fledglings (Wheelwright et al. 2003).

TABLE 1. The effects of age post-fledging, brood number, year, sex, nestling mass, nest density, and age at fledging on distance from the nest (m) of *P. sandwichensis* fledglings on Kent Island, NB (n = 137 individuals, 1,903 observations). For smooth terms, *P*-values represent approximate significance (Wood 2013). Parameter estimates for factor variables reflect deviation coding. The intercept is the grand mean across all years, and each year's estimate is the deviation from the grand mean for that year. Estimates are on the model (log) scale.

Parametric coefficients	Estimate (β)	SE	95%CI	*z*-value	*P*-value
(Intercept)	3.971	0.055	(3.865, 4.078)	72.84	<0.001
Brood number—1	−0.123	0.052	(−0.224, −0.021)	−2.37	0.018
Year—2022	−0.221	0.264	(−0.739, 0.296)	−0.84	0.401
Year—2023	0.320	0.298	(−0.264, 0.904)	1.07	0.283
Sex—female	−0.099	0.046	(−0.190, −0.009)	−2.15	0.032
Weight	0.022	0.039	(−0.054, 0.098)	0.57	0.570
Age at fledging	0.091	0.062	(−0.031, 0.213)	1.46	0.144

Smooth terms	EDF	Reference df	*F*-value	*P*-value
Days post-fledging (global)	6.3	9	45.31	<0.001
Days post-fledging (individual-level)	231.6	864	2.14	<0.001
Days post-fledging by year	2.6	18	0.52	<0.001
Nest density	1.6	9	0.54	<0.001

R^2 adj = 0.79, Deviance explained = 77.9%.

day 20–30, while others remained near natal territories and did not make large daily movements (EDF = 96.9, $P < 0.001$; Figure 1B, Table 2; Supplementary Material Figure S3). Fledglings tended to move farther on days with more precipitation ($P = 0.077$; Figure 4A, Table 2). The effects of both mass and nest density on daily distance differed by age: mass and density had little effect on movement early in the post-fledging period, but after about day 20, lighter fledglings and fledglings from less-dense areas moved farther between days (mass * age: EDF = 1.8, $P = 0.004$; Figure 4B, Table 2; density * age: EDF = 1.7, $P < 0.001$; Figure 4D, Table 2). However, no pairwise comparisons between the minimum, mean, and maximum weights at selected ages (days 0, 25, and 50 post-fledging) were significant (all $P > 0.4$). Pairwise comparisons between the minimum, mean, and maximum nest densities were significant at day 0 and 25 post-fledging (all $P < 0.01$) and marginally significant at day 50 (all $P < 0.10$). The shape of the relationship between daily distance and age post-fledging differed between brood numbers (brood number * age smoother: EDF = 1.0, $P = 0.046$; Figure 4C, Table 2), with second-brood fledglings moving farther between days later into the post-fledging period. The overall mean daily distance did not differ between broods ($P = 0.306$, Table 2). The model for daily distance had a lower R-squared and explained less deviance than did the model for distance from nest (Tables 1 and 2). In particular, the model did not capture the single, large movements by fledglings around day 20–30 as they dispersed away from their natal territories (Figure 1B; Supplementary Material Figure S3).

