

RESEARCH ARTICLE

Geese migrating over the Pacific Ocean select altitudes coinciding with offshore wind turbine blades

Emily L. Weiser¹  | Cory T. Overton²  | David C. Douglas³  | Michael L. Casazza²  | Paul L. Flint¹ 

¹U.S. Geological Survey, Alaska Science Center, Anchorage, Alaska, USA

²U.S. Geological Survey, Western Ecological Research Center, Dixon, California, USA

³U.S. Geological Survey, Alaska Science Center, Juneau, Alaska, USA

Correspondence

Emily L. Weiser
Email: eweiser@usgs.gov

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Abstract

1. Renewable energy facilities are a key part of mitigating climate change, but can pose threats to wild birds and bats, most often through collisions with infrastructure. Understanding collision risk and the factors affecting it can help minimize impacts on wild populations. For wind turbines, flight altitude is a major factor influencing collision risk, and altitude-selection analyses can evaluate when and why animals fly at certain altitudes under certain conditions.
2. We used GPS tags to track Pacific Flyway geese (Pacific greater white-fronted goose, tule greater white-fronted goose and lesser snow goose) on transoceanic migrations between Alaska and the Pacific Coast of the contiguous United States, an area where offshore windfarm development is beginning. We evaluated how geographic and environmental covariates affected (1) whether birds were at rest on the water versus in flight (binomial model) and (2) altitude selection when in flight (similar to a step-selection framework). We then used a Monte Carlo simulation to predict the probability of flying at each altitude under various conditions, considering both the fly/rest decision and altitude selection.
3. In both spring and fall, geese showed strong selection for altitudes within the expected rotor-swept zone (20–200 m asl), with 56% of locations expected to be within the rotor-swept zone under mean daylight conditions and 28% at night. This indicates a high possibility that migrating geese may be at risk of collision when passing through windfarms. Although there was some variation across subspecies, geese were most likely to be within the rotor-swept zone with little wind or light tailwinds, low clouds, little to no precipitation and moderate to cool air temperatures. Geese were unlikely to be in the rotor-swept zone at night, when most individuals were at rest on the water.
4. *Synthesis and applications.* These results could be used to inform windfarm management, including decisions to shut down turbines when collision risk is high. The altitude-selection framework we demonstrate could facilitate further study of other bird species to develop a holistic view of how windfarms in this area could affect the migratory bird community as a whole.

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altitude selection, goose, migration, movement, offshore, turbines, wind energy, windfarms

1 | INTRODUCTION

To minimize climate change impacts, a shift from fossil fuels to renewable energy is underway. However, renewable energy facilities can pose threats to birds, most often through direct mortality caused by collisions (Conkling et al., 2022). In particular, wind turbines are a source of fatal collisions for many avian taxa, and established regulatory thresholds may not sufficiently protect wild birds from population-level effects (mortality 1%–5% higher than background levels; Schippers et al., 2020). Windfarms can also have sublethal effects if birds increase energy expenditure to avoid the area (Fox & Petersen, 2019) or if birds are displaced from foraging or breeding habitat (Furness et al., 2013; Shaffer & Buhl, 2016). Installing a new windfarm could therefore represent a trade-off between benefiting birds through reducing climate change and harm through direct and indirect effects on survival.

Predicting effects of energy facilities on birds can support management actions to identify and mitigate any expected harm. Avian collision risk depends on frequency of encountering a windfarm, altitudes at which birds fly (highest risk at an altitude coinciding with the turbine blades, i.e., the rotor-swept zone), turbine characteristics such as blade length and speed and any behavioural avoidance of turbines and blades (Desholm & Kahlert, 2005; Furness et al., 2013; Masden & Cook, 2016). Migrating birds often fly at higher altitudes than those making local movements (Hüppop et al., 2006; Sugimoto & Matsuda, 2011; Zehtindjiev & Whitfield, 2011), but migrating birds may fly at lower altitudes with headwinds, precipitation, cloud cover, twilight or night (or, in other cases, during the day) and cooler air temperatures (Galtbalt et al., 2021; Hüppop et al., 2006; Lindström et al., 2021; Marcelino et al., 2021). Wind speed and direction can vary with altitude, so migrants may also seek altitudes that provide the best wind support, where wind support is defined as the amount of assistance (or resistance) provided by the wind in the intended direction of flight (Senner et al., 2018). However, most studies to date have focused on terrestrial windfarms or seabirds making local movements, and information is limited for other taxa that migrate offshore. Most previous studies have also described flight altitude as a response to conditions experienced by a bird, rather than also considering conditions simultaneously available at other altitudes, and therefore do not fully represent factors that may affect flight altitude.

A more robust approach is an altitude-selection framework, which is similar to a step-selection framework (Thurfjell et al., 2014) in that ambient conditions at both used and available locations (altitudes) are considered. Application of this altitude-selection framework has been rare thus far, with only one published example that we are aware of (Galtbalt et al., 2021). That study found that favourable wind conditions were less important than previously thought; curlews first selected a flight altitude due to the inherent costs

versus benefits of that altitude, such as energetic cost of climbing, air density and thus flight efficiency, and water loss (Klaassen, 2004; Klaassen et al., 1999; Pennycuik, 1989), before selecting for any other ambient conditions. As new windfarms continue to be developed, further study of altitude selection would support evaluation of the risks of bird-turbine collisions. Models of altitude selection may be especially useful for contexts in which directly documenting bird mortality is difficult, such as for offshore windfarms where carcasses cannot be documented or retrieved.

We quantified altitude selection of Arctic geese on transoceanic migrations between Alaska and the Pacific Coast of the contiguous US Windfarm development is just beginning in this area, and little is known about flight characteristics of waterfowl during offshore migrations. We tracked altitude and geographic location of 45 individuals of three subspecies of two species: Pacific greater white-fronted goose (*Anser albifrons sponsa*, hereafter GWFG), tule greater white-fronted goose (*A. a. elgasi*, hereafter TWFG), and lesser snow goose (*A. caerulescens caerulescens*, hereafter LSGO). For both fall and spring migration, we quantified (1) the probability of being in flight versus at rest and (2) altitude selection. We evaluated the relationship between each behaviour and ambient conditions: wind support at various altitudes, distance from shore, air temperature, precipitation, cloud base height and daylight. We then predicted how often geese would be within the expected rotor-swept zone (20–200m above sea level [asl]) for offshore wind turbines (>1km from shore) under various conditions. Our results could be used to inform windfarm management, and our altitude-selection framework could be a valuable tool for studies of other species across the globe in both applied and theoretical contexts.

