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Low migratory flight altitudes may explain increased collision risk for *Scolopax minor* (American Woodcock)

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ABSTRACT

Understanding bird migration at low altitudes is critical to evaluating risk of collision with obstacles. Recent advances in satellite tracking technologies allow quantifying use of low altitudes by small migrating birds with a high level of precision, allowing species-level inference into potential collision risk based on flight altitude. *Scolopax minor* (American Woodcock) is suspected to be a low-altitude migrant due to its frequent collisions with buildings, and subsequent mortality during migration may be contributing to population declines. We investigated migratory flight altitudes using satellite transmitters deployed on woodcock in 2020–2024 and examined how flight altitudes compare to the heights of common airspace obstacles. Each transmitter recorded a nocturnal GPS location with an altitude reading every 1–3 days during fall and spring migrations. We implemented a Bayesian hierarchical mixture model to identify whether locations were recorded on the ground or during flight, isolate measurement error, and describe the distribution of flight altitudes. We found that migrating woodcock fly at mean altitudes of 379 m above ground level, flying higher during spring (mean: 444 m, 95% credible interval: 333–578 m) than fall (338 m, 95% CRI: 267–423 m). Woodcock flight altitudes were frequently lower than could be observed using weather radar (27% of observations), and 57% of observations fell within the altitude range of ≥1 airspace obstacle. Our results suggest that woodcock fly at altitudes lower than reported for most nocturnal migrants, which likely contributes to their vulnerability to obstacle collisions. *Scolopax minor* provide an example of how vulnerability to obstacle collisions during nocturnal migratory flights are often species-specific, and mitigation efforts should incorporate measures aimed at reducing collisions during both diurnal stopovers and nocturnal migratory flights to effectively reduce bird collision mortality.

Keywords: airspace, altitude, American Woodcock, collision, migration, *Scolopax minor*, transmitter

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LAY SUMMARY

- Collision with airspace obstacles (including buildings, wind turbines, and communication towers) is a major source of mortality for migratory birds.
- In this study, we examined the flight altitudes of *Scolopax minor* (American Woodcock) equipped with GPS transmitters in 2020–2024 and compared their flight altitudes to common airspace obstacles.
- We found that woodcock fly lower than most nocturnal migrants, and 57% of observations fell within the altitude range of at least one airspace obstacle.
- These low-altitude flights may contribute to woodcocks' increased vulnerability to collisions with airspace obstacles.

Las bajas altitudes de vuelo migratorio pueden explicar el mayor riesgo de colisión en *Scolopax minor*

RESUMEN

Comprender la migración de las aves a bajas altitudes es fundamental para evaluar el riesgo de colisión con obstáculos. Los avances recientes en las tecnologías de rastreo satelital permiten cuantificar con alta precisión el uso de bajas altitudes por parte de aves migratorias pequeñas, lo que permite hacer inferencias a nivel de especie sobre el riesgo potencial de colisión según la altitud de vuelo. Se sospecha que *Scolopax minor* es un migrante de baja altitud debido a sus frecuentes colisiones con edificios, y la mortalidad resultante durante la migración podría estar contribuyendo al declive de su población. Investigamos las altitudes de vuelo migratorio utilizando transmisores satelitales instalados en individuos de *S. minor* entre 2020 y 2024 y examinamos cómo se comparan estas altitudes con la altura de los obstáculos comunes en el espacio aéreo. Cada transmisor registró una ubicación GPS nocturna con una lectura de altitud cada 1 a 3 días durante las migraciones de otoño y primavera. Implementamos un modelo jerárquico bayesiano de mezcla para identificar si las ubicaciones se registraron en el suelo o en vuelo, aislar el error de medición y describir la distribución de las altitudes de vuelo. Encontramos que los individuos migratorios de *S. minor* vuelan a una altitud media de 379 m sobre el nivel del suelo, volando más alto en primavera (media: 444 m, intervalo de credibilidad del 95%: 333–578 m) que en otoño (338 m, ICR 95%: 267–423 m). Las altitudes de vuelo de *S. minor* fueron frecuentemente más bajas de lo que podría detectarse con radar meteorológico (27% de las observaciones), y el 57% de las observaciones se encontraron dentro del rango de altitud de ≥ 1 obstáculo aéreo. Nuestros resultados sugieren que *S. minor* vuela a altitudes más bajas que las reportadas para la mayoría de los migrantes nocturnos, lo que probablemente contribuye a su vulnerabilidad ante colisiones con obstáculos. *S. minor* es un ejemplo de cómo la vulnerabilidad a las colisiones con obstáculos durante los vuelos migratorios nocturnos suele ser específica de cada especie, y los esfuerzos de mitigación deberían incluir medidas dirigidas a reducir las colisiones tanto durante las paradas diurnas como en los vuelos migratorios nocturnos para disminuir eficazmente la mortalidad por colisión de estas aves.