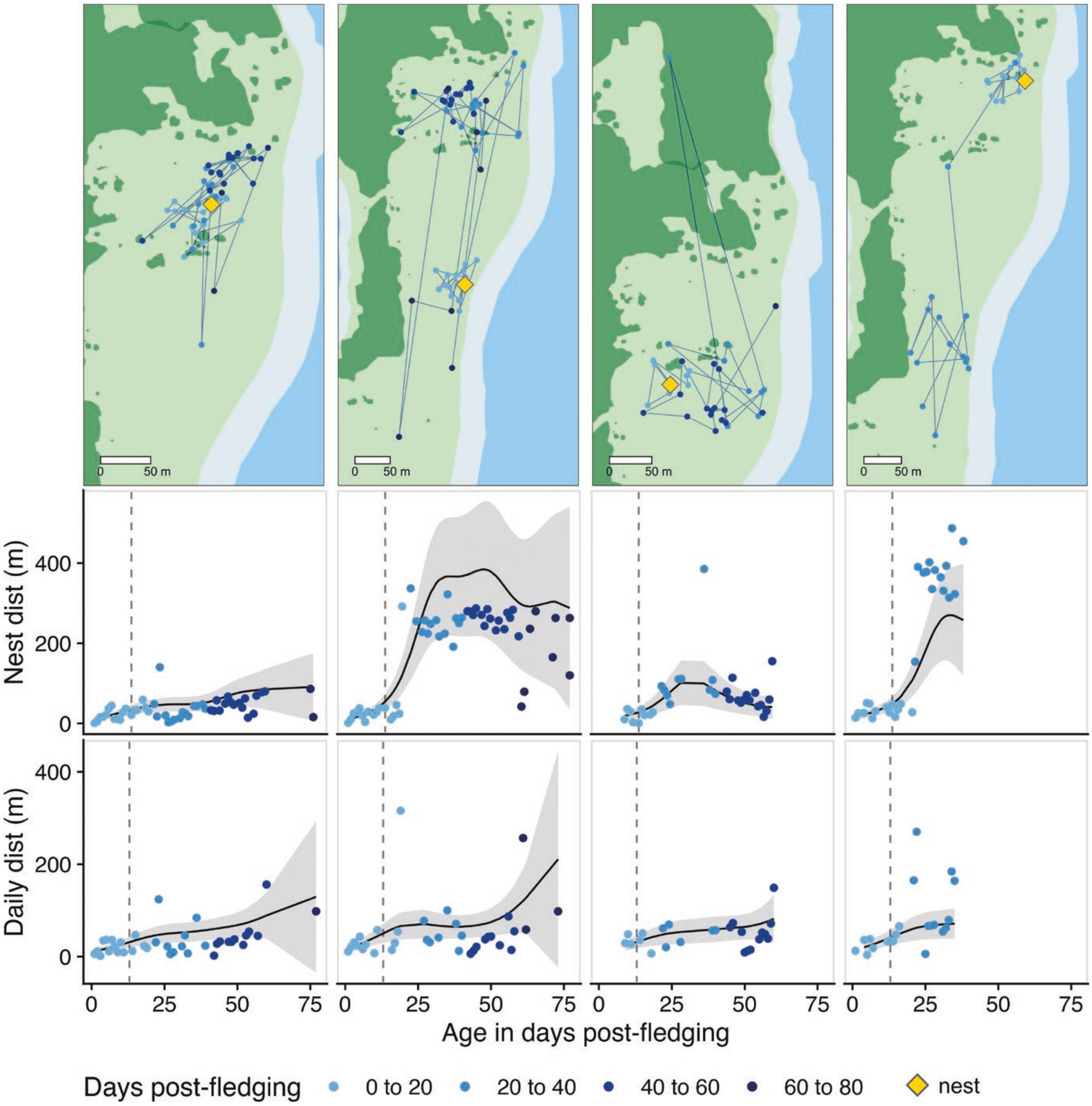

FIGURE 2. Maps and movement plots of 4 selected juvenile *P. sandwichensis* on Kent Island, NB, relative to their natal nests, with daily location points colored by age in days post-fledging and natal nest points mapped on the top panel, and plots of distance from the nest (middle panel) and distance between consecutive daily locations (bottom panel) versus age in days post-fledging for the same individual. The first and third individuals provide two examples of birds that remained near their natal nest throughout the study period; the second and fourth individuals provide examples of birds that moved away from their natal area.