2 | MATERIALS AND METHODS

We evaluated the relevance of patterns in altitude selection to anticipated offshore windfarm development off the west coast of North America (southeast Alaska, British Columbia, Oregon, Washington and California; hereafter the study area; Figure 1). Based on current and projected technologies, we expected that offshore wind turbines in these areas would have blades spanning 20–200m asl (hereafter the rotor-swept zone) and be placed at least 1km from shore, with no outer bound on the distance from shore. The final data set used in our analyses (over-ocean goose locations >1km from shore, with all associated environmental covariates) (Weiser et al., 2024a) and scripts to replicate the analyses and data simulations (Weiser, 2024) are publicly available.

Bird location data were obtained from three goose taxa (GWFG, TWFG and LSGO) that winter in the Sacramento Valley of California, USA and transit portions of the northeast Pacific Ocean

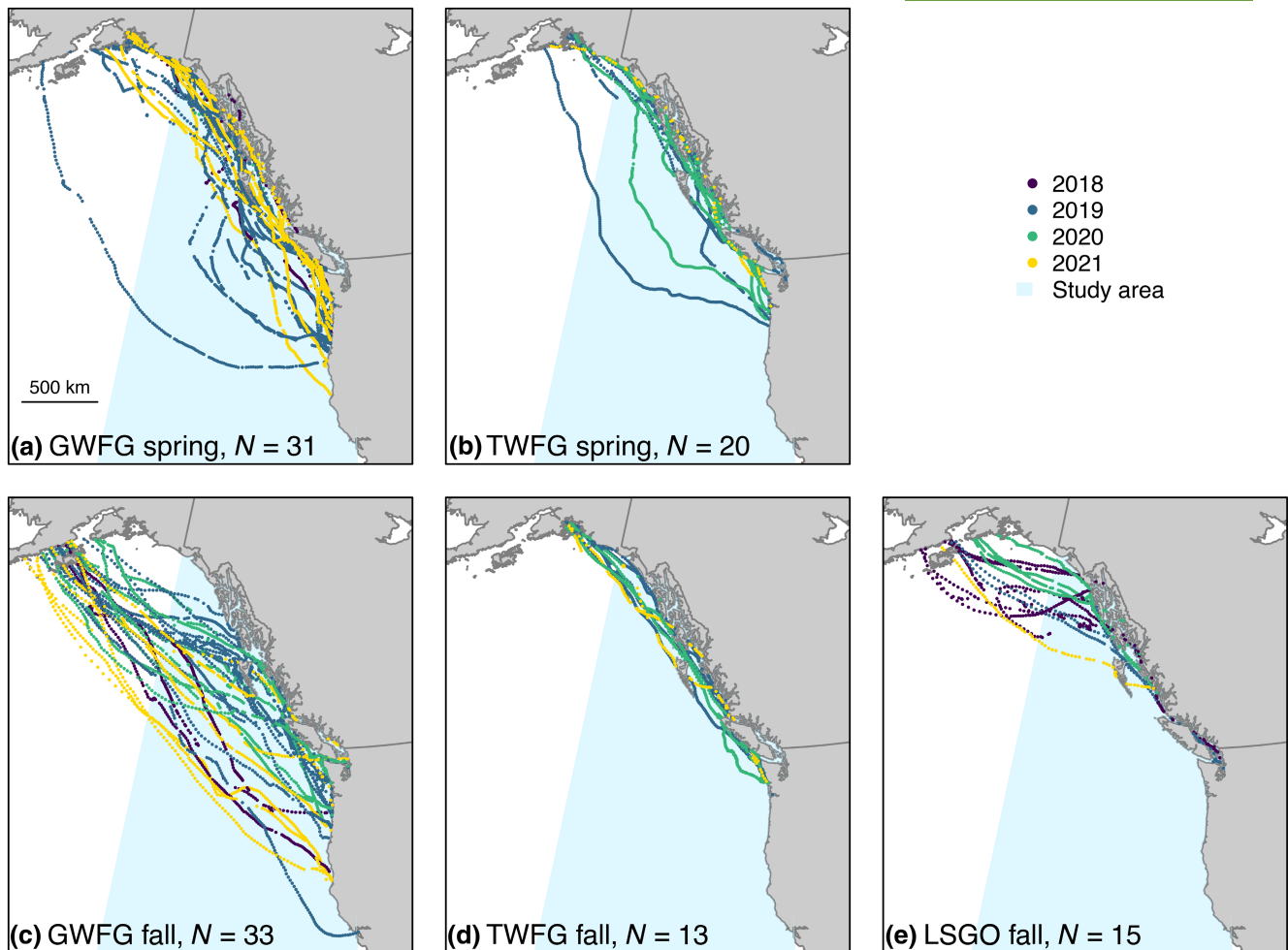


FIGURE 1 Mapped tracks for all offshore goose migration bouts (>1 km from the Pacific coast of the United States and Canada) (Weiser et al., 2024a). Points outside the study area (west of -141°) were excluded from the analysis. N is the number of migration bouts, where any given individual could have been tracked for multiple bouts (multiple years). LSGO in spring did not migrate over ocean and were thus excluded from this analysis. GWFG, Pacific greater white-fronted goose; LSGO, lesser snow goose; TWFG, tule greater white-fronted goose.

during migration to and from the Alaskan and Russian Arctic. We captured birds in late fall or early spring in the Sacramento Valley (all subspecies), early fall in Oregon (TWFG only), or late summer in the Western Arctic or Wrangel Island, Russia (LSGO only). We applied solar-charging Ornitela® GPS-enabled tracking collars (model N38 or N44 depending on goose size), which averaged 2% of bird body mass across individuals and never exceeded 2.75%. All animal procedures were reviewed and approved by the US Geological Survey Western Ecological Research Center Animal Care and Use Committee and conducted under Federal Banding Permit #21142 and California permit #SC-8090. We programmed the tags to collect the geographic position and altitude every 15 min when battery power was sufficient (87% of fixes were successfully completed at 15-min intervals). Data were stored on-board until the tag was within range of a GSM tower. For further details on tagging and data acquisition, see Appendix S1. For all analyses presented here, we used only migration bouts over ocean (>1 km from shore; 114 bouts by 45 birds), where a migration bout is a spring or fall migration (some individuals were tracked for multiple seasons).

Altitude values recorded by GPS units are subject to error, usually tens of meters (Lato et al., 2022), but our data set also showed more extreme apparent errors of hundreds to thousands of meters. As detailed in Appendix S1: Addressing altitude error, we evaluated errors for geese that were clearly resting on the ocean (based on instantaneous GPS speed) and used that information to identify process versus sampling error, which we used along with interpolation to produce an adjusted altitude estimate for each goose location.

