

**ATLANTIC BRANT WINTERING UPLAND FIELD USE AND
BIOENERGETICS**

by

David Jonas Weber

A thesis submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Master of Science in Wildlife Ecology

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Approved: _____
Christopher K. Williams, Ph.D.
Professor in charge of thesis on behalf of the Advisory Committee

Approved: _____
Jacob L. Bowman, Ph.D.
Chair of the Department of Entomology and Wildlife Ecology

Approved: _____
Brian E. Farkas, Ph.D.
Dean of the College of Agriculture and Natural Resources

Approved: _____
Louis F. Rossi, Ph.D.
Vice Provost for Graduate and Professional Education and
Dean of the Graduate College

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ABSTRACT

The need to understand waterfowl energetic demands and habitat use on the wintering grounds is increasingly important for conservation and management. Past research using scan-sampling techniques has produced important estimates of time budgets and daily energy expenditure, but modern technology can increasingly be used to obtain more precise movement data with multiple applications. Atlantic Brant (*Branta bernicla hrota*) increasingly use upland turfgrass fields, such as baseball fields and golf courses, throughout their wintering range and have undergone massive shifts in their food selection due to population declines caused by a loss of their preferred food, eelgrass, and severe winters. I sought to improve our understanding of Brant wintering ecology with an emphasis on upland turfgrass field use.

I used four years of wintering accelerometry data from 210 telemetered Atlantic Brant throughout New Jersey and New York, USA, to construct time budgets, estimate daily energy expenditure, and quantify habitat use. I also sampled turfgrass fields during the winters of 2021–22 and 2022–23 to explore the importance of field and grass characteristics in determining field use of Atlantic Brant in this urban ecosystem. I used Bayesian hierarchical modeling to quantify differences in daily energy expenditure and habitat use between sexes as well as among months and years.

I also explored the effects of environmental and temporal variables on energy expenditure.

I found the extrinsic characteristics of field size and distance to water to have consistently strong effects on field use in all models, while some intrinsic characteristics, such as grass height, live grass mass, clover mass, and carbon–nitrogen ratio had only moderate effects in some models. I found minimal to no effect of the mass of weeds, energy density, or distance to roost on field use. The average daily energy expenditure I calculated (1,238.2 kJ) was lower than in past observational studies, while the amounts of time spent in three behavioral states were comparable. Females had slightly higher average energy expenditure and spent notably more time in flight than males, and there were many notable differences among months and winters. My categorical model of behaviors predicted an increase in flight behavior at lower latitudes and higher tide levels, while a decrease was predicted during periods of rain and higher temperature. I found different trends of habitat use over time than previous studies on Atlantic Brant and found differences among regions to be the strongest driver of differences in habitat use.

I expect these results to help inform future management of Brant in the event of a decline in submerged aquatic vegetation or the Brant population. My improved energy expenditure estimate will allow future studies to more accurately estimate a wintering carrying capacity for Atlantic Brant. Explanations of differences in behavioral time budgets and habitat use will allow managers to consider more detailed effects, such as regional differences within the population and the importance of

environmental variables in affecting Brant behavior, energy expenditure, and habitat use.

Chapter 1

FACTORS INFLUENCING WINTERING UPLAND FIELD USE IN ATLANTIC BRANT

Introduction

Atlantic Brant (*Branta bernicla hrota*; hereafter “Brant”) breed in the eastern Canadian Arctic and spend the winter in shallow bays, lagoons, and tidal mudflats sheltered by barrier islands on the Atlantic coast of the United States (US) from Massachusetts to North Carolina. Typically arriving on the wintering grounds in late October, about 85% of the entire population winters in New Jersey and New York (Castelli et al. 2011). Brant populations can fluctuate wildly, in part due to severe winters and poor breeding seasons (Phillips 1932, Cottam et al. 1944, Kirby and Obrecht 1982). Such large population fluctuations led to concerns that the disappearance of preferred foods at wintering and staging areas may be linked to population declines (Cottam et al. 1944). Historically, wintering Brant fed primarily on abundant beds of eelgrass throughout their range. However, in the early 1930s, a wasting disease, likely caused by the protist *Labyrinthula zosterae*, decimated eelgrass populations throughout the eastern US and Europe (reviewed in Muehlstein 1989). While Brant continue to feed on eelgrass where it is present, the decline in eelgrass caused them to shift to primarily consuming other submerged aquatic vegetation (SAV), such as sea lettuces (*Ulva* spp. and *Enteromorpha* spp.), and saltmarsh grasses,

such as *Spartina alterniflora*. Increasingly, Brant have also been observed feeding on cultivated grasses and clover in parks, athletic fields, and lawns.

Studies on Brant foraging and diet in the US have primarily focused on SAV, not upland grasses. Therefore, little is known about how Brant select and use upland fields in their wintering range. However, Brant in the United Kingdom (UK) have made a dramatic switch to upland agricultural fields (St. Joseph 1979, Williams and Forbes 1980), leading to numerous studies examining field selection by Brant in order to provide suitable alternative foraging locations to dissuade geese from damaging agricultural crops. Brant in the UK and Canada geese (*Branta canadensis*) in the US select grass fields with higher nitrogen content. Other measures that are positively correlated with nitrogen, including protein content, percentage of live grass, and forage plant species, are also significant predictors of field choice in these species (Buchsbaum et al. 1981, Summers and Critchley 1990, Vickery et al. 1994, Riddington et al. 1997, Washburn and Seamans 2012). Grass height is also important, as shorter grass is preferred by geese because the apical halves of grass blades contain more nitrogen (Buchsbaum et al. 1986, Riddington et al. 1997). Mineral composition does not seem to play a significant role in food preference (Mathers and Montgomery 1997, McKay et al. 2001, Washburn and Seamans 2012).

Other factors can affect field selection and use but can be more difficult to measure than grass quality. For example, in their review of herbivorous waterfowl interacting with agriculture, Fox et al. (2017) noted that field selection is influenced by food intake rate, disturbance, food source depletion, snow cover, proximity to a safe

roost site, field size, and standing water. For example, Brant aggregate more where the percentage of live biomass is highest (Summers and Critchley 1990) and have less time to forage when they need to move among patches of food (Prop and Deerenberg 1991). Geese also tend to feed closer to roosts (Raveling 1969), on larger fields (Nilsson and Persson 1991), and on fields with standing water either on them or nearby. Therefore, when attempting to quantify Brant food availability and preference at a landscape level, both intrinsic factors (e.g., grass quality) and extrinsic factors (e.g., field or landscape characteristics) need to be considered.

Understanding how and why Brant use upland fields is essential for future management decisions on the wintering grounds. The North American Waterfowl Management Plan (United States Fish and Wildlife Service and Canadian Wildlife Service 1986) indicates that food is a limiting factor for populations, and determining the wintering carrying capacity for waterfowl is an important step in managing for a healthy population. Winter food availability can affect individual nutrition, body condition, distribution on the landscape, and migration timing (Williams et al. 2014). Malnutrition in the winter can lead to carryover effects that influence breeding success in the summer (Kaminski and Gluesing 1987, Anteau and Afton 2009).

I sought to determine variables that explain Brant upland field selection and use on the wintering grounds in New Jersey and New York. I hypothesized a negative effect of grass height, dead grass mass, carbon–nitrogen ratio, distance to the roost, and distance to open water on field use, as well as a positive effect of live grass mass, energy density, and field area. Understanding upland field selection and use is

essential for future management of Atlantic Brant populations, given the historical fluctuations in SAV abundance and more frequent interactions between Brant and humans in an increasingly urban environment. Furthermore, a better understanding of upland field use can allow for a more complete understanding of wintering food limitations and can be incorporated into future estimates of Atlantic Brant wintering carrying capacity.

Study Area

The study area included coastal New Jersey and the southern coast of Long Island, New York. Wintering Brant in this region are restricted to the immediate coast, generally on barrier islands and the bays that separate those islands from the mainland, and rarely travel inland more than a few kilometers from saltmarsh. Thus, the study area was further restricted to only the barrier islands, back bays, and upland turfgrass fields within ~8 km of the ocean (Figure 1.1).

The study area consists primarily of three habitat types: open water, estuarine marsh, and saltmarsh (Cowardin et al. 1979). The open water habitat consists of shallow subtidal embayments. The estuarine habitat contains intertidal streambeds, rocky shores, unconsolidated shores, and mudflats. The saltmarsh habitat consists of irregularly and regularly flooded intertidal emergent wetlands dominated by *Spartina* spp. Additionally, upland habitat adjacent to these habitats in urban and suburban areas is primarily turfgrass lawns, golf courses, and athletic fields predominantly covered by terrestrial grass (*Poa* spp.) and clover (*Trifolium* spp.).

The average winter low temperature in New Jersey (Atlantic City) is 0.1 °C, and the average high is 6.6 °C, with an average of 26.7 cm of winter rain. The average winter low temperature on Long Island (Wantagh Cedar Creek) is -1.3 °C, and the average high is 6.7 °C, with an average of 26.6 cm of winter rain (National Centers for Environmental Information 2021).