DISCUSSION

We found that the movement of *P. sandwichensis* fledglings was influenced by a variety of individual characteristics and external factors, including age, brood number, year, sex, mass, nest density, and precipitation. As we observed in *P. sandwichensis* fledglings, many juvenile birds disperse away from their nest after fledging (Fisher and Davis 2011, Jenkins et al. 2016, Raybuck et al. 2020, Fischer et al. 2022) and may then settle into a “post-dispersal home range” (Anders et al. 1998, White and Faaborg 2008, Styles et al. 2021). Beginning in mid-July to early August, fledglings were frequently observed in flocks of juveniles, in communal, non-territorial areas like lawns of buildings and intertidal areas, which are suitable for foraging but are not breeding habitat. After dispersing away from their natal areas, some fledglings, however, did settle in areas of suitable breeding habitat. The formation of post-dispersal home ranges could be a sign of territorial prospecting behavior (Styles et al. 2021) or could simply reflect spatiotemporal clumping of resources.

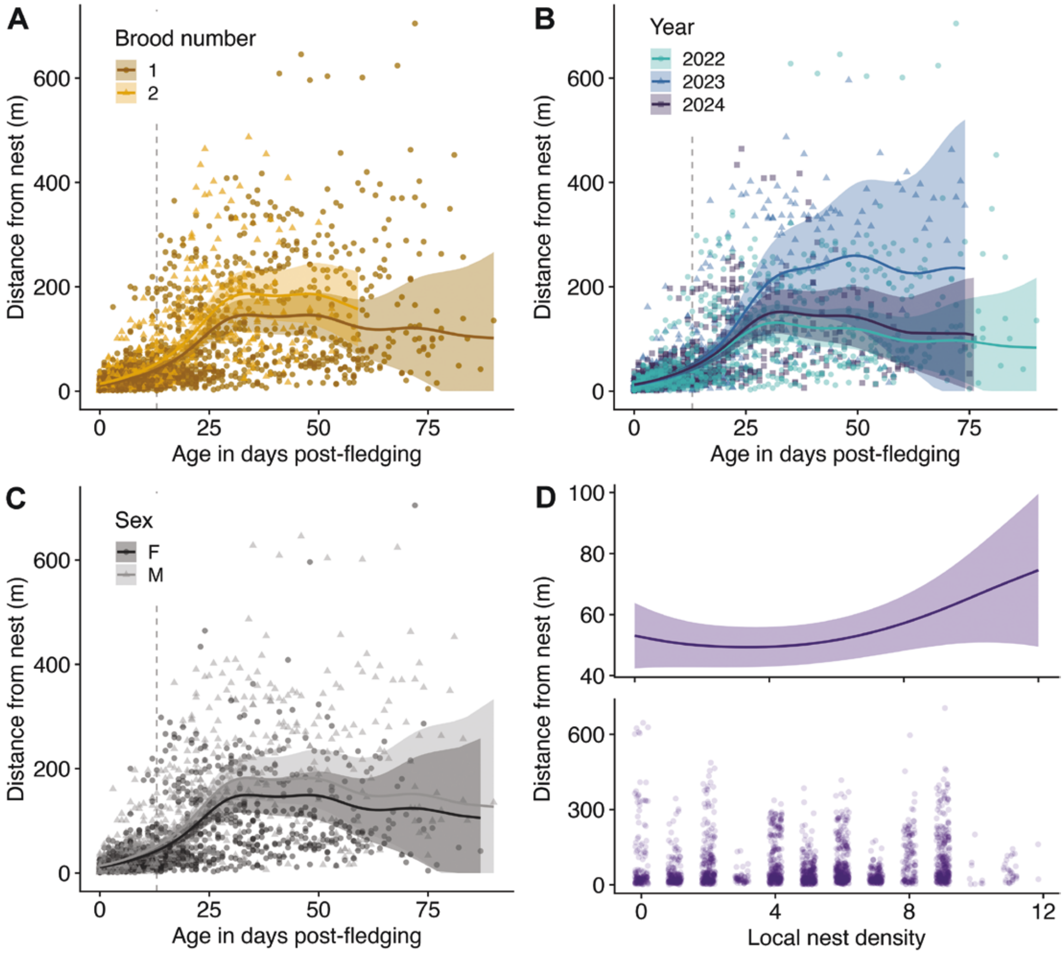

FIGURE 3. Factors influencing the distance moved away from the nest (in meters [m]; "distance from nest") of fledgling *P. sandwichensis* on Kent Island, NB. (**A**) Fledglings from second broods moved farther from their natal nests at all ages post-fledging than did fledglings from first broods (hierarchical generalized additive model, HGAM, $p = 0.01$). (**B**) The shape of the relationship between fledglings' distance from their natal nests and their age post-fledging differed between years ($p < 0.001$), with fledglings moving similar distances away from the nest between years in the early post-fledging period but, beginning around day 20–25 post-fledging, moving farther in 2023 than in 2022 or 2024. The overall mean distances across all ages did not differ ($p = 0.29$). The error in model estimates for fledglings in 2023 increased dramatically at higher ages because sample sizes of older fledglings were low due to low survival rates that year. (**C**) Male fledglings moved farther from their nests at all ages than did females ($p = 0.03$). (**D**) Fledglings from areas of high nest density moved farther from their natal nests than did fledglings from areas of medium or low nest density ($p = 0.001$). In the top panel, lines and shaded 95% CI are predictions based on the final HGAM. In the bottom panel, points are the distance from nest versus age for all individual birds. The dashed line at 13-day post-fledging represents the approximate age of independence for *P. sandwichensis* fledglings (Wheelwright et al. 2003).