We also determined whether the bird was at rest by using instantaneous ground speed as recorded by the tag. Our data showed a natural break where most speeds were <3 m per second (mps) or ≥ 5 mps (Figure S4), which agreed well with a previously used threshold of >4 mps (assuming very slow speeds could be due to measurement error or ocean currents). To avoid ambiguity, we assigned <3 mps as at-rest and ≥ 5 mps as in-flight, and excluded fixes with speeds between those values (0.7% of locations) from all analyses. We also excluded records with speed <3 mps and altitude >100 m (0.3% of locations), assuming those records reflected ambiguity in whether geese were in flight (at-rest

records with altitude >0 but $<100\text{m}$ could result from noise in altitude measurements).

For each goose location, we used data from the ERA5 reanalysis (Hersbach et al., 2020, 2022) as provided by Movebank's (Kays et al., 2022) Env-Data tool to calculate wind support at several altitude bands using inverse distance weighted calculations in x , y , z , and time dimensions (Safi et al., 2013). We used altitude bands of 10m asl, 100–2000m asl in 100m increments and 2500–5000m asl in 500m increments, thus providing finer resolution at lower altitudes (used more frequently by geese) while reducing demand on the Env-Data portal by using coarser bands at higher altitudes. For all altitude bands at each goose location, we retrieved the u (eastward) and v (northward) wind components, which together define wind speed and direction. Sometimes Env-Data returned missing data for low altitudes, in which case we substituted the ERA5 10-m modelled wind values for $\leq 25\text{m}$ altitudes or the modelled 100-m winds for 25–150m altitudes. We used u and v to calculate wind support in meters per second, where negative values indicate a headwind (Safi et al., 2013). We assumed the bird's direction of flight was directly toward the subsequent GPS location if the bird was in-flight. If the bird was at rest, we assumed its direction of travel was -50° (relative to 0°N) in spring (i.e., general compass bearing from northern California to the Alaska Peninsula) or the reverse at $+130^\circ$ in fall. Wind support was significantly correlated with altitude, with larger wind support at higher altitudes, but the correlation was weak ($|r| < 0.10$). Wind support was also strongly correlated between adjacent altitude bands ($r > 0.97$) and moderately correlated between the lowest (10m asl) and highest (3500m asl) altitudes used by geese ($r = 0.69$), indicating limited altitudinal variation in the wind support available to each goose at any given place and time.

We also annotated each goose location with the distance to coast from Movebank (Kays et al., 2022; NASA Goddard Space Flight Center Ocean Ecology Laboratory Ocean Biology Processing Group, 2009), in case birds changed altitude in preparation for flying over coastal terrain and to potentially inform decisions for the distance from shore at which to place wind turbines. We also calculated the daylight level based on time of day and location with the 'solarpos' function in R package *mapproj* v. 1.1-3 (day, civil twilight, or night; Bivand & Lewin-Koh, 2022). Finally, we retrieved weather data directly from ERA5 (single levels, hourly data, $0.25^\circ \times 0.25^\circ$ resolution; Hersbach et al., 2022): hourly mean air temperature at 2m asl, total hourly precipitation (mm) and cloud base height (m asl). For each goose location, we assigned the weather value from the corresponding ERA5 cell and hour (no spatial or temporal interpolation). The weather covariates were uncorrelated or weakly correlated with one another across all goose locations ($|r| < 0.23$).

2.1 | Statistical analysis: Probability of being in flight

First, we evaluated effects of environmental covariates (Table 1) on whether geese were in flight versus at rest at each recorded location over the ocean ($>1\text{km}$ from shore). We modelled each

subspecies and season separately, as we expected that responses to conditions might vary across subspecies (due to different migratory routes or physiology) and seasons (due to different migratory routes, conditions and constraints on timing). We standardized each covariate to mean = 0 and SD = 0.5 so that the magnitudes of the estimated effect sizes would be directly comparable across covariates measured on various natural scales, including for binary covariates. We used a generalized linear mixed model (GLMM) with a binary response variable (at rest = 0, in flight = 1) and an auto-regression term to account for autocorrelation via *glmmTMB* v. 1.1.3 (Brooks et al., 2017) in R v. 4.1.3 (R Core Team, 2022). We tested for effects of wind support at sea level, daylight and hourly precipitation. Daylight was a categorical covariate with three levels: day (sunrise to sunset), civil twilight and night (including nautical and astronomical twilight). Our dataset involved repeated measures of individuals and multiple individuals per year, so we included random effects of individual and year to account for pseudoreplication (with 1–15 individuals in each group in each year). To aid interpretation of results, we used parametric bootstrapping of the effect size estimates to predict the probability that geese would be in flight under a range of values of each covariate.

2.2 | Statistical analysis: Altitude selection

To evaluate altitude selection for geese in flight ($\geq 5\text{ mps}$) over the ocean ($>1\text{km}$ from shore), we used a step-selection framework to evaluate conditions used by geese versus matched conditions that were available but unused. The step-selection framework was relevant because we were assessing spatiotemporal series of individual locations, though here we were not interested in turn angles or step lengths, which are often considered in a step-selection function. A similar analysis has previously been applied to altitude selection in a conditional logistic mixed-effects model (Galtbalt et al., 2021), but we used a conditional Poisson mixed-effects model, as Muff et al. (2020) found that to be analytically equivalent but better able to handle a large dataset like ours (thousands of locations).

We followed Muff et al. (2020) to implement the analysis in a Bayesian framework using integrated nested Laplace approximation via *INLA* v. 22.03.16 (Rue et al., 2009) in R version 4.1.3 (R Core Team, 2022). For each subspecies and season, we applied the model to our dataset containing one record for each point at which geese were recorded in flight over open ocean, plus one record for every unused altitude band at the same location and time. Our response variable was binary, where used altitudes were set to 1 and available unused altitudes were set to 0. Available altitudes were identified by the bird's previous altitude, elapsed time, and a maximum climb rate threshold of 1.16 mps. This reflected the largest mean climb rate +2 SD empirically estimated for migrating brant (*Branta bernicla*; mean = 0.62, SD = 0.27; Green & Alerstam, 2000), as no climb-rate data were available for our study species. We did not limit the potential descent rate, assuming that geese could reach sea level from any used altitude (up to 3500m) within the 15-min interval between records.

TABLE 1 Covariates tested for the probability of being in flight or altitude selection by migrating geese.