Palabras clave: altitud, colisión, espacio aéreo, migración, *Scolopax minor*, transmisor

INTRODUCTION

Avian migratory flights can be studied using a wide range of techniques, including GPS and satellite telemetry, altimeters, imaging, and radar (Thaxter et al. 2016). These tools can be used to describe the altitudinal distributions of nocturnal avian migrants and examine how those altitudes shift in response to wind, weather, and artificial light during migration (Bauer et al. 2019). Research has focused on how these factors influence the risk of bird collision with obstacles (Lao et al. 2020), although there are still knowledge gaps regarding low-altitude flights that put birds within range of airspace obstacles (<200 m above ground level). Obstacles present at these altitudes include buildings (365–988 million bird collisions per year; Loss et al. 2014), wind turbines (234,000 bird collisions per year; Loss et al. 2013), and communication towers (4–5 million bird collisions per year; Gehring et al. 2011). Flights at obstacle height can be difficult to study due to blind spots in weather radar at low altitudes (Rogers et al. 2020), although some radar studies have had success in quantifying their prevalence. Cohen et al. (2022) estimated that 35% of birds migrating along the Great Lakes shorelines passed through the rotor-swept zone of a wind turbine at some point during their migratory flight, and White et al. (2020) found that migrating bird densities near Lake Erie were greatest below 400 m, even during peak migratory periods. Despite the utility of these studies, radar is generally limited to making inferences about overall patterns in bird migration and cannot provide insights into susceptibility to obstacle collisions at a species level. Species-level insight is particularly important as not all species are equally susceptible to obstacle collisions; Nichols et al. (2018) identified 13 species and 7 genera as "supercolliders," or taxa that are found more often after obstacle collisions than expected, given their population size. Gathering species-level data regarding use of low altitudes would allow one to determine whether flight altitude is contributing to the increased risk of collision with obstacles for these species.

Gaining species-level insight into flight altitudes requires the use of bird-borne telemetry equipment, usually altimeters or GPS transmitters (Thaxter et al. 2016). Transmitters come with their own set of drawbacks: they are expensive to deploy, collect far less data than other techniques, and are usually limited to birds above a specific mass. However, telemetry equipment can be used to make inferences about species-specific flight altitude, including both high and low altitudes, and in the case of GPS transmitters, can often do so with very high precision. Several studies have described low-altitude flights using GPS transmitters, including Bowlin et al. (2015), who found that of 13 tracked *Catharus ustulatus* (Swainson's Thrush) migratory

flights, one individual spent over an hour flying at altitudes <100 m before rising to altitudes of 300–500 m. A second thrush spent its entire ~2 hr migratory flight at an altitude of ~40 m. Galtbalt et al. (2021) found that *Numenius phaeopus* (Whimbrel) and *N. madagascariensis* (Far Eastern Curlew) have overwater median flight altitudes of 132 m and 156 m above sea level, respectively, although those altitudes increase to 718 m and 538 m when flying over land. Further transmitter studies focusing specifically on birds that are highly susceptible to collisions with airspace obstacles may allow one to better understand the prevalence of low-altitude flights among these species, and how those flights influence collision risk.

Scolopax minor (American Woodcock) is an upland Scolopacid species distributed throughout eastern North America. They are among the earliest avian migrants in spring (February–May) and the latest migrants in fall (October–December), likely timing their migration based on the availability of earthworms, which are their preferred prey (Fish et al. 2024, Berigan 2024, McAuley et al. 2020). Woodcock has long been thought to migrate at low altitudes; even before tracking data were available, Mendall and Aldous (1943) estimated that woodcock migrate at altitudes of 12–15 m based on the high rate of woodcock collisions with power, telephone, and telegraph lines. Woodcock deaths are frequently attributed to building collisions in major USA cities, such as Minneapolis (Loss et al. 2019) and Chicago (Van Doren et al. 2021), and mass building-collision events occurred when woodcock were caught in snowstorms during their early spring migration (Loss et al. 2020). Woodcock migratory mortality could contribute to their decline of 0.8% yr^{-1} since the 1960s (Cooper and Rau 2012, Loss et al. 2020). No studies, to the best of our knowledge, have quantified woodcock flight altitudes, or examined how those altitudes might impact their vulnerability to collision with airspace obstacles.