As in other songbird species, our estimates of movement patterns were strongly influenced by age (Kershner et al. 2004, Fisher and Davis 2011, Jenkins et al. 2016). Distances moved, however, vary widely between species and ecological contexts. At 4 weeks post-fledging, *P. sandwichensis* fledglings were 138 ± 12 m (mean ± SE) from their natal nests (min: 5 m, max: 408 m). This is similar to the few estimates available for other sparrows (Morton et al. 1991, Anthony et al. 2013) but is much lower than the typical dispersal distances for thrushes or warblers, which range from about 1–2 km to over 200 km (Anders et al. 1998, White and Faaborg 2008, Brown and Taylor 2015, Raybuck et al. 2020, Fiss et al. 2020). In songbird fledglings, distance moved between daily locations also generally increases in the first 1–3 weeks post-fledging, with daily movements ranging from about 20 to 100 m on average but up to 200–400 m in the third week (Kershner et al. 2004, Fisher and Davis 2011, Jenkins et al. 2016, Raybuck et al. 2020), similar to *P. sandwichensis* (in first 3 weeks, mean: 17–44 m, max: 316 m). After fledglings disperse from their natal territories and settle into post-fledging home ranges, generally 30–40 days post-fledging, daily distance may level out, as we have reported in *P. sandwichensis*, or may even decline (Styles et al. 2021). Few studies, however, have tracked daily movement rates this late into the post-fledging period.

Fledgling movement patterns varied based on individual characteristics, including brood number, sex, and mass as a nestling. First, distance from the nest was, on average, greater for second brood than first brood fledglings, and second brood fledglings continued to move greater distances between days later into the post-fledging period than did first-brood fledglings. Food availability may be lower later in the season for second brood fledglings (Rossmanith et al. 2007, Harriman et al. 2017), requiring them to travel farther to find sufficient resources (Jenkins et al. 2016). Later-fledging, second-brood young also have a shorter timeline between fledging and migration, which may necessitate higher movement rates

TABLE 2. The effects of age post-fledging, brood number, year, sex, nestling mass, nest density, daily mean temperature, and daily precipitation on distance between daily locations (m) of *P. sandwichensis* fledglings on Kent Island, NB (n = 116 individuals, 1,202 observations). For smooth terms, P-values represent approximate significance (Wood 2013). Parameter estimates for factor variables reflect deviation coding. The intercept is the grand mean across all years, and each year's estimate is the deviation from the grand mean for that year. Estimates are on the model (log) scale.