Methods

Capture and telemetry

The New Jersey Division of Fish and Wildlife and New York Department of Environmental Conservation captured Brant between January and April 2020–23 by using nets propelled by rockets armed with nitrocellulose fuel, typically on upland athletic fields or at freshwater inlets, with decoys and/or an electronic calling device. All captured birds were banded, and ~60 birds/year received Global Positioning System–Global System for Mobile Communications (GPS–GSM) backpacks, including Cellular Tracking Technologies ES-400 GPS–GSM + ACC telemetry systems and Ornitela OrniTrack 25 solar-powered transmitters. Backpacks were attached via an over-wing harness. Most instrumented birds were also marked with individually numbered tarsal bands to allow for individual identification in the field. Some units were deployed opportunistically on the breeding grounds in Canada by Environment and Climate Change Canada during the summer. Telemetry units were <3% of body weight, per Bird Banding Laboratory recommendations. Latitude and

longitude were recorded by the telemetry units every 30 min throughout the wintering period.

Intrinsic field characteristics

I collected grass samples from one “used” field, defined as having two or more GPS points from at least one telemetered bird, and one “unused” field, defined as having zero GPS points and no Brant feces present, within a telemetered Brant’s diurnal 99% kernel density estimate home range calculated using GPS points from the first 14 days of each month, November–April 2021–23. I collected samples during the remaining 14–17 days of each month after the construction of the home range. I sampled only Brant with at least one used and unused field within a home range to ensure pairing of samples. When the home ranges of multiple telemetered Brant overlapped and they were using the same upland fields, the birds were considered to be in the same flock and were treated as a single bird for sampling purposes to avoid pseudoreplication. Using home ranges to determine sampling locations allowed me to be certain that a field was available to be used by one or more Brant but was not used. I randomly sampled fields among used fields and unused fields within the home range that were safely accessible. Many predetermined random locations were inaccessible, and I chose alternative locations as needed. I calculated home ranges in the statistical software R (R Core Team 2021) using the “adehabitat” package (Calenge 2006) and mapped them in QGIS (QGIS Development Team 2022) for visual interpretation. For

home range calculations, I used only diurnal GPS points because *a priori* observations of Brant indicated rare or no use of upland feeding sites at night (unpublished data).

I collected grass samples for used fields within 20 m of a randomly selected GPS point. I collected samples for unused fields at a location determined by a random directional bearing and a random number of steps out into the field. Each sample consisted of three subsamples, all collected within a 20 m radius of the starting point by choosing a random bearing and number of steps to walk, in order to better capture within-field variation. In each subsample, I measured the tallest blade of live grass to the nearest millimeter with a ruler before cutting. I clipped subsamples at the soil line with a pair of scissors within a 10 × 10 cm quadrat and then placed them together in a labeled zip-closed plastic bag that was frozen at the end of the day.

After thawing the grass samples, I separated dead (brown) material from live (green) material and sorted the live material into grass (Poaceae), clover (*Trifolium* spp.), and other herbaceous plants (i.e., weeds). I dried the samples at 60 °C until a constant mass was achieved (typically after ~24 h) and weighed the samples to the nearest 0.001 g. Dead material was then discarded. I homogenized dried samples by grinding them in a Wiley mill (Thomas Scientific, Swedesboro, NJ, US). Subsamples of each sample were sent to the University of Delaware Core Laboratory for Soil, Plant, and Water Analysis to obtain the percentages of total nitrogen and total carbon per sample using an Elementar Vario-Max CN Cube (Elementar Americas, Ronkonkoma, NY, US). Samples were additionally placed into gelatin capsules and

combusted in an oxygen bomb calorimeter (Parr Instrument Company, Moline, IL, US) to calculate energy density in kJ/g.

Extrinsic field characteristics

I calculated three extrinsic factors that may influence field use using QGIS and R: field area, distance to open water, and distance to the nightly roost. I manually drew a polygon around each sampled field in QGIS, and field area was calculated in square meters for each polygon. In order to calculate distance to water, I calculated the minimum distance between the field polygon and a raster layer of open saltwater and freshwater ponds and lakes from the National Wetlands Inventory (United States Fish and Wildlife Service 2023) using the “sf” package in R (Pebesma 2018). Distance to the nightly roost was calculated as an average distance from the centroid (mean) of all nighttime points in the same 14-day period for which the diurnal home ranges were calculated. In some instances, Brant spent one or more nights in disparate locations (~5+ km) from the primary area where the grass sample was collected. This was often associated with birds that permanently moved from one area to another or with birds that ranged widely and frequently moved back and forth between disparate sites. In such instances, those entire nights were removed for the calculation of the mean nightly roost. In other words, only the closest nightly roosts associated with a sampled field were included when multiple distinct roosting locations occurred in the two-week period. If a bird moved between those two disparate locations during a single night, that night was kept in the dataset.

Statistical analyses

I modeled Brant field use as a function of intrinsic and extrinsic field characteristics using logistic regression in a Bayesian hierarchical analysis. Intrinsic field data included only data obtained from grass sampling, including average grass height (mm), live grass dry weight (g), dead grass dry weight (g), clover dry weight (g), other herbaceous plant dry weight (g), grass energy density (kJ/g), and grass carbon–nitrogen ratio, while extrinsic factors included field area (m²), distance to the roost (m), and distance to water (m).

To assess which factors influenced field use, several Bayesian hierarchical models were constructed and run using the “brms” package in R (Bürkner 2017). The global model included all intrinsic and extrinsic factors as population-level (fixed) effects (see formula below). The intrinsic model included only intrinsic factors that were measured from grass samples as fixed effects, while the extrinsic model included only extrinsic factors as fixed effects. The slope model was identical to the global model but also allowed for varying slopes of the predictors for each month in order to evaluate whether there were any temporal effects on the direction and intensity of the relationship between the predictors and field use. Some fields ($n = 28$) were sampled repeatedly over the sampling period (95/138 total samples). However, due to most fields (43 of 71) being sampled only once, I was unable to include varying intercepts for each field. Sample number was included as a random effect to account for the paired nature of my study design ($n = 69$ pairs). Month was also included as a random effect to account for unequal sampling effort among months (range 16–32 samples).

Only four fields were sampled as both a used and unused field during the study period; the remaining fields were only ever sampled as either used or unused.

These models used a Bernoulli distribution with a logit link to determine the probability of a field being used. All predictors were scaled to a mean of 0 and standard deviation (SD) of 1. Weakly informative priors of a normal distribution with a mean of 0 and SD of 3 were used for the slopes of the predictors. In the probability space, this prior assigns more probability closer to 0 and 1 and away from 0.5; in other words, I expected the predictors to have either a positive or negative effect on field use slightly more than I expected them to have no effect on field use, based on the literature. Similarly, I used a normal prior with a mean of 0 and SD of 2 for the intercept to assign slightly more probability to intermediate levels of field use when all predictors were at their mean value of 0. I used the default brms prior of a Student's t -distribution with 3 degrees of freedom, a mean of 0, and a SD of 2.5 for all group-level effects. The global model can be expressed in formula notation as $\text{field use} \sim 1 + \text{height} + \text{weight} + \text{clover} + \text{other} + \text{dead} + \text{CN} + \text{energy} + \text{roost} + \text{area} + \text{water} + (1 | \text{SID}) + (1 | \text{month})$, where *height* is average grass height, *weight* is grass weight, *clover* is clover weight, *other* is weight of other herbaceous plants, *dead* is weight of dead herbaceous material, *CN* is the carbon–nitrogen ratio, *energy* is energy density of the live herbaceous material, *roost* is the distance to the nightly roost, *area* is the area of the field, *water* is the distance to open water, *SID* is the sample number, and *month* is the month of the year the sample was collected. Each model was run with 10,000

iterations, of which 5,000 were warm-up iterations, across four Markov chain Monte Carlo (MCMC) chains, for a total of 20,000 draws.

For the sake of comparison, I also created a field use intensity model that contained only used field samples ($n = 69$) to explore the effects of all intrinsic and extrinsic factors on field use intensity, defined as the average number of GPS points per bird that used the sample field during the two-week period used to estimate home ranges and select sampling locations. This model was identical to the above global model but used a Poisson distribution with a log link to predict field use intensity and had normal priors with a mean of 0 and SD of 3 for both the intercept and the predictors.

Model comparison using leave-one-out cross validation or widely applicable information criterion was not reliable due to high Pareto k -values (six Pareto k -values >0.7 for the global and extrinsic models and 23 for the monthly slopes model) and therefore is not reported. This suggests that some individual data points highly influenced the results and that leaving out one data point could affect model inference.

All MCMC chains were examined using trace plots, and all R -hat values were approximately 1.0, which indicates model convergence. For each fixed effect, I report the mean effect size (estimate), 80% credible interval (CI), and proportion of the posterior distribution (PPD) on the same side of 0 as the estimate. I considered an effect to explain substantial, notable variation in Brant field use if its PPD was ≥ 0.8 .

Results

Field area had the strongest positive effect on field use in all nearly models, increasing the predicted field use to >95% when the field area was only 1 SD above the mean, and increasing the predicted number of use points by 143% per SD increase in the Poisson model of field use intensity. Distance to water had a negative effect on field use across all models, decreasing predicted use by >9% for each SD increase above the mean distance to water. Distance to the nighttime roost had a negative effect on field use in only the model with varying monthly slopes and the field use intensity model. The height of grass had a negative effect on field use, with a >17% reduction in the probability of field use per SD increase in grass height, and a strong positive effect on field use intensity, increasing the predicted number of points by 173% per SD increase. The weight of live grass had a weak positive effect on field use (>6% field use increase per SD), but it had a moderate negative effect on field use intensity (a 26% decrease in the number of used points per SD). The weight of clover had a negative effect on field use in the intrinsic and monthly slopes models, but it had a small positive effect on field use intensity. Carbon–nitrogen ratio had a negative effect of field use in the global model. All variables had PPD > 0.8 in the monthly slope and field use intensity models; see Table 1.1 for the mean effect size. All model results are summarized in Table 1.1 (with model-specific results listed in Tables A1–A6). The conditional effects of each significant predictor in the global model are shown in Figure 1.2.