Here we investigated the propensity for *S. minor* to fly at low altitudes during migratory flights and examined how flight altitudes compared to the altitudinal distributions of common airspace obstacles. We also quantified the proportion of woodcock flight locations that fell below a threshold detectable by weather radar to provide some context for comparing our estimates to other studies. We hypothesized that woodcock flight altitudes would fall below mean estimates for nocturnal migrants (418–459 m above ground level; Horton et al. 2016) and would frequently fall within altitudinal ranges corresponding with obstacles, such as buildings, wind turbines, and communication towers, based on high rates of collisions for this species (Mendall and Aldous 1943, Loss et al. 2020). We also postulated that woodcock flight altitudes would be lower in fall than spring, in accordance with general trends in nocturnal migrants (Horton et al. 2016), and that flight altitudes would be similar among age and sex classes due to minimal differences in morphological characteristics among these classes (McAuley et al. 2020, Agostini et al. 2023). Our analysis aimed to determine the vulnerability of woodcock and other nocturnal migrants to airspace collisions during migratory flights, and the necessity for further study of low-altitude movements of birds in general.

METHODS

Data Collection and Preprocessing

We collected *S. minor* locations with altitude readings from 2020 to 2024 using GPS transmitters as a part of a larger collaborative effort by the Eastern Woodcock Migration Research Cooperative (Blomberg et al. 2023, Clements et al. 2024, Fish et al. 2024). We captured woodcock at 100 sites across the eastern portion of their range, including Alabama, Florida, Georgia, Louisiana, Maine, Maryland, New Jersey, New York, North Carolina, Nova Scotia, Ontario, Pennsylvania, Québec, Rhode Island, South Carolina, Vermont, Virginia, West Virginia, and Wisconsin. We caught woodcock using a combination of spotlighting and mist netting (McAuley et al. 1993). We aged and sexed birds upon capture, where we classified birds undertaking their first fall and spring migrations as juveniles, and all other birds as adults. We then attached 4–7 g PinPoint transmitters (Lotek Wireless Inc., Newmarket, Ontario, CA) using a rump-mounted leg loop harness (Fish et al. 2024).

We programmed transmitters to collect locations every 1–3 days during migration, with locations alternating between diurnal (1300–1500 hours Eastern Time) and nocturnal (0000–0100 hours) times. Transmitters recorded time, latitude, longitude, and GPS-derived altitude above the WGS84 ellipsoid, and transmitted data back to the ARGOS satellite constellation after every third location. We subset these locations to include only those within the migratory classification dataset produced by Berigan (2024). This dataset classified individual locations as migratory or nonmigratory based on the assumption that migration starts after the first ≥16.1 km movement and ends after the final ≥16.1 km movement of the season. We used ArcGIS Pro 3.2.1 (ESRI 2024a) to calculate the difference between the altitude and orthometric elevation recorded for each location (ESRI composite elevation layer; ESRI 2024b), providing a measurement of altitude above ground level for each point.

We classified data for our models based on prior descriptions of woodcock activity patterns. Woodcock are ground-feeding birds that rarely fly outside of crepuscular hours (Rabe et al. 1983). When rare diurnal flights do occur, these are generally brief, comprising 1–3% of diurnal time budgets, and close to the ground (McAuley et al. 2020). We therefore made a modeling assumption that all diurnal locations could be treated as though they were known to be recorded on the ground (hereinafter "known ground locations"). As woodcock are nocturnal migrants, we define potential flight locations as all points that were nocturnal, occurred during migration based on the classification in Berigan (2024), and were preceded and followed by >6.68 km steps (defined as lines connecting consecutive locations). The 6.68 km threshold was based on the 99th percentile of step lengths recorded within a stopover site (Berigan 2024). Ensuring that the preceding and following steps were >6.68 km increased the likelihood that the bird had moved away from a stopover site before the point was recorded.