Covariate	Description	Source	Tested for effects on:	
			Probability of being in flight	Altitude selection
Altitude	Grouped into bands with the following means: 10, 20, 50–250 by 50s, 300–2000 by 100s, 2500, 3000, 3500m asl	GPS tracking collars (this study)	Yes	Yes
Wind support	Assistance provided by the wind based on wind speed, wind direction, and the direction to the bird's next location (mps). One value per altitude band	ERA5 (<i>u, v</i>) via Movebank	10m asl only	All used and available altitude bands at each bird location
Daylight	Categorical: day, civil twilight, night	<i>maptools</i>	Day, civil twilight, night	Day + civil twilight pooled, night
Distance to coast	km from the bird's location to the nearest coastline	Movebank	–	Yes
Cloud base height	Height of the base of the lowest cloud layer (m asl)	ERA5 (<i>cbh</i>)	–	Yes
Temperature	Hourly mean air temperature at 2 m asl (°C)	ERA5 (<i>t2m</i>)	–	Yes
Precipitation	Hourly total precipitation (mm)	ERA5 (<i>tp</i>)	Yes	Yes

Sources: This study (Weiser et al., 2024a), ERA5 (Hersbach et al., 2022), Movebank (Dodge et al., 2013; Kays et al., 2022), *maptools* (Bivand & Lewin-Koh, 2022).

Abbreviation: asl, above sea level.

We included a fixed effect for each standardized covariate of interest (Table 1). Two covariates (altitude and wind support) varied by altitude band and thus were represented by both linear effects and quadratic effects. We also tested an interaction between altitude and wind support. The remaining covariates (day vs. night, distance from coast, hourly mean air temperature, hourly total precipitation and cloud base height) were constant across altitude bands, and thus were represented only by interactions with altitude, excluding a main effect of each covariate. We also included random effects of year and individual on the linear effects of altitude and wind support to account for pseudoreplication. Following Muff et al. (2020), we used an uninformative prior with a mean=0 and precision=0.0001 for each slope coefficient, and a penalized complexity prior of PC(3, 0.05) for the precision of the random component of each slope. To allow inference from the random-slopes model, we built the model such that the intercept was interpreted as a random effect with precision fixed at 10^{-6} (Muff et al., 2020). After running the full model for each subspecies and season, we removed covariates with backwards stepwise selection until only significant terms remained (95% CI excluded zero).

2.3 | Predictions

From the final model for each subspecies and season, we generated predictions for the altitude selected by geese (and the 95% CI) across the observed ranges of the other included covariates, using a Monte Carlo simulation approach following Signer et al. (2017). A simulation approach was necessary to estimate selected altitudes because the modelled parameter estimates refer to relative selection strength (RSS) and cannot easily be translated to raw altitude. We simulated each species and season by (1) calculating the RSS for each altitude

band (0–3500m asl) under certain conditions, (2) randomly drawing starting altitudes for 500 individuals based on the RSS values, specified values of environmental covariates and estimated effects of each covariate from the altitude selection model and (3) simulating altitudes at 1099 subsequent locations for each individual based on the current altitude, covariate values and covariate effects. We dropped the first 100 simulated locations for each individual as burn-in and used the remaining 1000 locations from 500 individuals to estimate the probability (proportion of locations) of geese flying at each altitude under each set of environmental conditions.

To begin evaluating potential conflicts with offshore windfarms, we also quantified the probability of a goose flying in the rotor-swept zone (20–200m) under various values of other covariates. For this exercise, we were interested in all geese, not only those in flight. We therefore repeated the simulation exercise as described above, but this time we also simulated a binomial process for whether a simulated goose was at rest (in which case it was assigned altitude=0) or in flight (in which case the goose's altitude was simulated as described above) based on covariate effects estimated by our model for the probability of being in flight. We then calculated the proportion of simulated goose locations that were within the rotor-swept zone under each set of environmental conditions.

3 | RESULTS

3.1 | Tracking data summary

Our data set included 114 migration bouts from 45 geese that migrated over the ocean (>1 km offshore) within our study area (Figure 1). Many birds spent most of their spring or fall migration far offshore, especially

GWFG in fall (Figure 1c). LSGO took more inland routes that mostly bypassed the study area in fall (Figure 1e) and stayed over land in spring so their spring migration is not included here. Some systematic differences were apparent across years or seasons in terms of the general routes taken; for example, GWFG generally used more inshore routes in spring than in fall, except in spring 2019 (Figure 1a,c). Variation was also evident across bouts; for example, two TWFG bouts extended far offshore while the others were inshore (Figure 1b,d).

During spring migration, GWFG and TWFG occurred in the study area from mid-April to mid-May. The three subspecies varied in when they were present in the fall, spanning late August to late October (Table 2). The proportion of locations that were in flight (versus at rest) varied from 0.49 to 0.65 across subspecies and seasons (Table 2). The mean of our corrected altitude values (241 m asl) was very close to the mean of the uncorrected values (246 m asl), indicating that our altitude correction process would not introduce bias into our results. For all subspecies-season groups, most in-flight locations within the study area were recorded at low altitudes: 30% within the rotor-swept zone (20–200m) and 22% below that zone, with some variation across subspecies and seasons (Table 2; Figure S5). Altitude-specific values of wind support were broadly distributed across subspecies and seasons, but with lower means in spring than fall (Figure S6). In-flight goose locations occurred disproportionately near the coast, without precipitation and with cloud base height below 1500 m asl (Figure S6).

3.2 | Probability of being in flight

The three covariates evaluated for the probability of geese being in flight versus at rest (wind support at sea level, hourly precipitation

and time of day) showed significant effects for nearly all subspecies-season groups (Table S1). Wind support had the strongest positive effects, where higher wind support was associated with considerably higher probabilities of flight (Figure 2a–c). Time of day had the strongest negative effects, where most geese were expected to be in flight during the day but very few during civil twilight or night (Figure 2g–i). Precipitation had moderate negative effects for GWFG and TWFG in spring, but no effect in fall for those subspecies and an uncertain negative effect for LSGO in fall (Figure 2d–f).

3.3 | Altitude selection

For each subspecies-season group, altitude selection was significantly affected by several covariates (Figure 3; Table S2). The two strongest effects were altitude, where all groups selected lower altitudes (sometimes with a small quadratic effect) and wind support, where all groups selected altitudes with higher wind support.

The remaining covariates did not vary with altitude and thus could be tested only as an interaction with altitude, not as a main effect (see Section 2.2). The interactions between altitude and hourly precipitation or day versus night were retained for all groups, and other covariates were retained for a subset: air temperature and cloud base height for all but LSGO in fall, and distance from coast for GWFG in spring and TWFG in fall. In many cases, the interaction between altitude and another covariate had a statistically significant but weak effect on altitude selection, likely due to our large dataset (thousands of locations) enabling detection of weak relationships. This meant that the covariates were selected for retention in the model, but predictions for the probability of use of each altitude band were similar regardless of the value of the interacting covariate

TABLE 2 Study subspecies and summary statistics for Pacific Flyway geese migrating offshore; the full data set is publicly available (Weiser et al., 2024a).

