# Low migratory flight altitudes may explain increased collision risk for American Woodcock

# Abstract

Understanding bird migration at low altitudes is critical to evaluating risk of collision with obstacles; however, quantifying flight at low altitudes is often complicated by difficulty measuring low altitude flight using weather radar. Recent advances in satellite tracking technologies for avian species allow quantifying use of low altitudes by nocturnal migrants with a high level of precision, allowing species-level inference into potential collision risk based on use of risky altitudes. The American Woodcock (*Scolopax minor*) has long been considered 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 379m (SD: 393m), flying higher during spring (mean: 444m, 95% credible interval: 333–578m) than fall (338m, 95% CRI: 267–423m). 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. Woodcock 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

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

# 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 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 American Woodcocks’ increased vulnerability to collisions with airspace obstacles.

# 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 (<200m above ground level, hereafter AGL). Obstacles present at these altitudes include buildings (365–988 million bird collisions per year, Loss et al. 2014), wind turbines (234 thousand 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 sweep of a wind turbine at some point during their migratory flight, and White et al. (2020) found that migrating bird densities near Lake Erie remained highest below 400m, 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 birds are equally susceptible to obstacle collisions; Nichols et al. (2018) identified 13 species and 7 genera as “supercolliders”, or taxa which are found more often after obstacle collisions than expected given their population size. Gathering species-level data regarding use of low altitudes would allow us to determine whether altitude is contributing to the increased risk of collision with obstacles for these species.

Gaining species-level insight into bird flight altitudes requires the use of bird-borne telemetry equipment, usually either altimeters or satellite 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 size. 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), which found that of 13 tracked Swainson’s Thrush (*Catharus ustulatus*) migratory flights, one bird spent over an hour flying at altitudes <100m before rising to altitudes of 300–500m. A second thrush spent the entirety of its ~2 hour migratory flight at an altitude of ~40 m. Galtbalt et al. (2021) found that Whimbrel (*Numenius phaeopus*) and Far Eastern Curlew (*Numenius madagascariensis*) have overwater median flight altitudes of 132m and 156m above sea level, respectively, although those altitudes increase to 718m and 538m when flying over land. Further transmitter studies focusing specifically on birds that are highly susceptible to collisions with airspace obstacles may allow us to better understand the prevalence of low altitude flights among these species, and how those flights influence collision risk.

The American Woodcock (*Scolopax minor*, hereinafter woodcock) has long been thought to migrate at low altitudes, and thus may face increased collision and mortality risks. Even before tracking data were available, Mendall and Aldous (1943) estimated that woodcock migrate at altitudes of 12–15m based on the high rate of woodcock collisions with power, telephone, and telegraph lines. Woodcock are among the most frequently found species due to building collisions in major US 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 has been suggested as a potential causal factor in their declines of 0.8% per year since the 1960s (Cooper and Rau 2012, Loss et al. 2020). No studies to date have quantified woodcock flight altitudes, or examined how those altitudes might impact their vulnerability to collision with airspace obstacles.

Here we investigate the propensity for the American Woodcock to fly at low altitudes during migratory flights and examine how flight altitudes compare to the altitudinal distributions of common airspace obstacles. We also quantify the proportion of woodcock flight locations that fall 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 (418–459m AGL; 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 will be lower in fall than spring, in accordance with general trends in nocturnal migrants (Horton et al. 2016), and that flight altitudes will 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 sheds light on the vulnerability of woodcock and other nocturnal migrants to airspace collisions during their migratory flights, and the necessity for further study of low altitude movements of birds in general.

# Methods

## Data collection and preprocessing

We collected woodcock locations with altitude readings from 2020–2024 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 spotlights and mist nets (McAuley et al. 1993) and attached 4–7 g PinPoint transmitters with altimeters (Lotek Wireless Inc., Newmarket, Ontario, CA) using a rump-mounted leg loop harness (Fish et al. 2024). We aged and sexed birds upon capture, where juveniles were birds undertaking their first fall and spring migrations, after which they were considered adults.

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) locations. We subset these readings to include only locations in which birds had a known migratory or non-migratory state, based on the hidden Markov model delineations of migratory tracks derived in Berigan (2024). We used ArcGIS Pro 3.2.1 (ESRI 2024a) to calculate the difference between the recorded altitude and orthometric elevation for each location (elevation layer; ESRI 2024b), providing a measurement of height above ground level for each point. To ensure computational tractability, we divided all observed altitudes by the maximum altitude in the dataset (2183m), allowing estimated flight altitudes to scale between 0 and 1.