Modeling Altitude Distributions

Our model of woodcock flight altitudes included both potential flight locations and known ground locations, with each class of data informing a different aspect of the model. Known ground locations were assumed to always have a true altitude of 0 m, making their recorded altitudes A_r solely attributable to measurement error ε by the GPS units. The recorded altitude of a ground location i can be modeled as follows:

$$A_{ri} \sim \text{StudentT}\left(\nu_\varepsilon, \mu_\varepsilon, \sigma_\varepsilon\right) \quad (1)$$

where ν_ε represents degrees of freedom, μ_ε is the mean error observed across all observations, and σ_ε is the scale parameter

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associated with the error. As such, the known ground locations can be used to directly inform the measurement error term ε_i, which we assume remains consistent between ground and flight locations. We chose to model ε_i using a Student's *t*-distribution due to the distribution's flexibility in modeling heavy tails, which are frequently observed in altitudinal measurement error distributions (Péron et al. 2017).

For potential flight locations there are two possible outcomes. They can be recorded on the ground, in which case $A_{ri} = \varepsilon_i$, or recorded in flight with altitude A_f, in which case $A_{ri} = A_{f_i} + \varepsilon_i$. This can be modeled as follows:

$$A_{ri} \sim \begin{cases} \text{StudentT}\left(\nu_\varepsilon, \mu_\varepsilon, \sigma_\varepsilon\right) & \text{if} \quad \text{Flight}_i = 0 \\ \text{StudentT}\left(\nu_\varepsilon,\ \mu_\varepsilon + A_{f_i}, \sigma_\varepsilon\right) & \text{if} \quad \text{Flight}_i = 1 \end{cases} \tag{2}$$

$$A_{f_i} \sim \text{Lognormal}\left(\mu_f, \sigma_f\right) \tag{3}$$

where A_f for each location i that is identified in flight (i.e., $\text{Flight}_i = 1$) is drawn from a log-normal distribution with location parameter μ_f and scale parameter σ_f. We chose a log-normal distribution because it accommodated a heavy right tail, which is a common feature of bird altitude distributions (White et al. 2020). The flight status of the birds is the function of a Bernoulli distribution

$$\text{Flight}_i \sim \text{Bernoulli}\left(p_f\right) \tag{4}$$

where p_f is the proportion of true flight locations among all potential flight locations. As the programming language we used (i.e., Stan) does not support sampling discrete parameters, we expressed Equation (4) through a latent discrete parameterization described in Stan Development Team (2024).

All parameters in the model received vague priors. The measurement bias in the data, μ_ε, and location parameter for the flight distribution, μ_f, both received normal priors with mean 0 and standard deviation 1. The standard deviation of the measurement error, σ_ε, and the scale parameter for the flight distribution, σ_f, both received half-normal priors with mean 0 and standard deviation 1. The proportion of true flight locations among all potential flight locations, p_f, received a beta distribution prior where both the α and β shape parameters were set to 2. The degrees of freedom in the measurement error distribution, ν_ε, received a gamma distribution prior with an α of 2 and a β of 0.1, following suggestions for vague priors of ν in Juárez and Steel (2010).

Season, age, and sex models received a similar formulation to the base model, with the only difference being the use of group-specific (g) μ_f, σ_f, and p_f parameters

$$A_{f_i} \sim \text{Lognormal}\left(\mu_{f_g}, \sigma_{f_g}\right) \tag{5}$$

$$\text{Flight}_i \sim \text{Bernoulli}\left(p_{f_g}\right) \tag{6}$$

where the μ_{f_g}, σ_{f_g}, and p_{f_g} parameters were dependent on the season, age, or sex class associated with any given altitude observation. This model structure allowed the distribution of flight altitudes to be estimated for each season, age, and sex class separately, but with shared inference of error terms μ_ε and σ_ε as we had no a priori reason to believe that GPS measurement error would change as a function of these classes.