	GWFG: Pacific greater white-fronted goose		TWFG: Tule white-fronted goose		LSGO: Lesser snow goose
	Spring	Fall	Spring	Fall	Fall
Individuals	20	18	14	9	11
Bouts	32	34	20	13	15
Locations	3073	2347	1509	1030	486
Dates in study area	17 Apr–13 May	13 Sept–8 Oct	14 Apr–12 May	29 Aug–20 Sept	3 Oct–27 Oct
Proportion in flight	0.55	0.65	0.64	0.49	0.62
Maximum flight altitude (m asl)	3175	3418	2393	2676	3520
Observed in-flight proportion in rotor-swept zone (20–200m)	0.31	0.32	0.24	0.31	0.23
Observed in-flight proportion < 20m	0.31	0.12	0.20	0.24	0.08
Predicted per cent in rotor-swept zone under mean conditions (95% CI):					
Daylight	63 (60–66)	61 (58–64)	48 (45–51)	46 (43–49)	60 (57–63)
Night	10 (8–11)	44 (40–47)	18 (15–20)	12 (10–14)	56 (53–59)

Note: 'Migration bouts' were tallied per individual and season when a bird was tracked during the transoceanic portion of its migration. Some individuals were tracked for more than 1 year (e.g., two spring tracks) and thus are represented more than once here. The predicted proportions are from simulations using parameters estimated by (1) the model for the probability of being in flight and (2) the altitude selection model.

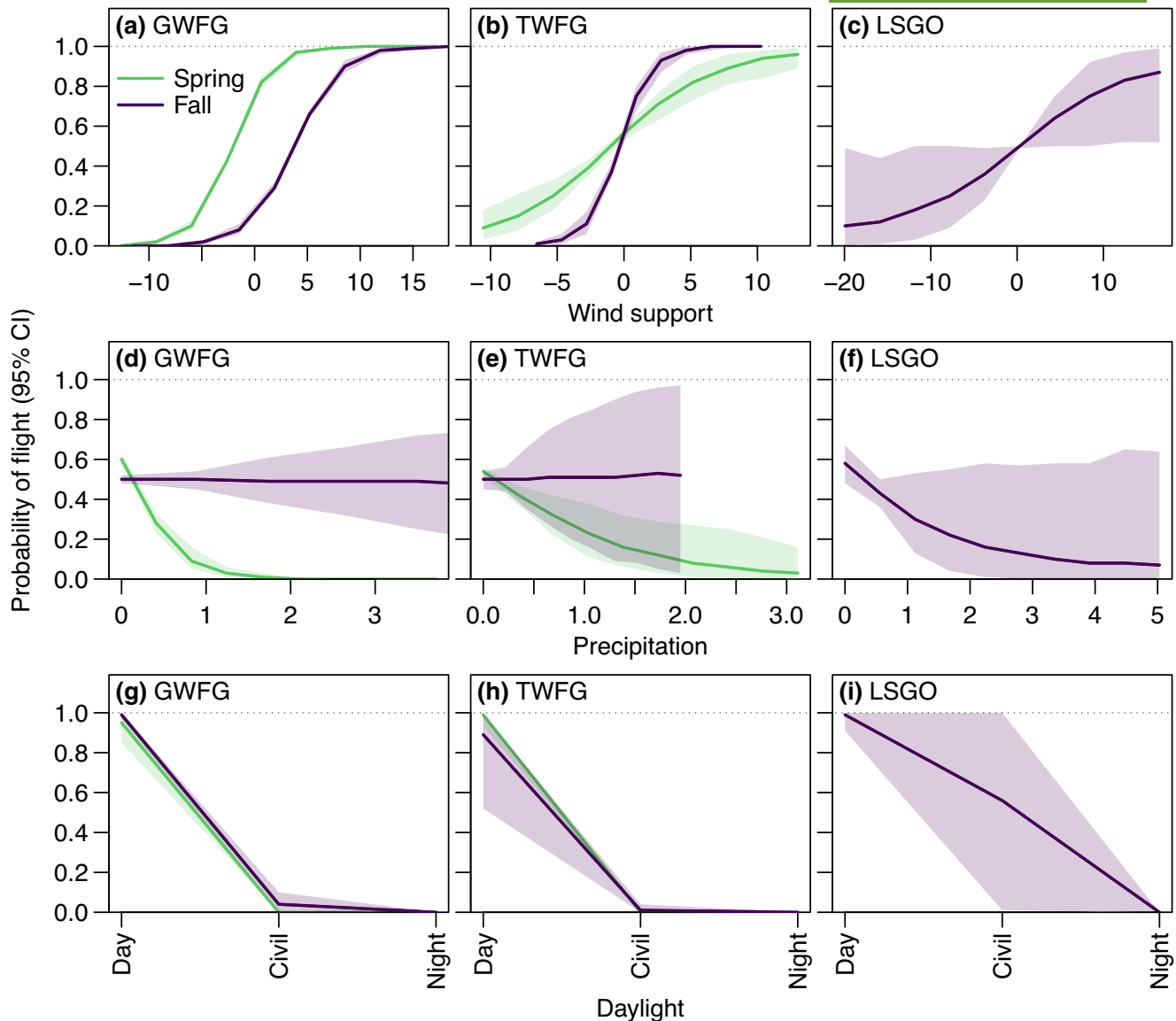


FIGURE 2 Predicted probability of being in flight (vs. at rest) for geese of each subspecies in each season across ranges of each covariate. These predictions were generated with parametric bootstrapping from a GLMM accounting for autocorrelation. In each panel, values of other covariates were fixed at the mean. The dotted horizontal line is for reference at the maximum possible probability of 1. GWFG, Pacific greater white-fronted goose; LSGO, lesser snow goose; TWFG, tule greater white-fronted goose.

(Figure 4). The strongest interactions were evident for TWFG in fall, which used higher altitudes when wind support at those altitudes was high and when near the coast (Figure 4f). TWFG showed a moderately increased probability of using higher altitudes during the day in both seasons (Figure 4i,j), with warm air temperatures in both seasons (Figure 4l,m) and with little to no precipitation in spring (Figure 4p).