We classified data for our models based on prior descriptions of woodcock activity patterns. Woodcock are ground feeding birds which rarely fly outside of crepuscular hours (Rabe et al. 1983). When rare diurnal flights do occur they are generally brief, comprising 1–3% of diurnal time budgets, and close to the ground (McAuley et al. We therefore made a modeling assumption that all diurnal locations could be treated as known ground locations. As woodcock are nocturnal migrants, we define potential flight locations as all points which were nocturnal, occurred during migration, and were preceded and followed by steps longer than 99% of stopover movements (6.68 km, Berigan 2024).

## 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 0m, making their recorded altitudes solely attributable to measurement error by the GPS units. The recorded altitude of a ground location *i* can be modelled as follows:

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|  |  | Eq. 1 |

where represents degrees of freedom, is the mean error observed across all observations and is the scale parameter associated with the error. As such, the known ground locations can be used to directly inform the measurement error term , which we assume remains consistent between ground and flight locations. We chose to model 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 = , or recorded in flight with altitude , in which case = + . This can be modelled as follows:

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|  |  | Eq. 2 |

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|  |  | Eq. 3 |

Where for each location *i* that is identified in flight (i.e., = 1) is drawn from a log-normal distribution with location parameter and scale parameter . 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

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|  |  | Eq. 4 |

Where 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 Eq. 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, , and location parameter for the flight distribution, both received normal priors with mean 0 and standard deviation 1. The standard deviation of the measurement error, , and the scale parameter for the flight distribution, both received half-normal priors with mean 0 and standard deviation 1. The proportion of true flight locations among all potential flight locations, , 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, , 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*) , , and parameters

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|  |  | Eq. 5 |

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|  |  | Eq. 6 |

where the , , and 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 and 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 the R package *rstan* (Stan Development Team 2024, 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 & Gelman 1998). We ran models using the scaled height above ground level estimates for , and back-transformed all parameter estimates into meters AGL for evaluation. We described the posteriors of flight altitude distribution parameters by simulating a log-normal distribution for each posterior value of and , 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 by the number of potential flight locations in each dataset. We summarized posteriors for all parameters using median values and highest density credible intervals (HDI) 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

Using the posterior distribution of predicted flight altitudes (calculated as Lognormal()), we evaluated 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 compared woodcock flight altitudes to the minimum altitude (120m) detected by Horton et al. (2016) using the Next Generation Weather Radar (NEXRAD) system, a weather radar system in the United States frequently used to study bird migration (DeMott et al. 2022, Horton et al. 2023). We quantified the proportion of woodcock flight locations that fell below a 120m 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 non-residential buildings ≤11 stories) result in the majority of window collision mortalities in the United States (Loss et al. 2014), we also quantified the proportion of locations at an altitude below that of an 11-story building (47m). We estimated the proportion of woodcock flight locations which fell within the rotor sweep of the average land-based wind turbine installed in 2022 (32–164m; Wiser et al. 2023). Finally, we measured the proportion of woodcock flight locations that fell below the height of a 305m 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, with 258 possible migratory locations (106 individuals). The base model predicted that 144 of these locations were most likely recorded when the bird was in flight (95% CRI: 127–161; estimates from all models in Supplemental Material Table S1). Estimated median flight altitude was 262m, and mean flight altitude was 379m (Table 1). Woodcock flew at mean altitudes of 338m in fall and 444m in spring, with 94% probability that mean flight altitudes are lower in fall than spring. Adult woodcock flew at mean altitudes of 431m while juveniles flew at altitudes of 371m, with 79% probability that mean flight altitudes are higher for adults than juveniles. Male woodcock flew at mean altitudes of 417m while females flew at altitudes of 352m, with 82% probability that mean flight altitudes are higher for males than females (Figure 1).

Over half (57%) of woodcock flight locations were at altitudes below 305m, posing potential risks for collisions with low-rise buildings, wind turbines, and communications towers (Table 2, Figure 2). Woodcock were equally likely to fly within range of low-rise buildings in fall and spring, while they were 6% more likely to fly at wind turbine altitude and 9% more likely to fly at communication tower altitude during fall. 27% of woodcock locations were below the minimum flight altitude reported in Horton et al. (2016) and likely would not have been detectable using NEXRAD weather radar.