We implemented these models in a Bayesian framework using package *rstan* (Stan Development Team 2024) in R version 4.4.1 (R Core Team 2024) running 4 chains at 15,000 iterations with 7,500 warmup iterations. We checked all models for convergence using trace plots and ensured that potential scale reduction values were <1.1 (Brooks and Gelman 1998). As Bayesian models often perform better with scaled variables, we scaled our estimated flight altitudes between 0 and 1 for modeling, and back-transformed all parameter estimates into meters above ground level for evaluation. We described the posteriors of flight altitude distribution parameters by simulating a log-normal distribution for each posterior value of μ_f and σ_f, and sampling the mean, median, standard deviation, and skewness of each simulated distribution. We estimated the number of flight locations from the base, season, age, and sex models by multiplying posterior values of p_f by the number of potential flight locations in each dataset. We summarized posteriors for all parameters using median values and highest density credible intervals (CRI) since they allow for more conservative estimates when posterior densities are skewed (Kruschke 2014, Makowski et al. 2019). We also calculated the probability of superiority, or the likelihood of one group having a higher parameter value than another group, for season, age, and sex models following Ruscio (2008).

Comparison of Flight Altitudes to Weather Radar and Airspace Obstacles

We used derived metrics from our model to assess how often woodcock flight altitudes occurred in the altitude range typically detected by ground-based radar and how they coincided with height intervals associated with common airspace obstacles that pose collision risk. We calculated these metrics by simulating a log-normal distribution for each posterior value of μ_f and σ_f, and measuring the proportion of each simulated distribution that fell below or within the given height interval. We compared woodcock flight altitudes to the minimum altitude (120 m) detected by Horton et al. (2016) using the Next Generation Weather Radar (NEXRAD) system, a weather radar system in the USA frequently used to study bird migration (DeMott et al. 2022, Horton et al. 2023). We quantified the proportion of simulated flight altitudes that fell below a 120-m threshold, representing the proportion of locations that would not be detectable by weather radar. As low-rise buildings (defined as residential buildings 4–11 stories and nonresidential buildings ≤11 stories) result in the highest number of window collision mortalities in the United States (Loss et al. 2014), we also quantified the proportion of simulated flight altitudes below the height of an 11-story building (47 m). We estimated the proportion of simulated flight altitudes that fell within the rotor-swept zone of the average land-based wind turbine installed in 2022 (32–164 m; Wiser et al. 2023). Finally, we measured the proportion of simulated flight altitudes that fell below the height of a 305-m communication tower, as these towers are responsible for 5–70x as many collisions as shorter towers (Gehring et al. 2011).

RESULTS

We collected 16,293 GPS locations with altitude recordings from 344 individuals. Most of these locations (9,658) were recorded at 1300–1500 Eastern Time and were classified as known ground locations. Of those locations remaining, 258 met the criteria to be possible migratory locations (106 individuals). These locations were broadly distributed throughout the eastern portion of the woodcock's range (Supplementary Material Figure S1). The base model predicted that 144 of

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TABLE 1. Sample size and distribution of *Scolopax minor* (American Woodcock) altitudes above ground level during migratory flights, measured using the base model as well as season, age, and sex models. Estimates indicate the median value of the posterior distribution, whereas the highest density credible intervals are provided in parentheses. Note that some individuals were missing age and sex data and were excluded from respective models. Altitude data were collected using GPS transmitters in the eastern portion of the woodcock's range in 2020–2024.

Model	Individuals [a]	Locations [b]	Estimated number of flight locations [c]	Mean altitude (m)	Median altitude (m)
Base	106	258	144 (127–161)	379 (320–447)	262 (218–304)
Season					
Fall	54	118	76 (65–88)	338 (267–423)	242 (188–296)
Spring	59	140	67 (54–80)	444 (333–578)	295 (220–376)
Age					
Adult	44	98	55 (45–65)	431 (317–581)	291 (218–374)
Juvenile	49	134	75 (63–88)	371 (295–465)	266 (210–324)
Sex					
Male	52	121	72 (61–83)	417 (326–532)	289 (225–356)
Female	49	128	66 (54–78)	352 (270–456)	247 (184–310)

[a]Number of individual birds with recorded potential flight locations.
[b]Number of potential flight locations. The criteria for potential flight locations included being (1) recorded at night, (2) recorded during migration, and (3) preceded and followed by >6.68 km steps.
[c]Calculated by multiplying posterior values of p_{fg} by the number of potential flight locations in each dataset (Equation 6).