Discussion

My study provides the first examination of factors influencing Brant upland field use in the US. My models support results similar to those found in other Brant and goose populations in different habitats, despite the urban turfgrass park system being quite different from natural grasslands and agricultural fields. While the model results differ subtly, they present a clear picture of the importance of extrinsic field characteristics and aspects of the surrounding landscape in predicting upland field use by Brant.

Field area consistently had the greatest effect size in explaining field use. The larger the field, the more likely the field was to be used. This relationship was expected based on previous studies of geese (Nilsson and Persson 1991, Gill 1996, McKay et al. 1996), and larger fields may impart additional protection from predators and human disturbance by permitting greater visibility (Wisiz et al. 2008). Most of the largest fields in the study area were golf courses and parks (~4.5–42.5 ha), which have regular human traffic but likely are large enough to allow Brant the ability to use parts of the fields farthest from humans at any time. In contrast, an average baseball field (~1 ha) would leave little to no room for Brant if even one or two people were actively using the field. Field area may also be a proxy for other unmeasured field characteristics, such as habitat closure, distance to roads, and amount of visual obstruction (Wisiz et al. 2008). Many smaller fields are part of a complex of fields separated by fences, sidewalks, and/or ornamental trees and bushes, which may interfere with predator visibility, while larger fields tend to have less visual

obstruction from such objects, although this varies among fields. Furthermore, Brant are social foragers, remaining in flocks ranging from a dozen to several thousand birds. Because geese are attracted to areas where other geese are congregating, as the presence of other geese may suggest high-quality habitat (Wisz et al. 2008), larger fields may simply have greater food availability and thus provide long-term energetic benefits (Amano et al. 2006, Chudzińska et al. 2015, Harrison et al. 2018).

Fields closer to open water and closer to the nighttime roost had a higher likelihood of being used and being used more heavily. Open water allows refuge from predators (Fox et al. 2017), and Brant roost in saltmarsh that is surrounded by open water. Many goose species are also well known to exploit fields closer to the roost before searching for food farther afield (Raveling 1969, Fox et al. 2017). However, Atlantic Brant generally have more limited habitat requirements (they are restricted to only coastal saltmarshes), which suggests they would not travel as far to exploit additional fields, particularly since fields appear to be a secondary food preference (Smith et al. 1985, Ladin 2010, Ladin et al. 2014). Whether Brant field use is influenced by existing roost sites or if access to fields influences the choice of a roost site early in the winter remains unknown and likely varies among individuals and regions. Regardless, these relationships make sense by implying that Brant prefer to stay closer to their primary food sources in and around the saltmarsh.

Overall, the quality of the grass in the fields had a less clear effect on Brant field use. Grass height was the strongest and most consistent intrinsic characteristic affecting Brant field use, with shorter grass being preferred. Geese have been shown to

prefer shorter grass (Buchsbaum et al. 1986, Riddington et al. 1997). However, among used fields, fields with taller grass were used more heavily, which may imply that Brant may be spending more time where grass has not yet been eaten by other geese. The mass of live grass also had a consistent effect on field use among models, with more grass leading to a higher likelihood of use but the reverse effect on field use intensity. Increased standing biomass has been shown to increase field usage (Summers and Critchley 1990), and it does not make sense for Brant to feed more heavily where there is less food unless it is caused by a feedback loop: the more Brant eat there, the less food is present when I go to take a sample of grass. It is also possible that my results for field intensity are not completely representative, as my study was not designed specifically to test use intensity and was instead done opportunistically with the available data. However, my model results do suggest that grass and field characteristics affect use and use intensity differently.

Among the other variables tested, only the carbon–nitrogen ratio significantly affected field use when extrinsic characteristics were also included (the global model), and incorporating random slopes for each month only increased the strength of this negative effect. While the direction of the effect was reversed in the intensity model, it was extremely weak. These results suggest that Brant in my study area prefer higher levels of nitrogen when selecting food, which has been shown previously for other populations of Brant (Riddington et al. 1997, Durant et al. 2004, Hassall and Lane 2005). The amount of clover in the field had a negative effect on field use but a small positive effect on field use intensity. Previous studies have found Brant to prefer

clover to grass in the UK (McKay et al. 2001), but this does not appear to be the case in my study area, although the overall minimal presence of clover in my samples (median 1.1%, mean 5.9%, range 0–50.5%) may imply that clover is too scarce for Brant to reliably select.

I hypothesized that an increase in non-grass, non-clover herbaceous plants (i.e., weeds) would lead to a decline in field use, potentially due to being thicker or less palatable than grass and clover (Conover 1991), and I found no mention in the literature of Brant foraging on these plants. I found no effect of having more weeds in two of the four models that included it and an extremely weak effect barely surpassing my 80% PPD threshold in the other two models, implying that weeds have little influence on Brant field use and use intensity in New Jersey and New York. Surprisingly, energy density had a weak or no effect in most models, but had a somewhat stronger negative effect on field use intensity. Previous research has found that Brant choose more energetically dense foods (Fox et al. 2017), so these results may suggest that Brant in my study area are choosing fields based on characteristics other than nutrition, which is further supported by the stronger effects of extrinsic characteristics in all models.

The amount of dead herbaceous material in a field had a weak but notable positive relationship with field use in two of my models. While I expected *a priori* a negative relationship, a positive relationship could be explained by the mowing of grass, which is frequent in this urban turfgrass system and would reduce grass height while increasing the amount of dead grass in a field, as my sampling methodology did

not differentiate between standing dead grass and older, cut dead grass. It is also worth noting that I was unable to incorporate the influence of resampling fields into my models, which may suggest that some aspect of the fields I resampled influenced my models disproportionately in comparison to fields that never were resampled, thereby skewing my results.

There may be further explanations of Brant field use that were not captured by my models. There is a possibility of cultural transmission of field selection in my study area. Brant, like most migratory geese, winter with their offspring from the preceding summer. Geese have been shown to learn novel behaviors from their parents (Fritz et al. 2000), and geese often learn their migratory routes and foraging locations by following their parents or other conspecifics (Warren et al. 1993, Aplin 2019). Thus, it is possible that young Brant learn to forage on specific fields, either from their parents or by observing other adults, and continue to pass this knowledge to their offspring, allowing the behavior to spread rapidly through the population (Smith et al. 1985). This transmission is possible because there is little to no change among years in these turfgrass ecosystems, unlike in agricultural systems, which vary greatly among years in both their forage species and the total amount of forage available.

Additionally, my study design may have hindered my potential to elucidate the importance of intrinsic field characteristics. Splitting sampling evenly between used and unused fields for every telemetered bird and month may have obscured some effects of month and individual on field use. A better approach may be to sample all used and unused fields within an individual's home range, rather than just one of each,

to better understand field use on a more individual and local level and to better quantify the variation between used fields and unused fields while increasing the overall sample size. Resampling fields may also have biased my results; fully randomized sampling or consistent resampling of every field may provide better data for modeling. While I explored field use intensity using the average number of GPS locations logged on each used field, using feces to determine the intensity of field use (e.g., Summers and Critchley 1990, Vickery et al. 1994, McKay et al. 2001) or observational counts of Brant (e.g., McKay et al. 1996) may provide clearer and more consistent use intensity data. Likewise, an experiment manipulating grass characteristics, such as mowing regime, fertilization, or Brant exclusion, may provide additional clarification of my results. Finally, I treated the entire Brant population in my study area as a single population. However, it is possible that there are local or regional differences in characteristics influencing field use, even within my study area, such that some field characteristics may be more important in certain locales than others, depending upon the local availability of fields and quantity of SAV in the surrounding saltmarshes.

My results further our understanding of Brant wintering ecology and potential energetic carrying capacity for future population management. If available SAV or the Brant population were to decline again significantly in the future, we may be able to better predict and understand upland field selection and use. Managers might also be able to supplement Brant forage by altering management of existing turfgrass fields and by creating additional grasslands in nearby agricultural fields.