Table 1. Characteristics of American Woodcock (*Scolopax minor*) altitudes above ground level during migratory flights, measured using the base model (bold) as well as season (Fall/Spring), age (Adult/Juvenile), and sex (Male/Female) models. Estimates indicate the median value of the posterior distribution, while credible intervals reflect highest density intervals.

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| Metric | Estimate | 95% Credible Interval |
| **Median flight altitude** | **262m** | **218–304m** |
| *Fall/Spring* | 242/295m | 188–296/220–376m |
| *Adult/Juvenile* | 291/266m | 218–374/210–324m |
| *Male/Female* | 289/247m | 225–356/184–310m |
| **Mean flight altitude** | **379m** | **320–447m** |
| *Fall/Spring* | 338/444m | 267–423/333–578m |
| *Adult/Juvenile* | 431/371m | 317–581/295–465m |
| *Male/Female* | 417/352m | 326–532/270–456m |
| **Standard deviation** | **393m** | **279–540m** |
| *Fall/Spring* | 328/491m | 210–504m/292–825m |
| *Adult/Juvenile* | 465/358m | 262–805m/233–546m |
| *Male/Female* | 429/352m | 269–674m/211–567m |
| **Skewness** | **3.95** | **2.64–6.53** |
| *Fall/Spring* | 3.65/4.34 | 2.33–6.24/2.48–8.38 |
| *Adult/Juvenile* | 4.19/3.63 | 2.33–7.86/2.31–6.12 |
| *Male/Female* | 3.93/3.80 | 2.40–6.95/2.20–6.77 |

Table 2. Proportion of American Woodcock (*Scolopax minor*) migratory flight altitudes within height intervals related to weather radar and airspace obstacles. Metrics are measured using the base model (bold) as well as season (Fall/Spring), age (Adult/Juvenile), and sex (Male/Female) models. Estimates indicate the median expected value, while credible intervals reflect highest density intervals for each estimate.

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| Metric | Estimate | 95% Credible Interval |
| **Below NEXRAD detection altitude (120m)1** | **27%** | **20–35%** |
| *Fall/Spring* | 29/24% | 19–40/13–35% |
| *Adult/Juvenile* | 24/25% | 13–35/15–36% |
| *Male/Female* | 23/29% | 14–34/17–41% |
| **Below height of low-rise buildings (47m)2** | **2%** | **0–5%** |
| *Fall/Spring* | 2/2% | 0–6/0–6% |
| *Adult/Juvenile* | 2/2% | 0–6/0–5% |
| *Male/Female* | 2/2% | 0–5/0–7% |
| **Within sweep of land-based wind turbines (32–164m)3** | **28%** | **21–35%** |
| *Fall/Spring* | 31/25% | 22–41/15–35% |
| *Adult/Juvenile* | 25/27% | 15–35/18–36% |
| *Male/Female* | 25/30% | 16–34/20–41% |
| **Below height of large communication towers (305m)4** | **57%** | **50–64%** |
| *Fall/Spring* | 61/52% | 51–71/40–63% |
| *Adult/Juvenile* | 52/57% | 41–64/46–66% |
| *Male/Female* | 53/60% | 42–63/49–71% |