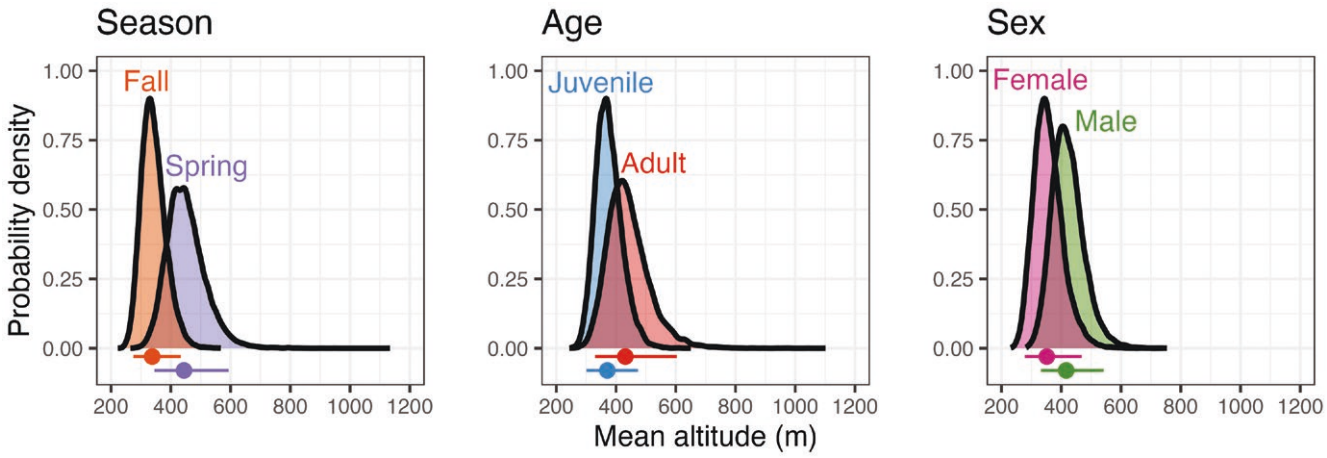

FIGURE 1. Posterior distributions for mean flight altitude of *Scolopax minor* (American Woodcock) flight locations, subdivided by season, age, and sex. Density plots represent posterior distributions of parameters, whereas point intervals represent the medians and 95% highest density credible intervals of the posteriors. Altitude data were collected using GPS transmitters in the eastern portion of the woodcock's range in 2020–2024.

these locations were most likely recorded when the bird was in flight (95% CRI: 127–161; Table 1). Estimated median flight altitude above ground level was 262 m, and mean flight altitude was 379 m. Woodcock flew at mean altitudes of 338 m in fall and 444 m in spring, with 94% probability that mean flight altitudes were lower in fall than spring. Adult woodcock flew at mean altitudes of 431 m, while juveniles flew at altitudes of 371 m, with 79% probability that mean flight altitudes were higher for adults than juveniles. Male woodcock flew at mean altitudes of 417 m, while females flew at altitudes of 352 m, with 82% probability that mean flight altitudes were higher for males than females (Figure 1). Additional statistics describing the shape of these distributions are provided in Supplementary Material Table S1.

Over half (57%) of simulated flight altitudes were below 305 m, posing potential risks for collisions with low-rise buildings, wind turbines, and communications towers (Table 2; Figure 2). *Scolopax minor* were equally likely to fly within range of low-rise buildings in fall and spring, while they were 6% more likely to fly within the rotor-swept zone of wind turbines and 9% more likely to fly at communication tower altitude during fall. Twenty-seven percent of simulated flight altitudes were below the minimum flight altitude reported by Horton et al. (2016) and likely would not have been detectable using NEXRAD weather radar.

DISCUSSION

We found that mean woodcock flight altitudes above ground level fell below those typical of most migrating birds during fall (woodcock: 338 m; all birds: 418–491 m) and spring (woodcock: 444 m; all birds: 438–559 m; Horton et al. 2016). This result may be due, in part, to the increased representation of lower altitude flight locations in our data, as 27% of woodcock flight locations fell below the minimum altitude normally observed via weather radar (120 m; Horton et al. 2016). However, given preexisting information about woodcock's high susceptibility to collisions with anthropogenic structures (Mendall and Aldous 1943, Loss et al. 2020) we believe that some portion of

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TABLE 2. Proportion of *S. minor* flight altitudes above ground level within height intervals related to weather radar and airspace obstacles. We calculated these metrics by simulating a log-normal distribution for each posterior value of μ_f and σ_f, and measuring the proportion of each distribution which fell below or within the given height interval. Results are included for the base model as well as season, age, and sex models. Estimates indicate the median expected value, while credible intervals reflect highest density intervals for each estimate. These derived metrics are based on altitude data collected using GPS transmitters in the eastern portion of the woodcock's range in 2020–2024.