Tables

Table 1.1 Comparison of model results among six field use models for Brant in New Jersey and New York from 2020–23. Est. is the mean scaled parameter estimate (i.e., relative effect size), and PPD is the percent of the posterior distribution that is above or below 0. Bold values indicate high certainty of effect (PPD > 0.8).

| Variable | Global | | Intrinsic | | Extrinsic | | Slope | | Intensity | |
|-----------------------|--------------|-------------|--------------|-------------|-------------|-------------|--------------|-------------|--------------|-------------|
| | Est. | PPD | Est. | PPD | Est. | PPD | Est. | PPD | Est. | PPD |
| Intercept | 0.69 | | -0.01 | | 0.64 | | 0.73 | | 2.84 | |
| Grass height | -0.71 | 0.98 | -0.78 | 1 | | | -1.13 | 1 | 0.55 | 1 |
| Grass weight | 0.34 | 0.88 | 0.32 | 0.90 | | | 0.47 | 1 | -0.30 | 1 |
| Clover weight | -0.16 | 0.76 | -0.29 | 0.92 | | | -0.19 | 1 | 0.10 | 1 |
| Other weight | -0.06 | 0.58 | 0.05 | 0.59 | | | -0.02 | 0.80 | 0.02 | 0.80 |
| Dead weight | 0.11 | 0.67 | 0.09 | 0.66 | | | 0.09 | 1 | 0.19 | 1 |
| Carbon–nitrogen ratio | -0.24 | 0.83 | -0.13 | 0.73 | | | -0.45 | 1 | 0.07 | 1 |
| Energy density | -0.09 | 0.62 | 0.09 | 0.65 | | | -0.04 | 1 | -0.23 | 1 |
| Distance to roost | 0.07 | 0.63 | | | -0.06 | 0.63 | -0.20 | 1 | -0.23 | 1 |
| Field area | 3.47 | 1 | | | 3.15 | 1 | 4.54 | 1 | 0.36 | 1 |
| Distance to water | -0.37 | 0.92 | | | -0.5 | 0.98 | -0.53 | 1 | -0.85 | 1 |

Figures

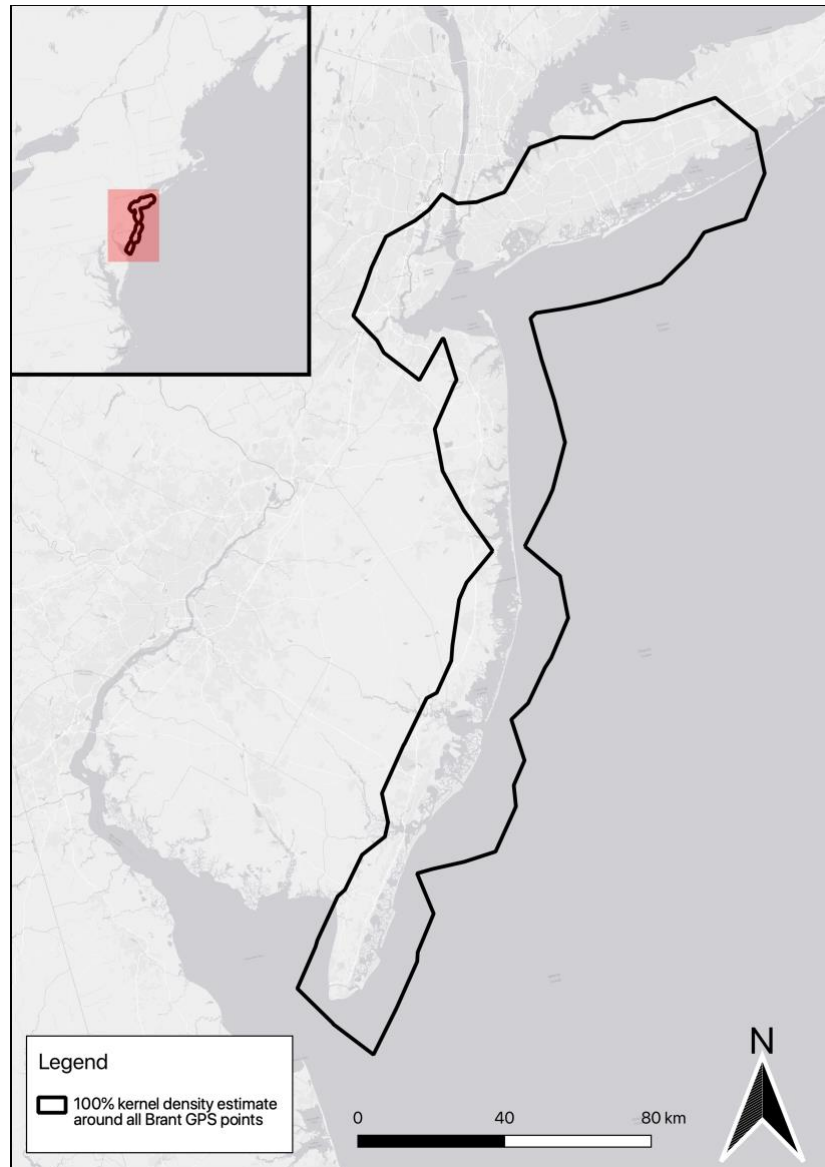


Figure 1.1 Study area represented as a 100% kernel density estimate around all GPS points obtained from telemetered Brant in New Jersey and New York from 2020–23.

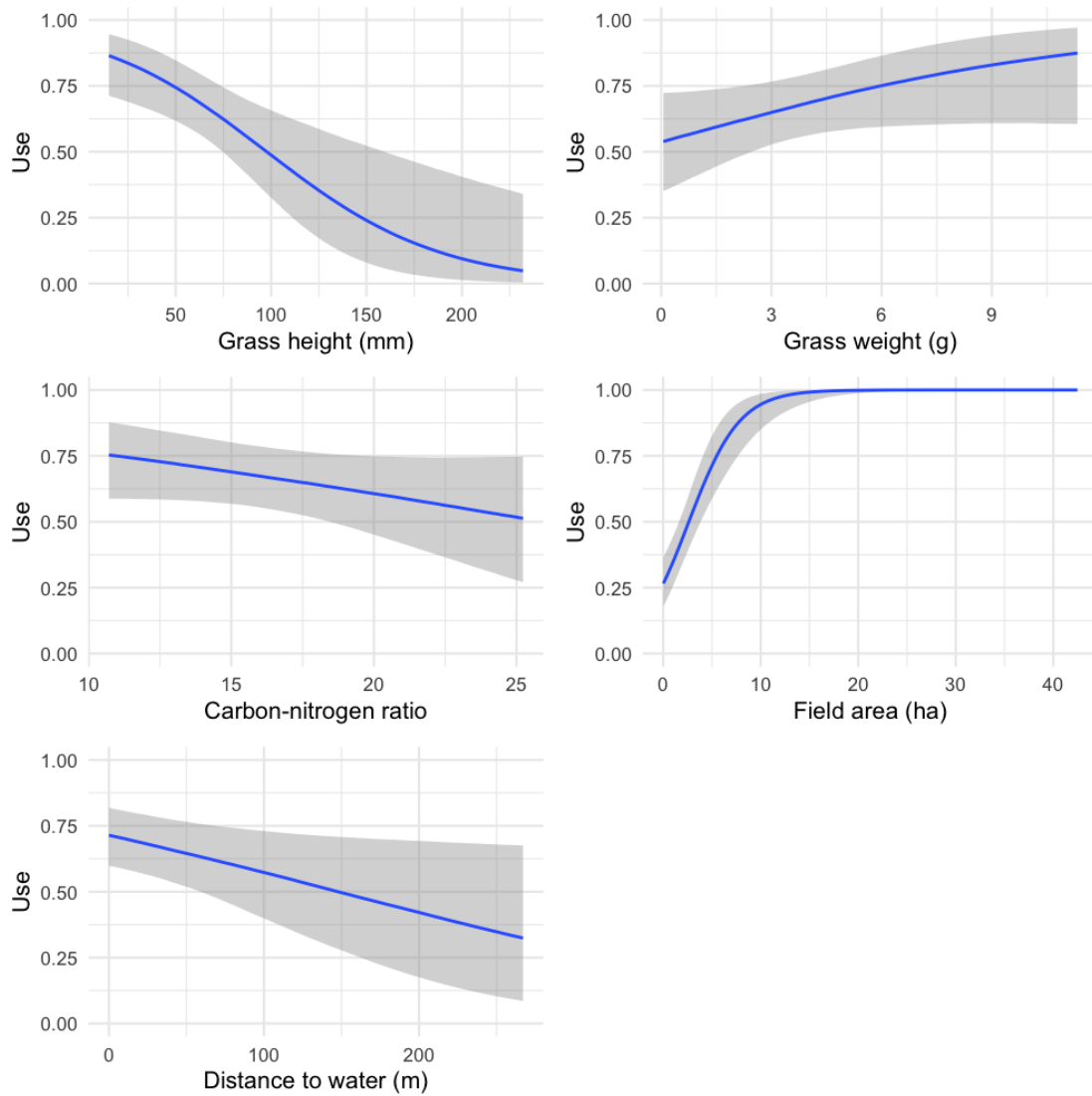


Figure 1.2 The conditional effects of each significant predictor in the global model of field use for Brant in New Jersey and New York from 2020–23 when all other predictors are at their mean value. The shaded area represents the 80% prediction credible interval.

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Chapter 2

DIFFERENCES IN DAILY ENERGY EXPENDITURE AND BEHAVIORAL TIME BUDGETS OF WINTERING ATLANTIC BRANT USING TRI-AXIAL ACCELEROMETRY

Introduction

The availability of food on the wintering grounds is thought to be a significant limiting factor for waterfowl populations (Williams et al. 2014). Malnutrition during the wintering period can have negative cross-seasonal effects, such as reduced nesting success in the summer (Kaminski and Gluesing 1987, Anteau and Afton 2009), and can lead to population declines (Sedinger and Alisauskas 2014). Therefore, numerous waterfowl joint ventures prioritize understanding wintering waterfowl habitat use and food requirements (Williams et al. 2014). In order to determine the wintering carrying capacity of a population, knowledge of both the energy available on the landscape and the daily energy expenditure (DEE) of a given species is required. Using this information, waterfowl managers can focus on increasing food resources on the wintering grounds to boost carrying capacity if the population exceeds the available resources.