1 Minimum NEXRAD detection height is based on the lowest altitude detected by Horton et al. (2016).

2 Height of low-rise buildings is determined based on that of an 11-story building, based on Loss et al. (2014).

3 Sweep of wind turbines is based on the average land-based turbine constructed in 2022 (Wiser et al. 2023).

4 Height of large communication towers based on Gehring et al. (2011).

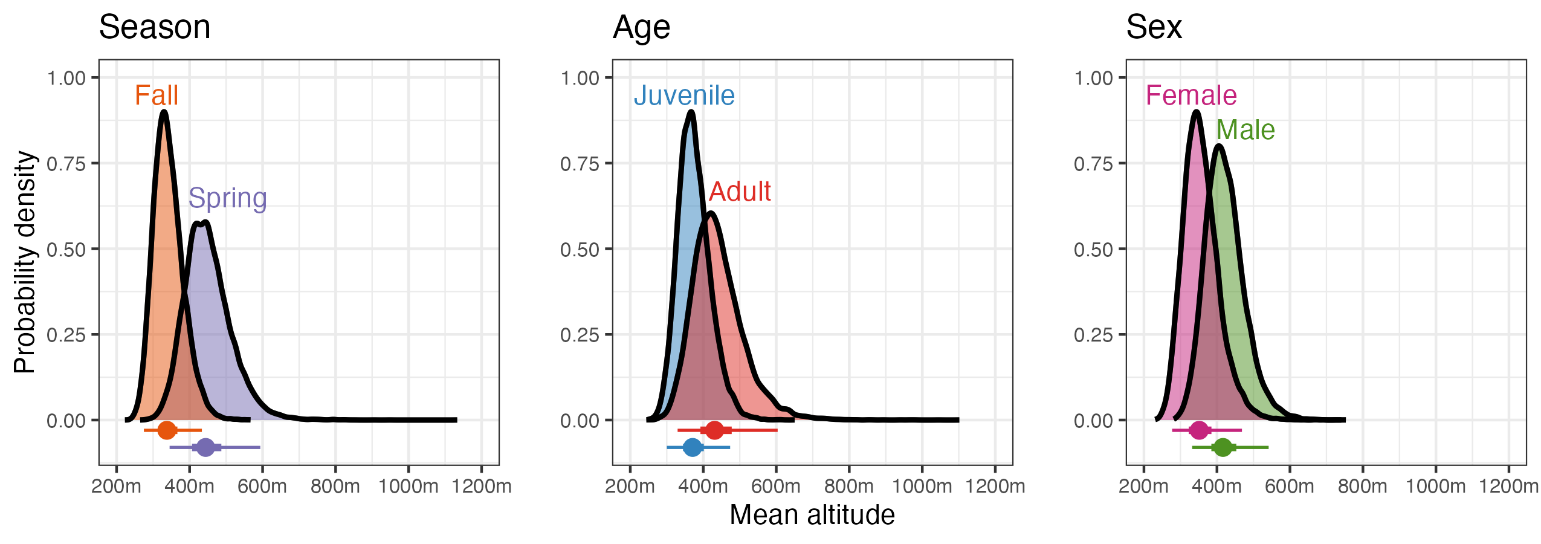


Figure 1. Posterior distributions for mean flight altitude of American Woodcock (*Scolopax minor*) flight locations, subdivided by season, age, and sex. Density plots represent posterior distributions of parameters, while point intervals represent the medians (points), 50% highest density credible intervals (thick lines), and 95% highest density credible intervals (thin lines) of the posteriors.