The combination of (1) the probability of being in flight and (2) altitude selection for birds in flight often resulted in strong variation in the expected probability of a given goose location being within the rotor-swept zone (20–200m asl). For three groups (GWFG in both seasons and TWFG in fall), moderate wind support values were strongly associated with a higher probability of being in the rotor-swept zone (Figure 5a). TWFG in fall were less likely to be in

the rotor-swept zone when very near the coast (Figure 5b), and all groups were less likely to be in the rotor-swept zone at night than during the day (Figure 5c). Higher clouds had weak to moderate negative effects (Figure 5d). TWFG were less likely to be in the rotor-swept zone with warmer temperatures in both seasons (Figure 5e). The effect of precipitation was generally negative, but it was weak for GWFG and LSGO in fall and parabolic for TWFG in spring (Figure 5g). During daylight and under mean observed values of the other covariates, 56% (95% CI=44%–65%) of goose locations across all groups were expected to be in the rotor-swept zone. Across groups, this predicted percentage varied from 46% (95% CI=43%–49%) for TWFG in fall to 63% (95% CI=60%–66%) for GWFG in spring (Table 2). The predicted overall percentage dropped to 28% (95% CI=8%–58%) at night, when more geese were expected to

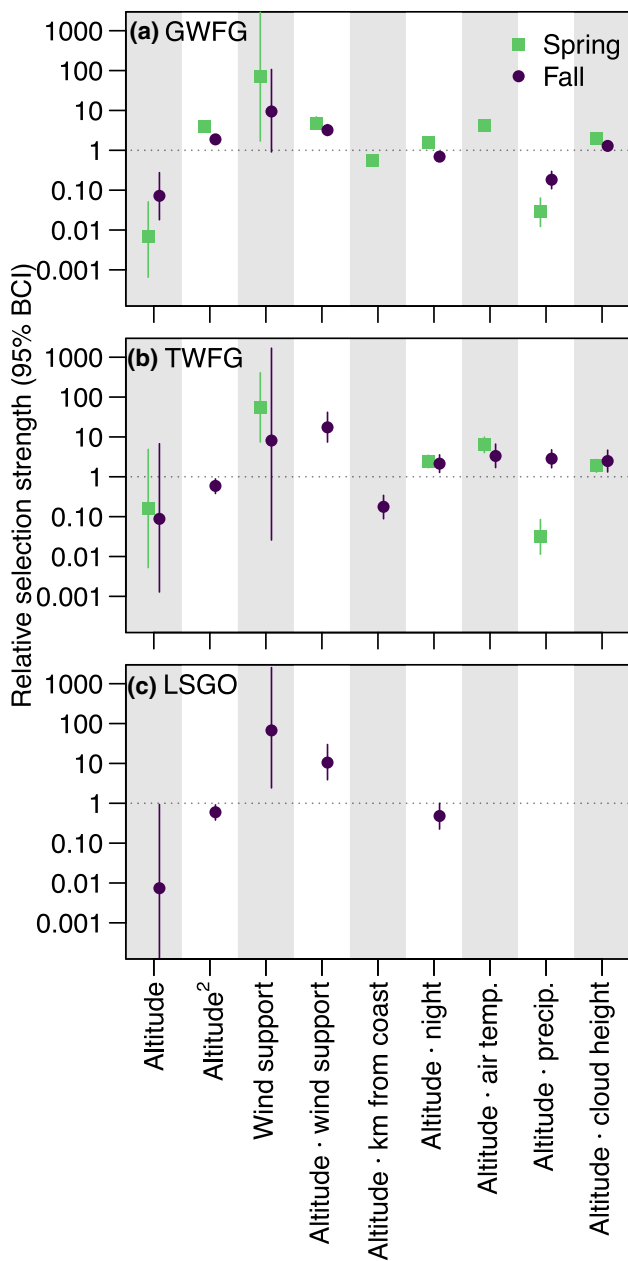


FIGURE 3 Effects of altitude, wind support at each altitude and covariates interacting with altitude on the relative selection strength for geese in flight over the study area. Effects are plotted on the log scale as multiples of the baseline value of 1 and indicate selection for values one unit (2 SD) from the mean of available altitudes. For example, a value of 0.10 would indicate that an altitude 2 SD higher than the mean available altitude had a probability of use of 1/10th of that of the mean available altitude. GWFG, Pacific greater white-fronted goose; LSGO, lesser snow goose; TWFG, tule greater white-fronted goose.

be at rest on the water. Given that the altitude of the rotor-swept zone may vary across windfarms or with changing technology, we developed a web-based application to summarize the proportion of goose locations expected to be within a user-specified altitude band in daylight and mean environmental conditions for each subspecies (<https://www.usgs.gov/apps/RotorZone/>; Weiser et al., 2024b).

4 | DISCUSSION

The Pacific Flyway geese we tracked showed extensive use of offshore areas during their transoceanic migrations. Under mean conditions, 56% of all goose locations in offshore areas were expected to be within the rotor-swept zone during daylight and 28% at night, indicating a potentially high diurnal risk of collision with wind turbines. The predicted probability of flying in the rotor-swept zone increased when conditions favoured flight and selection of low altitudes. Many relationships were similar across subspecies and seasons, but some varied, indicating that our results have some generalizable applicability, but taxon- and season-specific assessments will continue to be useful.

Of the three subspecies, LSGO spent little time in the offshore study area, instead migrating mostly over land. This not only reduced our statistical power to evaluate covariates affecting altitude selection in this population, but also indicated that LSGO would not likely be affected by offshore windfarm development except in the northern edge of our study area (off the coast of Southeast Alaska). In contrast, both GWFG and TWFG spent substantial time in the study area. TWFG were generally closer to shore than GWFG and thus would more often coincide with windfarm development on the continental shelf, though GWFG also migrated along the continental shelf in spring and crossed that area in fall.

Across subspecies, the geese we tracked spent one-half to two thirds of their over-ocean migration time at rest, when they would not be at risk of colliding with wind turbines. Resting was especially common at night or with negative wind support (headwinds) at sea level. Wind turbines operating at night or with strong winds against the direction of migratory travel (i.e., NW winds in the spring and SE winds in the fall in the Gulf of Alaska and northeast Pacific) are therefore unlikely to result in mortality of migrating geese. Precipitation was also often associated with more geese being at rest, especially in spring.

Time at rest could also be affected by extreme conditions not considered here. For example, dense wildfire smoke in fall 2020 that coincided with TWFG migration in our study area caused individuals to stage for extended periods on the water (Overton et al., 2022). We did not evaluate wildfire smoke in our analysis due to its rarity, but a response to smoke was reflected in our raw data set, where considerably more fall TWFG locations were at rest in 2020 (65%) than in 2019 and 2021 (35%). Extended offshore staging could increase the period of risk if resting birds periodically ascend into or through the rotor zone in search of suitable flight conditions.