Parametric coefficients	Estimate (β)	SE	95%CI	z-value	P-value
(Intercept)	3.564	0.047	(3.472, 3.656)	76.19	<0.001
Brood number—1	−0.144	0.141	(−0.420, 0.132)	−1.02	0.306
Year—2022	−0.070	0.057	(−0.182, 0.042)	−1.23	0.221
Year—2023	0.059	0.062	(−0.064, 0.181)	0.94	0.347
Sex—female	−0.007	0.041	(−0.087, 0.073)	−0.16	0.870
Temperature	−0.003	0.011	(−0.024, 0.017)	−0.33	0.745
Precipitation	0.009	0.005	(−0.001, 0.019)	1.77	0.077

Smooth terms	EDF	Reference df	F-value	P-value
Days post-fledging (global)	4.5	9	26.93	<0.001
Days post-fledging (individual-level)	96.9	715	0.29	<0.001
Days post-fledging by brood number	1.0	9	0.22	0.046
Mass	0.0	9	0.00	0.335
Days post-fledging by mass	1.8	16	0.34	0.004
Nest density	0.0	9	0.00	0.103
Days post-fledging by nest density	1.7	16	0.95	<0.001

R^2 adj = 0.26, Deviance explained = 43.1%.

to begin preparing and fueling for migration (Jenkins et al. 2016). Additionally, first-brood fledglings may remain on their natal territories longer if their parents stay on the territory to initiate a second brood, while second-brood fledglings may be led away from the territory by parents that have ceased breeding (third broods are rare in this population). Second brood fledglings may also be able to disperse farther if neighboring breeding pairs do not attempt a second brood and become less territorial. Next, sex influenced overall distance from the nest, with males traveling on average farther than females, but did not influence daily distances. This pattern is opposite to the expectation of female-biased dispersal in birds (Greenwood and Harvey 1982) and could possibly reflect differences in boldness or exploratory behavior between sexes (Nilsson et al. 2014). Finally, lighter fledglings moved greater daily distances later in the post-fledging period. Lighter fledglings may be forced to move farther to find sufficient resources due to lower competitive ability; however, the size of this effect was small and may not be biologically meaningful.

External factors, including year, local nest density, and precipitation, also influenced movement patterns. The differences in distance from the nest between years exhibited by *P. sandwichensis* may be due to annual variation in environmental conditions. Weather conditions differed substantially between years, with 2022 and 2024 being sunny and dry relative to 2023, which was particularly foggy and rainy (total precipitation across the tracking period: 180 mm in 2022, 390 mm in 2023, 240 mm in 2024; Environment and Climate Change Canada 2024). Additionally, population density was much higher in 2023 than in other years: there were 110 breeding adults in 2023, compared to only 76 in 2022 and 81 in 2024. Cold, rainy weather and increased competition for food likely made it more difficult for parents to find sufficient food for dependent fledglings and for independent fledglings to feed themselves. As a result, survival of fledglings was lower in 2023, and thus average tracking times were shorter (S.D.M., D.R.N., personal communication). After becoming independent, surviving fledglings in 2023 may have had to travel further from the nest to find sufficient resources. Alternatively, surviving fledglings may have been those that were in the best condition and, thus, capable of traveling farther. Although fledglings in 2023 travelled farther from their nests, their daily distances travelled did not differ. This suggests that fledglings moved in a directed manner away from nests in 2023, perhaps while searching for limited food resources, but remained nearer natal territories in 2022 and 2024.

Local nest density influenced both distance from nest and daily distances, though in opposite directions. Birds from high-density areas travelled farther from their natal nests, supporting the idea that fledglings may disperse to avoid intraspecific competition (Ausprey and Rodewald 2013). However, birds from low-density areas moved more between days after independence. Individuals from low-density areas may move more between days but stay within the nest area—having more space to move due to low density—while individuals from high-density areas may move relatively shorter distances between days but in a strongly directional manner away from the nest to avoid high levels of competition. Finally, precipitation also influenced movement patterns somewhat, with birds tending to move greater distances between days with greater precipitation. This pattern is contrary to the prediction that fledglings would seek shelter during inclement weather, but could reflect greater energetic needs and thus increased movement to seek food or shelter. Additionally, if invertebrate prey are more active after rain events, fledglings may move farther to take advantage of increased foraging opportunities.