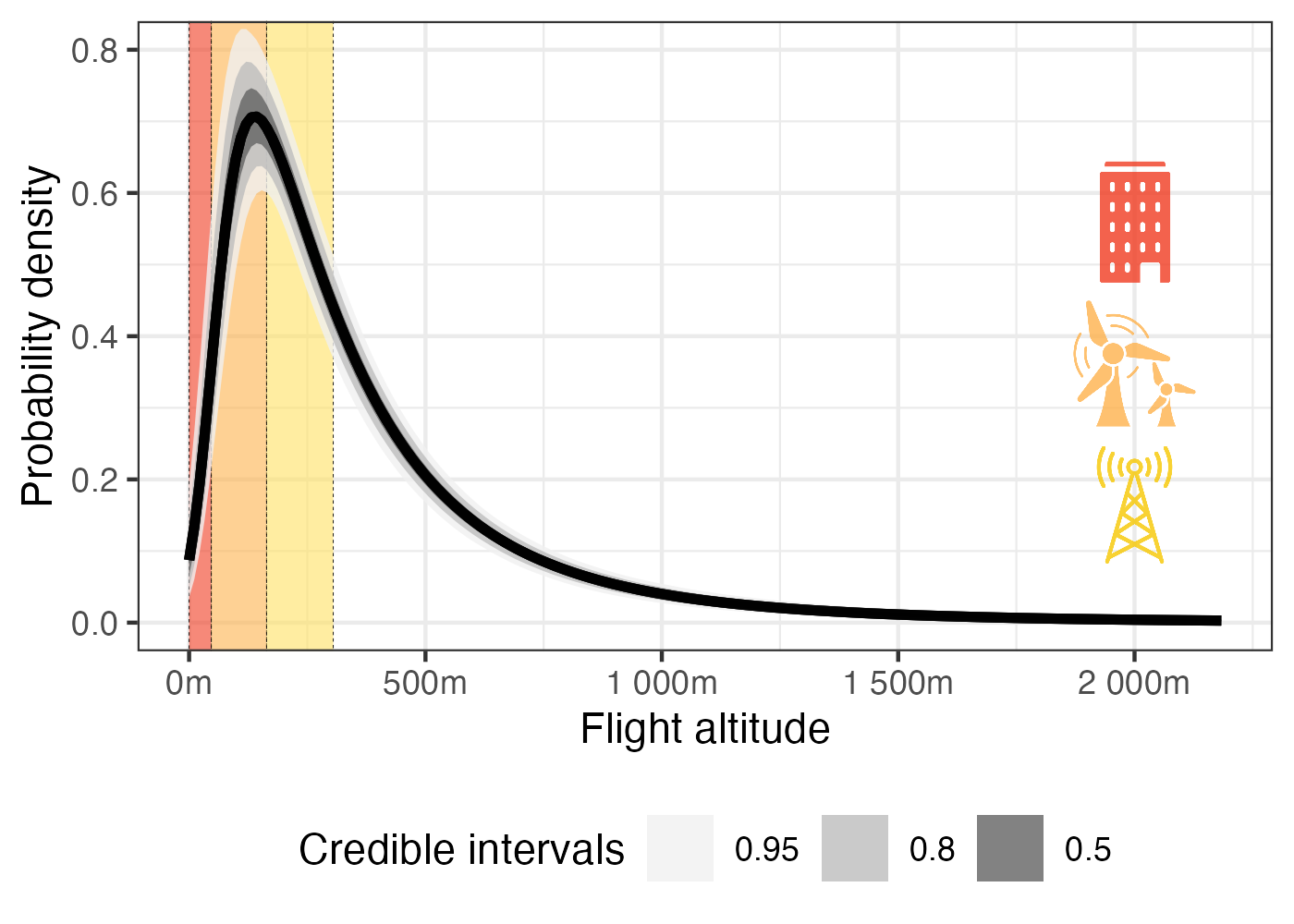


Figure 2. Distribution of woodcock flight altitudes above ground level compared to the heights of low-rise buildings (red; 47m), land-based wind turbines (orange; 32–164m), and large communications towers (yellow; 244m). The dark line represents the median flight altitude distribution calculated using the base model, while ribbons represent 50%, 80%, and 95% highest density credible intervals for the distribution.

# Discussion

We found that mean woodcock flight altitudes fell below those typical of most migrating birds during fall (woodcock: 338m; all birds: 418–491m) and spring (woodcock: 444m; all birds: 438–559m; Horton et al. 2016). This result may be due, in part, to the greater 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 (120m; 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 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 greater 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 non-migratory gamebirds or ducks, with the most similar species in terms of wing loading and mass being the non-migratory Rock Pigeon (*Columba livia*; Poole 1938). As high wing loading is speculated to be associated with migratory inefficiency (Bowlin & Wikelski 2008), woodcock may be inefficient fliers and choose 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: 444m, 95% CRI: 333–578m) than fall (mean: 338m, 95% CRI: 267–423m). This matches seasonal variation in flight altitudes observed via radar (Horton et al. 2016), presumably due to migrants utilizing southerly jet streams present at higher altitudes in the spring (La Sorte et al. 2014). As a result of these seasonal differences, woodcock are more likely to fly at altitudes that intersect 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, Loss et al. 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. 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). Woodcock also conduct lengthy aerial displays during the spring, which may provide an additional opportunity for collision with buildings.

Despite a mean flight altitude of 379m, we found that 57% of woodcock flight altitudes occurred below 305m. The occurrence of so many flight locations within the range of anthropogenic obstacles during peak times for migratory flight (12–1am 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 three types of structures examined here are responsible for substantial migratory bird mortality, collisions with these structures are likely caused by different mechanisms. Low-rise buildings, for example, are responsible for more collisions than any other structure examined in this study (est. 339 million per annum, Loss et al. 2014) despite having the lowest height (47m). The exceptional rate of mortality associated with low rise buildings is likely the joint function of their prevalence (est. 15.1 million low rise buildings in the United States, 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 annum) and are less prevalent on the landscape (>26 thousand in the United States) 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, which 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, Gehring et al. 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.

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