For geese in flight, collision risk is partly driven by flight altitude. Our finding that geese strongly selected low altitudes aligns with previous work showing that migrating birds often select altitude itself over other covariates. Flying at higher altitudes incurs inherent costs such as the energetic expense of climbing, reduced air density (reducing lift) or higher water loss (Galtbalt et al., 2021; Klaassen, 2004). These costs would be affected by body mass and relative wing-loading (Norberg, 1990), and so could be particularly pronounced in geese, though strong altitude selection has also been

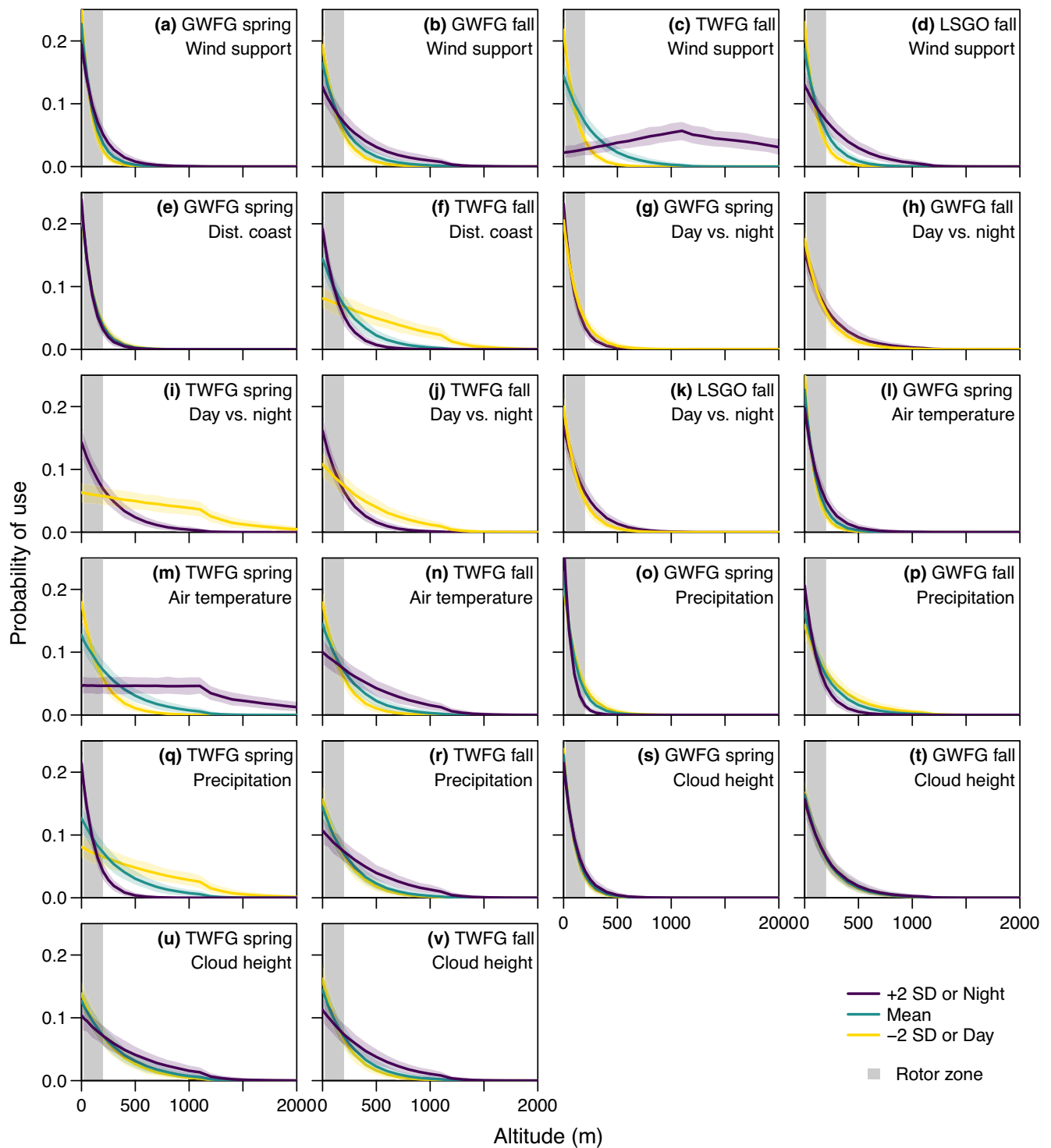


FIGURE 4 Predicted probability of use of each altitude (0–3500m) for each subspecies and season, depending on each covariate that was retained in the final model, assuming geese are in flight. Each panel shows a line for three values of the indicated interacting covariate: –2 SD, mean, and +2 SD, as calculated across all available points in the dataset; or two lines for day versus night for the binary daylight covariate. Missing panels indicate cases where a covariate was not retained for a given subspecies and season. To improve legibility, the x-axis is truncated (maximum predicted altitude was 3500m). In most cases, geese were most likely to fly in the rotor-swept zone (vertical grey bar; 20–200m), but with some variation depending on values of some covariates. GWFG, Pacific greater white-fronted goose; LSGO, lesser snow goose; TWFG, tule greater white-fronted goose.