There was wide variation in movement patterns between individual fledglings that was not explained by any of our predictors. Differences between individuals could simply

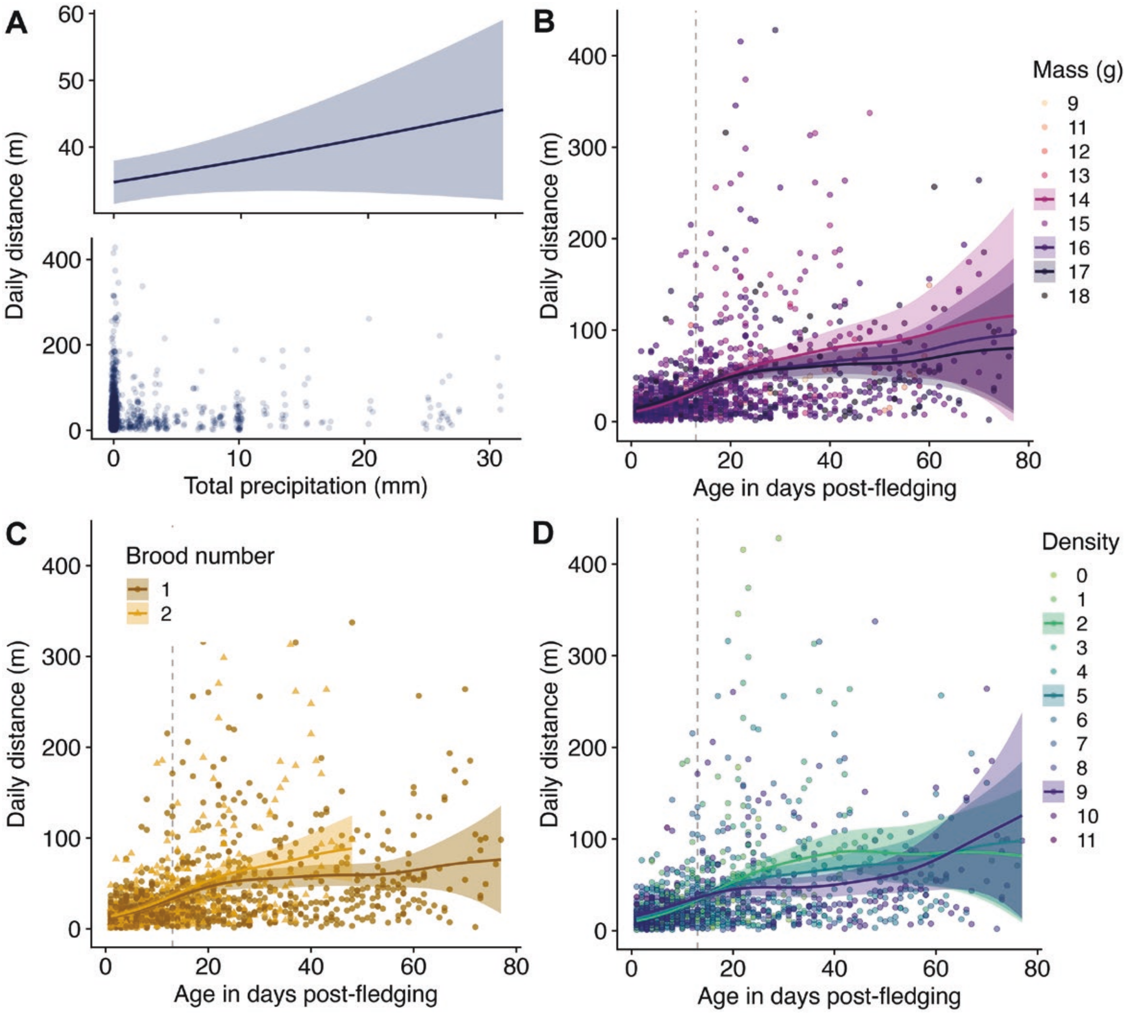

FIGURE 4. Factors influencing distance moved between consecutive daily locations (in meters [m], "daily distance") of fledgling *P. sandwichensis* on Kent Island, NB. (**A**) Fledglings tended to move farther on days with higher precipitation (hierarchical generalized additive model, HGAM, $p = 0.08$). (**B**) Mass had little effect on daily distance moved early in the post-fledging period, but after about day 20, lighter fledglings moved farther between days ($p \leq 0.01$). (**C**) Second-brood fledglings moved farther between days later into the post-fledging period than did first-brood fledglings ($p = 0.05$), but the overall mean daily distance did not differ between broods ($p = 0.31$). (**D**) Local nest density (birds ha^{-1}) had little effect on daily distance moved early in the post-fledging period, but after about day 20, fledglings from less-dense areas moved farther between days ($p < 0.01$). Lines and shaded 95% CI are predictions based on the final HGAM, and points are the distance between consecutive locations versus age for all individual birds. The dashed line at 13-day post-fledging represents the approximate age of independence for *P. sandwichensis* fledglings (Wheelwright et al. 2003).

represent "chaos" or random variation, which is often important but rarely examined in ecology (Munch et al. 2022). We observed some individuals that stayed near their natal territory for the entire study period, while others made large jumps in movement (Figure 2, Supplementary Material Figure S2), not clearly driven by any measured characteristics or external factors. These differences could be explained by covariates currently missing from the analysis, such as predation risk or vegetation characteristics. Variation between individuals could also be due to differences in personality traits, including boldness or activity level (Nilsson et al. 2014) or simply due to random wandering. Post-fledging movement patterns often show high among-individual variation. For instance, dispersal patterns of *Cardinalis cardinalis* (Northern Cardinal) fledglings varied between individuals, with some dispersing locally within their natal forest fragments and others making extended movements into the surrounding landscape (Ausprey and Rodewald 2013). Space use also differed between *Parus major* (Great Tit) families (van Overveld et al. 2011).