Atlantic Brant (*Branta bernicla hrota*; hereafter “Brant”) winter on the Atlantic coast of the United States from Massachusetts to North Carolina, using shallow bays, lagoons, and tidal mudflats sheltered by barrier islands. After a large decline in their preferred food, eelgrass (*Zostera* spp.), led to population declines

(Cottam et al. 1944), Brant switched to eating macroalgae (*Ulva* spp. and *Enteromorpha* spp.), saltmarsh grasses (*Spartina* spp.), and upland turfgrasses and clover in parks and lawns (Ladin et al. 2011). Due to this past loss of Brant food resources and subsequent large population declines, understanding energetic needs for Brant on the wintering grounds is of high priority.

DEE was traditionally estimated in the field by constructing a time–activity budget using instantaneous scan sampling. Using this method, Ladin et al. (2011) estimated an average DEE for Brant using diurnal scans ($1,530 \pm 64$ kJ), while Heise (2012) improved upon the methodology by incorporating nocturnal sampling ($1,358.61 \pm 46.84$ kJ). However, scan sampling is limited, requiring one or more birds to be close enough to an observation point to determine their behavior. Thus, nocturnal behaviors were traditionally ignored or sampled under conditions of limited visibility. Additionally, rarer behaviors, such as flight, may be missed using the common 10 min sampling intervals, especially when sampling smaller numbers of individuals. Thus, there is a need to further refine estimates of DEE and time budgets for Brant to improve future carrying capacity estimates.

More recently, tri-axial accelerometers on back- or neck-mounted GPS units have allowed for increased sampling of waterfowl behavior (Wilson et al. 2006, Brown et al. 2013). Accelerometers allow biologists to sample behaviors in otherwise inaccessible locations or times while also allowing more precise and frequent sampling of individual behavior that is free from bias due to the observer's presence and observer error (Brown et al. 2013). Accelerometers also allow simultaneous

sampling across a large geographic area while allowing for a direct link between location and behavior (VonBank et al. 2021, 2023). As such, these high-frequency data have the potential to provide unprecedented information at the level of an individual, which could provide new insights into behavior and energetics.

I used tri-axial accelerometry data from >200 Brant from 2020–23 wintering in New Jersey and New York, USA, to determine the time spent in different behavioral states and calculated DEE across each day for each individual to arrive at an overall mean DEE for wintering Brant to compare to past published DEE values. I explored differences between sexes and among months and years using Bayesian generalized linear mixed effect models on both DEE and time spent in three behavioral states. I predicted no difference between sexes and small differences among months and years. Finally, I modeled the probability of being in a particular behavioral state as an effect of environmental, temporal, and geographic variables in order to determine the impact of these variables on Brant behaviors. These results can be compared to those from previous scan-sampling studies and can be used to improve carrying capacity estimates and future management decisions.

Study Area

The study area (Figure 2.1) was restricted to coastal New Jersey and the southern coast of Long Island, New York, which contains about 85% of the Atlantic Brant population during the winter (Castelli et al. 2011). Wintering Brant primarily use barrier islands and the bays that separate those islands from the mainland and

rarely travel inland more than a few kilometers from saltmarsh. There were three primary habitat types in the study area: open water, estuarine marsh, and saltmarsh (Cowardin et al. 1979). The open water habitat consisted of shallow subtidal embayments, while the estuarine habitat consisted of intertidal streambeds, rocky shores, unconsolidated shores, and mudflats. The saltmarsh habitat contained both irregularly and regularly flooded intertidal emergent wetland dominated by *Spartina* spp. Additionally, upland habitat adjacent to these habitats in urban and suburban areas was primarily turfgrass lawns, golf courses, and athletic fields covered by terrestrial grass (*Poa* spp.) and clover (*Trifolium* spp.). The average winter low temperature in New Jersey (Atlantic City) was 0.1 °C, and the average high was 6.6 °C, with an average of 26.7 cm of winter rain. The average winter low temperature on Long Island (Wantagh Cedar Creek) was -1.3 °C, and the average high was 6.7 °C, with an average of 26.6 cm of winter rain (National Centers for Environmental Information 2021).

Methods

Capture and accelerometry

The New Jersey Division of Fish and Wildlife and New York Department of Environmental Conservation captured Brant between January and March 2020–23 using rocket nets, typically on upland athletic fields or at freshwater inlets, with decoys and an electronic calling device. All captured birds were banded, and ~60

birds/year received Ornitela OrniTrack 25 solar-powered Global Positioning System–Global System for Mobile Communications (GPS–GSM) backpacks. Backpacks were attached via an over-wing harness. Most instrumented birds were also marked with individually numbered tarsal bands to allow for individual identification in the field. Additional units were deployed opportunistically on the breeding grounds in Canada by Environment and Climate Change Canada during the breeding season. Telemetry units were <3% of body weight, per Bird Banding Laboratory recommendations. Accelerometry data were recorded by the telemetry units every 6 min in 3 s bursts at 10 Hz throughout the wintering period.

Behavioral classification

In order to assign behaviors to corresponding accelerometry bursts, video of wild telemetered Brant was taken and the video matched to the corresponding accelerometry data of that individual. These data were supplemented with known flying data, collected when Brant were in active migratory flight (determined based on GPS data). Due to a deficit of stationary data in the video dataset, the data were supplemented with nighttime roosting data from calm nights (wind speed <3 m/s) and further hand-picked to be similar to known stationary data from the video dataset. The total accelerometry training dataset included 886 bursts across 20 individual Brant. All bursts were categorized into three behavior types: flying, stationary, and movement. Feeding, walking, swimming, and preening were all combined into the movement category to increase model accuracy.

With the training dataset of known-behavior accelerometry bursts, I built a random forest model using the “randomForest” package (Liaw and Wiener 2002) in the statistical software R (R Core Team 2021). I calculated 85 summary statistics from the raw accelerometry data then further reduced them to 31 statistics after removing highly correlated ($r > 0.9$) statistics and those that produced infinite values. In order to avoid artificially increasing model accuracy, the dataset was subsampled to include only 150 bursts per behavioral class (VonBank et al. 2023). The reduced training dataset ($n = 450$) was used to train the model, which was then tested against the remaining, unused data ($n = 436$). The final model had an overall classification accuracy of 90.2%, with similarly high precision and recall for each behavioral class (range 82.6–97.5).

Daily energy expenditure calculations

I predicted Brant behaviors for all accelerometry bursts using the random forest model. Using these predictions, I constructed time–activity budgets, consisting of the amount of time spent in each behavioral category, for each Brant on each day of the wintering period across all years. I included only days with 230–240 total bursts (~96–100% of the total possible daily bursts) in the final analyses to remove partial days or days with too many missing bursts. I calculated energetic costs for each burst, under the assumption that the behavior was constant until the next burst (i.e., the full 6 min), and summed for each day (midnight to midnight, EST) to obtain DEE in kJ/day

using the following equation adapted from scan-sampling studies (Albright 1981, Ladin et al. 2011, Clausen et al. 2012, Daniels 2014, Livolsi 2015):

$$DEE = \sum_{i=1}^n [(BMR \times a_j) + C_T] \times t_i \quad \text{Equation 1}$$

where n is the number of accelerometry bursts in a day, BMR is the basal metabolic rate in kJ/hr, a_j is the behavior-specific multiplier above BMR when engaged in behavior j , C_T is the cost of thermoregulation (kJ/h) when temperatures fall below the lower critical temperature (LCT), and t_i is the length in h of the i^{th} burst. The first and last burst of each day were also extended backward or forward, respectively, to midnight in addition to counting for the full 6 min burst to ensure a full 24 h measure of DEE. I calculated C_T only when the ambient temperature fell below the LCT, using the equation $C_T = 0.042 \times (LCT - T_a) \times 20.1$ (Morehouse 1974), where T_a is the ambient temperature and 20.1 is a constant to convert L O₂ to kJ/hr.

No studies have determined LCT, BMR, or energetic behavioral multipliers for Atlantic Brant. For Pacific Brant (*Branta bernicla nigricans*), LCT values vary: Irving et al. (1955) found an LCT of 6 °C in both winter and summer, while Morehouse (1974) determined LCTs of 2.5 °C, 8.2 °C, or 10.3 °C depending on sex, time of year, or locale. Similarly, American Black Duck (*Anas rubripes*) LCT values are often used for waterfowl without known LCT values. These also vary: Wooley and Owen (1977) determined an LCT of 12 °C for ducks acclimated to 19 °C but an LCT of 8 °C for ducks acclimated to 5 °C. Thus, it is apparent that acclimation to the local climate is important for determining LCT, perhaps more so than having species-specific values from a different locale or time of year. As American Black Ducks overlap in weight

with Brant and winter in similar habitats, and because temperatures in my study area are closer to 5 °C, I used 8 °C as the LCT for Brant in this study. This is also more conservative than using a lower LCT, such as 6 °C as determined by Irving et al. (1955), as it will increase DEE estimates and thus lower potential carrying capacity estimates.

Published BMR values for non-Atlantic populations of Brant vary greatly (11.38–29.92 kJ/h; reviewed in Miller and Eadie 2006). More typically, allometric equations are used to determine BMR based on mass (e.g., Ladin et al. 2011, Clausen et al. 2012, Heise et al. 2019). I used the allometric equation from Miller and Eadie (2006) for geese and ducks combined, $417 \times \text{mass}^{0.71}$, with the mean mass (in kg) at the time of capture for each sex to calculate BMR in kJ/h. Additionally, although McPherson (2020) found that the allometric equation of Miller and Eadie (2006) produced an estimated BMR ~64% higher than their actual measured BMR for American Black Ducks, I believe this is a conservative choice until further research is conducted on the energetics of Atlantic Brant.