Model	Percent below NEXRAD detection altitude (120 m)[a]	Percent below height of low-rise buildings (47 m)[b]	Percent within sweep of land-based wind turbines (32–164 m)[c]	Percent below height of large communication towers (305 m)[d]
Base	27 (20–35)	2 (0–5)	28 (21–35)	57 (50–64)
Season				
Fall	29 (19–40)	2 (0–6)	31 (22–41)	61 (51–71)
Spring	24 (13–35)	2 (0–6)	25 (15–35)	52 (40–63)
Age				
Adult	24 (13–35)	2 (0–6)	25 (15–35)	52 (41–64)
Juvenile	25 (15–36)	2 (0–5)	27 (18–36)	57 (46–66)
Sex				
Male	23 (14–34)	2 (0–5)	25 (16–34)	53 (42–63)
Female	29 (17–41)	2 (0–7)	30 (20–41)	60 (49–71)

[a]Minimum NEXRAD detection height is based on the lowest altitude detected by Horton et al. (2016).
[b]Height of low-rise buildings based on that of an 11-story building (Loss et al. 2014).
[c]Sweep of wind turbines is based on the average land-based turbine constructed in 2022 (Wiser et al. 2023).
[d]Height of large communication towers based on Gehring et al. (2011).

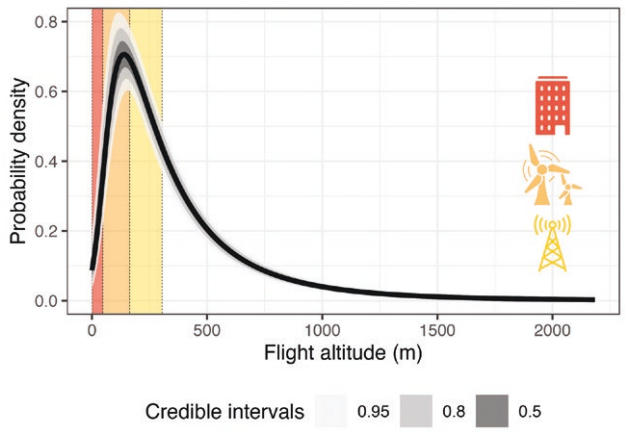

FIGURE 2. Distribution of *S. minor* flight altitudes above ground level compared to the heights of low-rise buildings (red; 47 m), land-based wind turbines (orange; 32–164 m), and large communications towers (yellow; 244 m). Dark line represents the median flight altitude distribution calculated using the base model, whereas ribbons represent 50%, 80%, and 95% highest density credible intervals for the distribution. We produced these distributions by simulating a log-normal distribution for each posterior value of μ_f and σ_f. Raw altitude data were collected using GPS transmitters in the eastern portion of the woodcock's range in 2020–2024.

this effect is due to a biological difference between the flight altitudes of woodcock and other nocturnal migrants. Woodcocks' unconventional use of low altitudes may be related to morphology, as they have a higher wing loading than 79% of species sampled by Poole (1938), and their wing loading appears to be considerably higher than other birds of comparable size. Birds with a higher wing loading than woodcock were generally nonmigratory gamebirds or ducks, with the most similar species in terms of wing loading and mass being the nonmigratory *Columba livia* (Rock Pigeon; Poole 1938). As high wing loading is speculated to be associated with migratory inefficiency (Bowlin and Wikelski 2008), woodcock may be inefficient fliers and fly at lower altitudes as a result (Grilli et al. 2017).

As anticipated, we found little support for an age or sex difference in woodcock flight altitudes but considerable support for a seasonal difference, with woodcock flight altitudes being higher during spring (mean: 444 m, 95% CRI: 333–578 m) than fall (mean: 338 m, 95% CRI: 267–423 m). This matches seasonal variation in flight altitudes observed via radar (Horton et al. 2016), presumably due to migrants using southerly low-level jet streams present at higher altitudes in the spring (La Sorte et al. 2014). Due to lower flight altitudes in fall, woodcock are more likely to fly at altitudes coinciding with wind turbines (31% vs. 25% of altitudes) and communication towers (61% vs. 52%) in fall than spring. Woodcock collisions with buildings appear to occur more frequently during the spring rather than fall (Loss et al. 2019, 2020), which is notable as flight altitudes are generally higher during spring. This may be due to a mismatch between the data collection windows for bird collision studies and the fall migratory periods of woodcock (Loss et al. 2020). These building collisions may also be associated with the frequency of migratory stopovers: woodcock spend longer migrating during spring, and the increased number of stopovers may expose woodcock to a greater risk of building collision during crepuscular flights (Berigan 2024). Other factors, such as seasonal weather (Loss et al. 2020) or male display behavior in the spring (McAuley et al. 2020) could be alternative drivers for seasonal differences in building collision rates.