We acknowledge some limitations of this study related to our methodological approach and the nature of the study site. First, our ability to make inferences about movement distances was somewhat constrained by having only one location per individual per day. A higher frequency of locations would have provided a more accurate picture of distance travelled and may have captured some movement behavior we missed, such as movement that could have occurred at night (Mukhin et al. 2005). Second, due to high mortality of fledglings (S.D.M., D.R.N, personal communication), our sample size late in the post-fledging period (after about day 70; Supplementary Material Figure S4) was quite small, making it more challenging to be confident in the patterns we have reported during this time. Finally, because our study population was on an island, post-fledging movement patterns may differ from those of mainland populations if movement was constrained by the size and shape of the island (Wheelwright et al. 2003). Our results, however, may have some relevance for bird populations breeding in fragmented habitats because fragmented habitats, like islands, can also constrain movement (Norris and Stutchbury 2002, Jenkins et al. 2016).

Our results demonstrate how post-fledging movement patterns and the factors influencing movement can change between the early, dependent post-fledging period and the relatively understudied late, independent post-fledging period. Many of the variables we examined (e.g., year, local density, brood number) more strongly influenced movement for older fledglings than for younger ones. Older fledglings also varied much more in their space use, with some fledglings dispersing long distances and others remaining near their natal territories. Improved understanding of factors that influence movement patterns is crucial to understanding the dynamics of the post-fledging period because of the influence of movement on survival: fledglings must move to find sufficient food resources, avoid predators, and prepare for migration. Future work could investigate whether the motivation for movement during the fledgling period is primarily driven by the search for food, predator avoidance, or prospecting for future territories. This would include assessing food availability, predation risk, individual condition and survival, and whether juveniles return to breed in areas they used during the post-fledging period.

Supplementary material

Supplementary material is available at *Ornithology* online.

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Ethics statement

The capture and handling of *P. sandwichensis* was conducted under Canadian Wildlife Service bird banding permits (no. 10789 and 10789-K) and was in compliance with the Animal Care Committee at the University of Guelph (Animal Use Protocol no. 4987).

Conflict of interest statement

The authors do not declare any conflict of interest.

Author contributions

SDM and DRN conceived the idea and designed the methods. SDM analyzed the data and wrote the paper. All authors contributed to data collection and editing the paper.

Data availability

All data, metadata, and R code used to generate results are available from Mueller et al. (2025).

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