I used the behavioral multipliers of Stahl (2001) for most behaviors. For flying, I used the allometric relationship $P_{\text{flight}} = 52.6 \times \text{mass}^{0.74}$, where P_{flight} is the power required for flight in W (Butler and Bishop 2000), using a mean mass of 1.393 kg for males and 1.301 kg for females (calculated from the weight of telemetered birds at the time of banding) to estimate the energetic costs of flight, and I then converted P_{flight} to kJ/hr and divided by the BMR to get the multiplier. I used the multiplier for swimming from McPherson (2020) for American Black Ducks. Individual behavioral multipliers

were averaged together to match the behavioral categories of this study: 1.82 for movement (swimming/walking/feeding/preening) and 1.65 for stationary (roosting/alert).

Analyses

Since my goal was to determine DEE and behavioral time budgets for the wintering period, I censored each individual bird down to its core range for each winter. Despite Brant wintering throughout the entire study area, many Brant exhibited stopover behavior and moved locations multiple times on the “wintering grounds.” For example, many birds spent 1–30 days in Jamaica Bay, New York, after arriving in October or November and before moving farther south or east to their core wintering area. Then, they moved back north, typically in March or April, to another stopover location, where they remained until departing for the breeding grounds in Canada (unpublished data). Thus, the core wintering area was typically defined as the southernmost or easternmost wintering location where a bird spent the majority of the winter (typically 2–3 months or more), which always overlapped the December–February period, which is the coldest part of the winter. Thus, I allowed an individual Brant’s behavior to determine the length of its wintering period rather than using a fixed wintering period that may have included non-wintering behavior. I used a changepoint analysis using the “changepoint” package in R (Killick et al. 2022) to assist with identifying these stopover sites, although the final date ranges were verified from manual inspection of the GPS data. Birds captured on the wintering grounds

were assumed to still be in their core wintering area at the time of capture, rather than in a spring or migratory stopover area. The data were further censored by removing one additional day after the banding date and one day prior to death or departure from the core wintering area. Birds with <7 days of accelerometry data were removed from analyses ($n = 7$).

Various differences in DEE and time spent on behaviors among groups were examined. To determine differences between sexes and among months and years while accounting for individual variation, various Bayesian generalized linear mixed-effect models were fit using the “brms” package in R (Bürkner 2017). To examine differences in DEE, an exponentially modified Gaussian (exGaussian) model with default (uninformative) priors was constructed using the equation $DEE \sim 1 + sex + month + winter + (1 | individual)$. To examine differences in time spent in the three behavioral classes, an exGaussian model with default priors was constructed using the equation $time \sim 1 + sex + month + winter + (1 | individual)$ for each behavior separately, where *time* is the number of h per day spent in a particular behavior.

Heise et al. (2019) examined the effects of environmental and temporal variables on Brant behavior, including temperature, ice cover, hunting season, wind speed, tide height, precipitation, and time of day, and primarily found effects of hunting season, time of day, and tide height. I sought to compare the effects of some of these variables on data derived from accelerometry and those of this previous observational study. To examine the effect of environmental variables on the probability of engaging in a particular behavior, a multinomial logistic regression (i.e.,

categorical) model was fit with the equation $behavior \sim 1 + temperature + precipitation + water\ height + wind\ speed + time\ of\ day + latitude + weekend + sex + (1 | individual)$, where *precipitation* and *weekend* were binary yes/no variables and *time of day* was a categorical factor that included the nocturnal period, the diurnal period, and the morning and evening crepuscular periods (sunrise and sunset \pm 30 min, respectively). Latitude was included to determine differences within the study area. Weekend was included as a proxy for human disturbance; I expected greater disturbance in all habitat types on weekends, potentially increasing flight behavior and decreasing stationary behavior. Temperature, precipitation, and wind speed were obtained by temporally and spatially matching accelerometry bursts with one of five NOAA weather stations in the study area (National Centers for Environmental Information et al. 2023). Water height data are relative to mean tide level and were downloaded using the NOAA Tides and Currents API (<https://api.tidesandcurrents.noaa.gov/api/prod/>) for five water level stations in my study area. I used a normal distribution with a mean of 0 and a standard deviation of 2 as priors for both the intercepts and predictor variables. Data for this model were subsampled to one data point per h, rather than per 6 min, to minimize temporal autocorrelation and decrease model run time. This reduced the dataset from >5 million observations to 515,883 observations.

For each fixed effect in the models of time spent in each behavioral state, I report the mean effect size (MES) of the beta estimates and their 80% credible

intervals (CI). I considered an effect to explain substantial variation in DEE or time spent on a behavior if its 80% CI did not overlap 0.

Results

There were 21,500 Brant-days included in the final analyses across 204 individuals (121 male, 83 female) and four winters. For the first winter of the study, 2019–20, only data from males from February–May were collected. All other winters had a mix of sexes and contained data from all months October–May. All R -hat values were <1.01 , which indicates model convergence.

Behavioral results

The observed average (\pm standard error, SE) amount of time spent in flight each day was 1.29 ± 0.01 h (5.4% of a day). The average amount of time spent moving (e.g., feeding or preening) was 18.0 ± 0.1 h (75.0%). The average amount of time spent stationary was 4.7 ± 0.03 h (19.6%). Averages by sex, month, and year are shown in Table 2.1.

Temporal differences in behaviors can be seen in Figure 2.2. Brant spent 31.8% of the nocturnal period stationary, compared to 15.9% of the morning, 10.0% of the evening, and 8% of the day on average. Likewise, flying accounted for 4.7% of the nocturnal period, 8.2% of the morning, 6.6% of the evening, and 5.7% of the day on average, while the remainder of time was spent moving (presumably primarily feeding).

The results of the categorical logistic regression model are presented in Figure 2.4 (for full model results, see Appendix Table A.10). Time of day had the strongest effect on probabilities of engaging in certain behaviors, predicting a 17% decrease in flight behavior, a 29% decrease in movement behavior, and a 323% increase in stationary behavior during the nocturnal period in comparison to the diurnal period. Latitude also had a strong effect on behavior; the model predicted a 138% increase in flight behavior, a 640% increase in stationary behavior, and a 22% decrease in movement behavior at the lowest latitudes in comparison the highest latitudes in my study area. Increasing water height from lowest to highest height predicted a 4% decrease in movement probability, a 9% increase in flight behavior, and a 46% increase in the probability of being stationary. The probabilities of flight and movement were predicted to increase with increasing wind speeds by 0.11% and 0.16% per additional m/s, respectively, while stationary behavior decreased by 0.26% per additional m/s. The presence of precipitation increased the probability of movement by 7%, while decreasing flight by 38% and stationary behavior by 44% in comparison to no precipitation. The probability of movement was predicted to increase by 0.04% for each additional °C, while the probability of flight decreased by 0.03% per °C. The weekend, when higher disturbance was expected, had little to no effect on behavioral probabilities (<1.2% change for each behavior). Being a male Brant predicted a 25% decrease in flight (a 1.6% decrease in probability) and an 11% decrease in stationary behavior compared to females.

I was unable to achieve model convergence for daily movement time. However, the model for daily flight time predicted many differences in flight time between sexes and among months and winters (Table 2.2, Figure 2.3). Males were predicted to fly much less than females (MES -0.34 , CI -0.43 to -0.24). October, February, April, and May were predicted to have lower flight time than January, while the remaining months were not notably different from January. All winters had notably lower predicted flight time than 2020. Winter 2021 (MES -0.05 , CI -0.07 to -0.03) and winter 2022 (MES -0.08 , CI -0.11 to -0.05) had smaller negative effects on flight time than winter 2023, which had a larger negative effect on flight time (MES -0.22 , CI -0.26 to -0.18). Further, the model of daily time spent stationary predicted notable differences between sexes and among months and years (Table 2.2). Male Brant were predicted to spend less time stationary than females (MES -0.88 , CI -1.24 to -0.53). October had the highest positive predicted difference from January (MES 0.87 , CI 0.65 – 1.08), while April (MES -0.42 , CI -0.50 to -0.34) and May (MES -0.55 , CI -0.64 to -0.46) had similarly high negative effects on time spent stationary. Winter 2021 showed more time stationary (MES 0.17 , CI 0.14 – 0.21) and 2023 much less time stationary (MES -0.33 , CI -0.39 to -0.28) in comparison to winter 2020.

Daily energy expenditure

The overall average DEE for Brant across the wintering period was $1,238.2 \pm 8.4$ kJ (mean \pm SE). The cost of thermoregulation (C_T) beyond BMR accounted for

4.17% of DEE on average, with a median of 2.23% (range 0–28.15%, Figure 2.5). Averages by sex, month, and year are shown in Table 2.1. Model results indicated that DEE varied by sex, month, and year (Table 2.2). DEE was predicted to be consistently slightly (~2%) lower in males than females (MES -21.7, CI -43.3 to -0.3). All months were predicted to have lower DEE than January, with May (MES -115.2, CI -121.0 to -109.3) and October (MES -108.6, CI -122.9 to -94.6) having the strongest predicted negative effect on DEE. In comparison to the reference winter of 2020 (2019–20), the model predicted weakly higher DEE values in 2021 (MES 6.3, CI 0.6–12.0) and stronger lower values in 2023 (MES -43.6, CI -53.2 to -33.9).