Despite a mean flight altitude of 379 m, we found that 57% of woodcock flight altitudes occurred below 305 m. The occurrence of so many flight locations within the range of anthropogenic obstacles during peak times for migratory flight (12–1 am Eastern Time) suggests that woodcock are not solely vulnerable to collision with these obstacles during takeoff and landing but throughout their migratory flights. While all 3 types of structures examined here are responsible for substantial migratory bird mortality, collisions with these

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structures are likely caused by different mechanisms. Low-rise buildings, for example, are responsible for more collisions of all taxa than any other structure examined in this study (estimated 339 million per year; Loss et al. 2014) despite having the lowest height (47 m). The exceptional rate of mortality associated with low-rise buildings is likely the joint function of their prevalence (estimated 15.1 million low-rise buildings in the USA; Loss et al. 2014) and a higher rate of mortality associated with birds undergoing stopovers, which can be lengthy and expose birds to mortality risk through the diurnal hours in addition to nocturnal migratory flights (Cusa et al. 2015). In comparison, communication towers kill fewer birds (4–5 million per year) and are less prevalent on the landscape (>26,000 in the USA) but are more likely to result in collisions during migratory flights, especially if guy wires are present (Gehring et al. 2011). Understanding these differing risk profiles is an important facet of interpreting the relative mortality risk of low-altitude flights and drawing connections between low-altitude flights and increased rates of bird collisions.

Low flight altitudes are one of several risk factors for obstacle collisions, and these factors may differ in importance based on whether collisions occur during diurnal stopovers or nocturnal migratory flights. A proper understanding of how collision risk changes between those periods, especially on a species level, is critical to the implementation of mitigation measures, as most measures will reduce obstacle collision chance during one period but not the other. Reduction of artificial light at night, as well as flashing lights and reduction of guy wires on communication towers, are all seen as potential mechanisms to reduce obstacle collisions during nocturnal migratory flights (Gehring et al. 2009, 2011, Van Doren et al. 2021). The application of ultraviolet reflective stickers to windows or the use of bird safe glass, on the other hand, focus on reducing obstacle collisions during diurnal hours (De Groot et al. 2022). As birds may differ in their vulnerability to obstacle collisions during diurnal vs. nocturnal hours (e.g., woodcock, which migrate at low altitudes and are likely more prone to nocturnal collisions), the impact of individual mitigation efforts on collision risk will be species-specific. A well-balanced effort focusing on reducing both nocturnal and diurnal collision risk while accommodating for local phenomena, such as migratory staging areas or reduced flight altitudes during overwater crossings (Howell et al. 2020, Galtbalt et al. 2021), will be required to effectively reduce bird collision mortality.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Conflict of interest statement

The authors declare no conflicts of interest.

Ethics statement

All capture and handling were conducted in accordance with protocols approved by the University of Maine Institutional Animal Care and Use Committee (Protocols A2017-05-02 and A2020-07-01) as well as permits from the USGS Bird Banding Laboratory and Canadian Bird Banding Office.

Author contributions

E.J., A.R., and L.B. initially conceived of this paper, and L.B. conducted the analysis with support from S.C. L.B. wrote the initial draft manuscript, and E.J. and A.R. provided substantive feedback on subsequent drafts. E.J., A.R., A.F., R.D., S.C., and L.B. contributed to the collection and maintenance of the Eastern Woodcock Migration Research Cooperative dataset. G.B., B.C., G.C., J.D., K.F., C.G., W.H., M.H., D.H., S. Maddox, S. McWilliams, S. Meyer, T.N, J.P., C.R., D.S., C.S., J. Stiller, J. Straub, M.T., D.W., and L.W. provided funding and/or logistic support for the acquisition and deployment of GPS transmitters on woodcock. All authors read and approved the final manuscript.

Data availability

The data underlying this article is publicly available at Berigan et al. (2025).

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