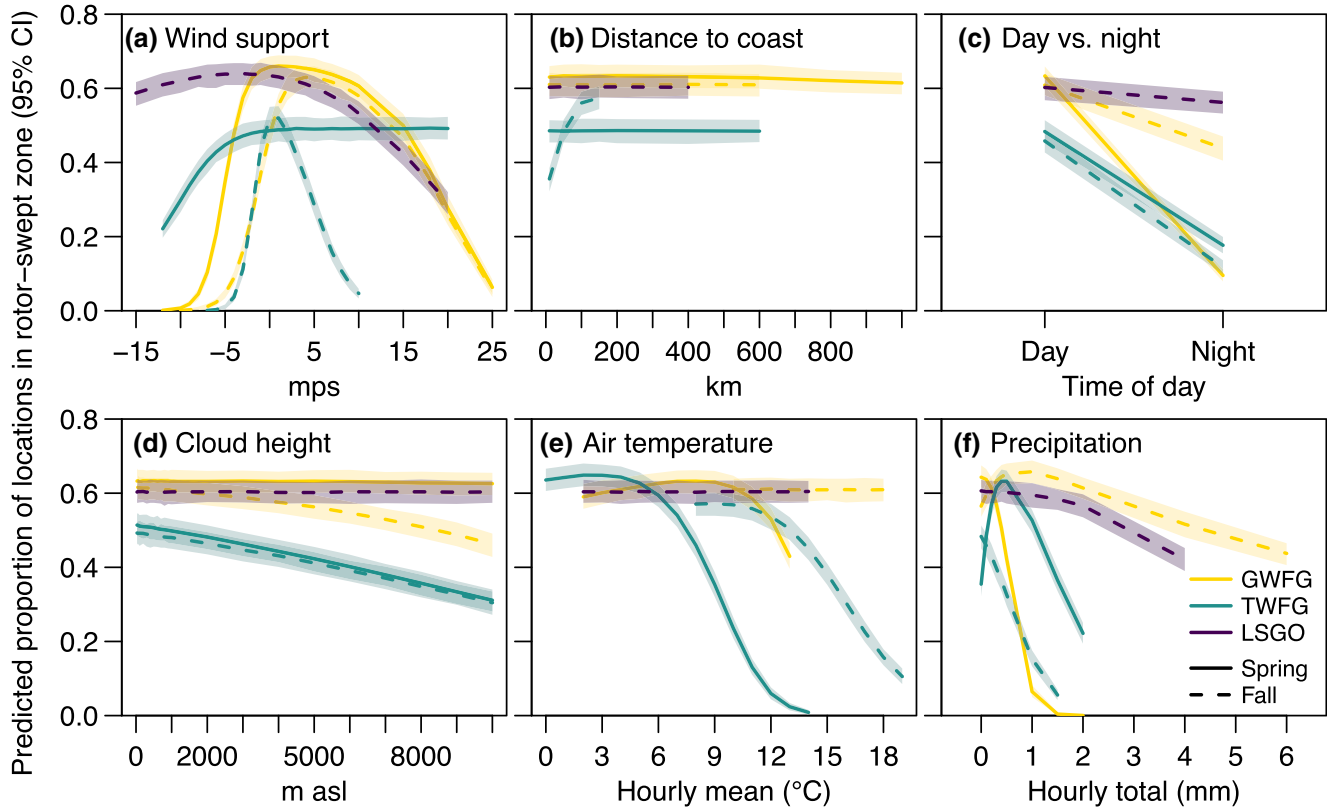


FIGURE 5 Predicted proportion of goose locations in the rotor-swept zone (20–200 m asl) under various conditions and for each subspecies and season, including all goose locations (in-flight and at-rest). Predictions are plotted only for the range of values observed for each subspecies-season group, and only for covariates retained in the final model for that group. In each panel, covariates other than those explicitly displayed were held at their mean value. GWFG, Pacific greater white-fronted goose; LSGO, lesser snow goose; TWFG, tule greater white-fronted goose.

found in a smaller species (curlews; Galtbalt et al., 2021). Evaluating other species in an altitude-selection framework would reveal the extent to which flight behaviour reflects strategies to minimize energetic and physiological costs.

The relationships we found between altitude selection and other covariates also revealed behavioural strategies and associated possibility of collision with future windfarms. First, calm winds prompted TWFG to fly in the rotor-swept zone, headwinds resulted in TWFG and GWFG flying below the rotor-swept zone, and strong tailwinds also resulted in geese flying above the rotor-swept zone, all likely resulting from strategies to optimize the trade-off between energetic costs and the need to complete migration. Higher flight with tailwinds has also been found in black brant, which initiated trans-Pacific migration on days with strong tailwinds and climbed to >1000 m (Dau, 1992), although it is unknown whether that behavioural response would continue throughout the migration bout. Second, geese tended to select higher altitudes (above the rotor-swept zone) with higher cloud base, even though flight altitudes were typically considerably lower than the cloud base, suggesting higher clouds may be associated with other conditions conducive to higher-altitude flight rather than directly affecting altitude selection. Third, warmer temperatures prompted higher flight in TWFG, possibly due to a thermoregulatory advantage of seeking cooler air at higher altitudes under those conditions (Senner

et al., 2018). Fourth, TWFG in fall selected higher altitudes when very near the coast. In fall 2020, TWFG near shore used high altitudes to avoid wildfire smoke (Overton et al., 2022), which could partly explain this relationship. More generally, our data set showed a tendency for TWFG to fly directly to inland sites without stopping at coastal wetlands, and so may have been gaining altitude near land in preparation for crossing the Pacific Coast Range.

Our study did not directly address the probability of geese migrating through a specific offshore wind development, but our birds' widely divergent migration paths suggest that only a small fraction of a population will likely encounter a specific windfarm in a given year. However, when geese and offshore windfarms coincide, we have demonstrated a high probability that geese will fly at altitudes in the rotor-swept zone. Mitigation measures to prevent collisions, such as shutting down turbines, could be targeted to conditions when geese are most likely to be in the rotor-swept zone: daylight, little wind or light tailwinds, low clouds, little to no precipitation and moderate to cool air temperatures. Alternatively, wind turbines may not operate with light winds or blade speeds may be slower, reducing the risk to geese under those conditions without additional management action. Our study was also conducted in the absence of wind turbines and assumed that migrating geese would not avoid windfarms. If GWFG, TWFG and LSGO show behavioural avoidance of turbines, as has

been documented in some other birds (BOWind, 2008; Chamberlain et al., 2006; Desholm & Kahlert, 2005; Plonczkier & Simms, 2012), the risk of collision would be reduced, though avoidance could incur other costs such as additional energetic expenditure or exposure to suboptimal migration conditions. Once construction of offshore windfarms begins in this region, further tracking studies could evaluate whether these goose species change their flight path or altitude to avoid turbines and thus reduce collision risk.

By demonstrating selection for the rotor-swept zone by geese during transoceanic migrations, this study sets the stage for evaluating and mitigating potential harmful effects of offshore windfarms on migrating waterfowl in the northeast Pacific. In quantifying collision risk under various conditions, our results can be used to mitigate risk through turbine management as well as furthering knowledge of how and why migrating birds select flight altitudes.

AUTHOR CONTRIBUTIONS

Cory T. Overton, Michael L. Casazza and Paul L. Flint conceived the study. Cory T. Overton collected the movement data. David C. Douglas compiled the geographic and wind support data. Emily L. Weiser compiled other environmental data, designed and performed the analysis and drafted much of the manuscript. All authors contributed critically to conceptualizing the analysis and writing the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data set (<https://doi.org/10.5066/P9VUNOQ9>), scripts used in the analysis (<https://doi.org/10.5066/P17VOLEY>) and web app

to explore the probability of geese flying in the rotor-swept zone (<https://www.usgs.gov/apps/RotorZone/>) are publicly available (Weiser, 2024; Weiser et al., 2024a, 2024b).

ORCID

Emily L. Weiser  <https://orcid.org/0000-0003-1598-659X>

Cory T. Overton  <https://orcid.org/0000-0002-5060-7447>

David C. Douglas  <https://orcid.org/0000-0003-0186-1104>

Michael L. Casazza  <https://orcid.org/0000-0002-5636-735X>

Paul L. Flint  <https://orcid.org/0000-0002-8758-6993>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Supplementary methods.

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