Discussion

Understanding the variables that impact waterfowl behaviors and energetics is a crucial aspect of waterfowl management (Williams et al. 2014). I found that flight, the most energetically costly behavior (~10–13× BMR in Brant), differed between sexes and among months and years and was predicted to increase with increasing wind and to decrease with increasing temperature, tide height, rain, and latitude. Brant were also predicted to fly more during the crepuscular periods than during diurnal or nocturnal periods. Changes in flight behavior directly affect DEE, which I found to be higher in females than males. The predicted difference of 22 kJ over the course of a 150-day winter would amount to an additional 2.7 days' worth of food that females must obtain compared to males based on the average DEE found in this study. While this relatively small difference may not be biologically significant, these regional, sex,

and temporal differences should still be considered in future energetics studies of Atlantic Brant to gain a more complete picture of carrying capacity in New Jersey and New York. Even a small difference in energy expenditure could lead to a large difference in carrying capacity estimates when extrapolated over the entire study area and Brant population.

Overall Brant DEE derived from accelerometry data (1,238 kJ) was 8.9% lower than DEE derived from scan-sampling efforts that incorporated nocturnal sampling of the same population of Brant (1,359 kJ; Heise 2012). However, this may be due to methodological differences, such as selecting fewer behavioral categories and using a different mean weight for each sex in the present study. This difference could also be attributed to differences in the estimated amount of flight time; Heise et al. (2019) found flight behavior to be 7.7% of a day, compared to 5.4% herein. Regardless, it is evident that this range of DEE is appropriate for future management decisions and carrying capacity estimates. Other behavioral data were quite similar to those of Heise et al. (2019): 17.3% stationary (resting + alert; compared to 19.6% in this study) and 75.0% movement (feeding + comfort + swimming + walking; compared to 75.0% in this study). Therefore, scan-sampling studies that choose to incorporate nocturnal sampling may provide good overall mean estimates of energetic demand (when simple DEE models are used) and behavioral time budgets that are comparable to those of accelerometry studies. However, because nocturnal scan sampling is logistically difficult and rarely conducted, accelerometry provides an

alternative for identifying behaviors across the entire 24 h period and may yield more precise estimates.

The use of accelerometry also allows for a comparison between sexes, which is not possible in scan-sampling studies of geese. Despite being a lower average weight, which directly reduces BMR and DEE, DEE of female Brant was slightly higher than that of males. This may be explained by the 32% increase in flight behavior displayed by females compared to males, as flight is the most energetically costly behavior. In all months except January, accelerometry data showed that females had an observed mean daily flight time greater than the highest monthly mean daily flight time of males (1.26 h in March). February showed the highest mean daily flight time for females (2.09 h). While little is known about pairing behavior in Brant on the wintering grounds, this aligns well with courtship and pairing in other species of waterfowl. McDuie et al. (2019) found that female Northern Pintail moved more than males after the hunting season (February–March) and attributed this to females moving to evade pursuit by courting males. As Brant were primarily banded in early February and equipping Brant with backpack telemetry units can potentially break pair bonds (Ward and Flint 1995, Lameris et al. 2018), it is possible that either males were pursuing females or females were in search of new mates, leading to greater flight behavior. However, this hypothesis would not explain females' greater flight times in all other months compared to males. One alternative explanation could be that females have different risk assessment than males and potentially respond to disturbances earlier, as has been shown in some waterfowl (e.g., Guay et al. 2013). Assuming that

this effect is not an artifact of sampling, these differences in behavior between sexes could be crucial for understanding Brant wintering behavior and energetics and should be considered instead of using population averages when possible.

While the differential effects of months and years on DEE could be attributed to differences in temperature or food availability (Ladin et al. 2011), differences in time spent in a behavioral state are less easily explained. In addition to the flight differences described above, Brant moved, and thus presumably fed, the least in February and March, with increased movement in April and May, which may be explained by the need to fuel up to prepare for their migration to the breeding grounds (Ladin et al. 2011). Brant were also the least stationary during December and January and flew the least in January, which aligns both with the coldest part of the winter and the hunting season. Heise et al. (2019) observed a decrease in stationary behavior during the hunting season in areas open to hunting, which aligns with my results, although they found little to no effect of temperature on behaviors. Further work is required to differentiate the effects of hunting and temperature on Brant behavior.

In my model of behavioral probabilities, latitude had a particularly strong effect on all behaviors, with birds at higher latitudes (e.g., Long Island) predicted to move more, fly less, and be less stationary. This strong effect suggests regional differences within the Brant population in my study area, which may be attributed to the availability and connectivity of different habitat types. For example, this result suggests that more northern birds do not have to fly as much to access abundant food sources and thus do not need to compensate additional flight costs with increased

stationary behavior to balance their energy budgets; therefore, they can spend the vast majority of their time feeding. In order to better elucidate this effect, further work on movement and behaviors in relation to habitat types is necessary (Sur et al. 2021).

Brant were predicted to fly slightly more often with higher tides and on the weekend, which could represent a small effect of disturbance. Weekends were added to the model as a proxy for increased human disturbance, particularly terrestrial disturbance during warmer weather and hunting pressure in colder months. High tide levels can obscure submerged aquatic vegetation, the preferred food of Brant, causing them to seek alternative foods (Clausen 2000, Colmorgen 2020).

Brant were also predicted to fly less during periods of rain and warmer temperatures. Heise et al. (2019) found the opposite effect of temperature, with Brant flying less often in colder weather. This difference could be attributed to increased detection from more frequent (consistent 6 min samples) and unbiased (following an individual regardless of location or time of day) sampling compared to scan-sampling methodology. Alternatively, it could be skewed by larger sample sizes and increased flight behavior in February, one of the coldest months. Regardless, this effect was fairly small and may not be particularly important in influencing Brant behavior. Furthermore, the strong negative effect of wind on stationary behavior predicted by the model may be attributed to a sampling issue, in which high winds may buffet a bird and make its telemetry backpack more likely to move (e.g., a bird rocking back and forth while resting on the ground or higher waves moving a bird while it is resting on water), rather than the bird itself actually moving.

Despite the continued improvement of DEE estimates for Brant, further refinement of these estimates is still necessary to achieve greater confidence. For example, I assigned behaviors to only three broad categories to improve the predictive accuracy of my random forest model; more fine-scale behavioral categories should be used when possible and would provide a richer dataset. Furthermore, BMR, LCT, and behavioral multipliers for Brant should be more directly determined using captive birds taken from New Jersey or New York in the winter. The current allometric approach, while widely used, could be overestimating BMR and thus DEE (McPherson 2020). Finally, there are many factors not currently considered in many DEE studies due to the difficulty of doing so: wind speed, water temperature, flocking effects, and solar radiation (but see, e.g., Wiersma and Piersma 1994, McKinney and McWilliams 2005). Future studies seeking to further refine DEE estimates should consider these additional variables if possible. Additionally, researchers and managers using accelerometry to determine time budgets and energy expenditure should consider both more frequent sampling regimes when possible (less than the 6 min used in this study) and an increased sampling frequency (>10 Hz) to capture a wider range of behaviors with greater accuracy (Yu et al. 2023).

My results lend further support to a DEE value around 1,200–1,300 kJ being an acceptable average for Atlantic Brant in New Jersey and New York in the winter. Future work on the availability of food on the landscape would therefore provide a good estimate of the carrying capacity for wintering Brant. Colmorgen (2020) estimated the carrying capacity of Brant in my study area to be around 165,000 based

on the availability of submerged aquatic vegetation using a predictive model of remote sensing data and a DEE estimate of 1,595 kJ. While Colmorgen (2020) acknowledges potential sources of bias that may have overestimated carry capacity, he did not consider upland grasses, an alternative food source that would increase the carrying capacity estimate. This additional food source combined with the lower DEE found in this study suggest that Brant may not be food limited on the wintering grounds, as evidenced by the 10-year average (2013–23) for the entire Atlantic Brant population in the US of 136,033 (U.S. Fish and Wildlife Service 2023), which is considerably lower than the prediction of 165,000 for just my study area. However, these estimates, both of food availability and energy expenditure, require further research and refinement to increase confidence in this conclusion and to inform future management decisions in the event of a population decline, an extremely cold winter, or another catastrophic decline of the preferred food of Brant.

Tables

Table 2.1 Means and standard errors of daily energy expenditure (DEE) and time (h per day) spent in three behavioral states by sex, month, and year calculated from accelerometry data for Brant in New Jersey and New York from 2020–2023.

| | Group | <i>N</i> (days) | Flight (h) | Stationary (h) | Movement (h) | DEE (kJ) |
|---------|----------|-----------------|-------------|----------------|--------------|----------------|
| Overall | | 21500 | 1.29 ± 0.01 | 4.7 ± 0.03 | 18.0 ± 0.1 | 1238.2 ± 8.4 |
| Sex | Male | 14403 | 1.17 ± 0.01 | 4.59 ± 0.04 | 18.2 ± 0.2 | 1236.5 ± 10.3 |
| | Female | 7097 | 1.55 ± 0.02 | 4.92 ± 0.06 | 17.5 ± 0.2 | 1241.7 ± 14.7 |
| Month | October | 129 | 1.10 ± 0.10 | 5.1 ± 0.5 | 17.9 ± 1.6 | 1155.9 ± 101.8 |
| | November | 1461 | 1.19 ± 0.03 | 4.5 ± 0.1 | 18.3 ± 0.5 | 1203.6 ± 31.5 |
| | December | 1969 | 1.17 ± 0.03 | 4.0 ± 0.1 | 18.8 ± 0.4 | 1253.4 ± 28.3 |
| | January | 1547 | 1.07 ± 0.03 | 4.0 ± 0.1 | 18.9 ± 0.5 | 1272.5 ± 32.4 |
| | February | 3883 | 1.53 ± 0.02 | 4.9 ± 0.1 | 17.6 ± 0.3 | 1331.3 ± 21.4 |
| | March | 5746 | 1.36 ± 0.02 | 5.2 ± 0.1 | 17.4 ± 0.2 | 1244.3 ± 16.4 |
| | April | 4849 | 1.24 ± 0.02 | 4.6 ± 0.1 | 18.2 ± 0.3 | 1183.5 ± 17.0 |
| | May | 1916 | 1.15 ± 0.03 | 4.5 ± 0.1 | 18.4 ± 0.4 | 1158.4 ± 26.5 |
| Winter | 2019–20* | 2980 | 1.09 ± 0.02 | 3.0 ± 0.1 | 19.9 ± 0.4 | 1200.3 ± 22.0 |
| | 2020–21 | 5895 | 1.22 ± 0.02 | 5.1 ± 0.1 | 17.7 ± 0.2 | 1248.1 ± 16.3 |
| | 2021–22 | 6272 | 1.51 ± 0.02 | 5.1 ± 0.1 | 17.4 ± 0.2 | 1283.6 ± 16.2 |
| | 2022–23 | 6353 | 1.24 ± 0.02 | 4.8 ± 0.1 | 18.0 ± 0.2 | 1202.0 ± 15.1 |

*This winter includes only the months of February–May and only male birds.

Table 2.2 Predicted mean difference from reference level of effects for each variable in models of daily energy expenditure (DEE), time in flight, and time stationary for Brant in New Jersey and New York from 2020–23. Sex is relative to females, month is relative to the reference month of January (1), and winter is relative to the reference winter of 2020 (2019–20).

| Variable | DEE (kJ) | Flight (h) | Stationary (h) |
|--------------|----------|------------|----------------|
| Sex: male | -22 | -0.33 | -0.88 |
| October | -109 | -0.13 | +0.87 |
| November | -68 | -0.03 | +0.22 |
| December | -28 | | -0.09 |
| February | -18 | -0.04 | +0.24 |
| March | -53 | -0.02 | +0.17 |
| April | -92 | -0.09 | -0.42 |
| May | -115 | -0.18 | -0.55 |
| Winter: 2021 | +6 | -0.05 | +0.56 |
| Winter: 2022 | | -0.08 | |
| Winter: 2023 | -44 | -0.22 | -0.62 |

Figures

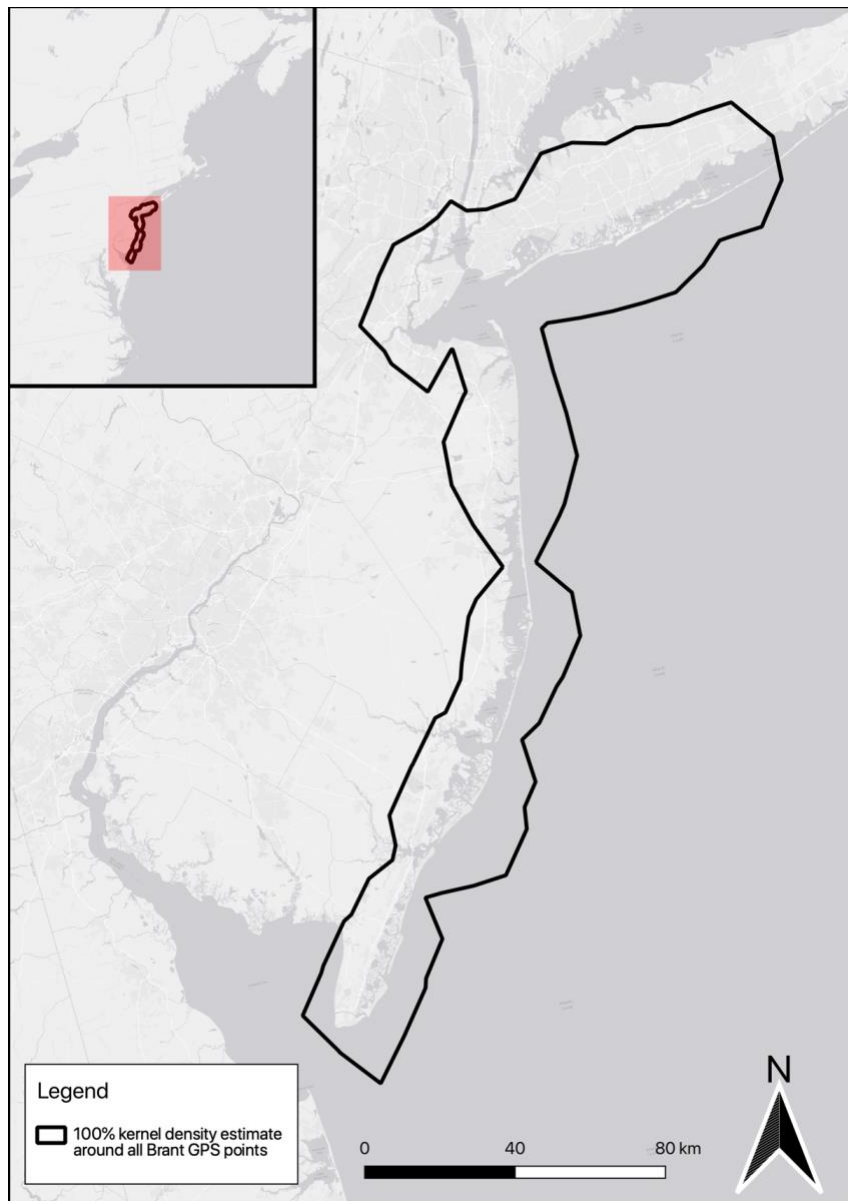


Figure 2.1 Study area represented as a 100% kernel density estimate around all GPS points obtained from telemetered Brant in New Jersey and New York from 2020–23.

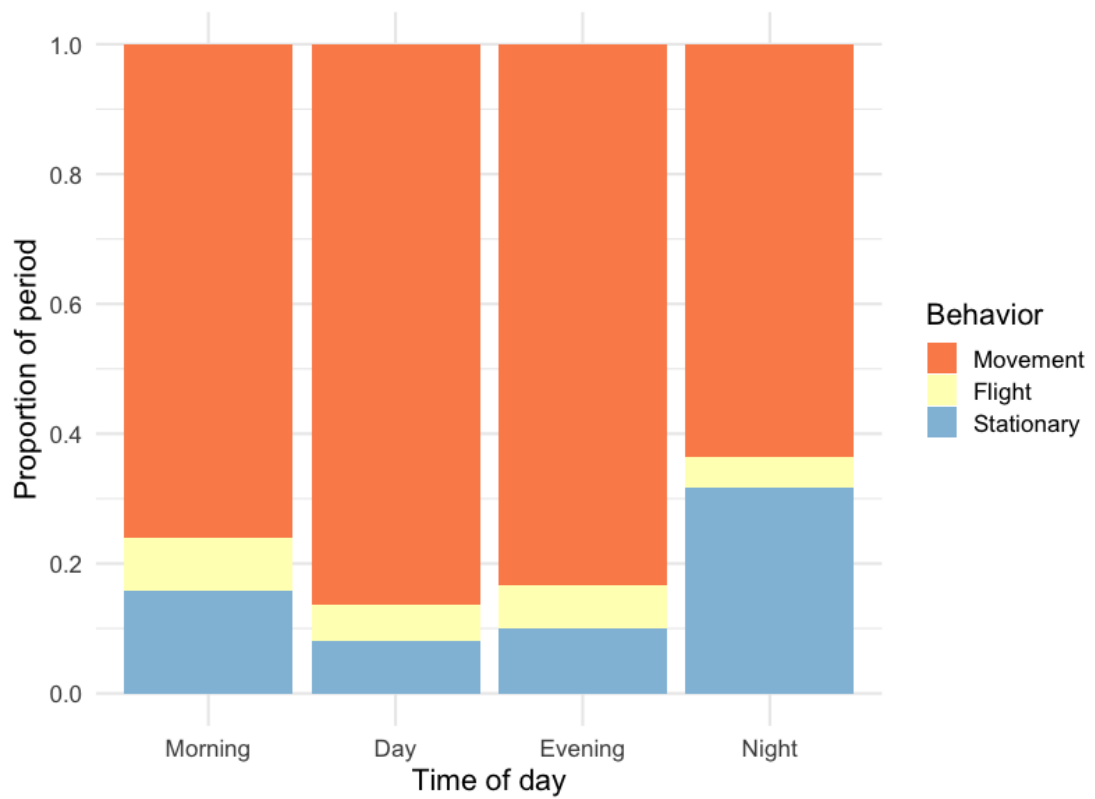


Figure 2.2 Average proportion of time spent in each of three behaviors during each period of the day calculated from accelerometry data for 204 Brant in New Jersey and New York across 21,500 total Brant-days from 2020–23.

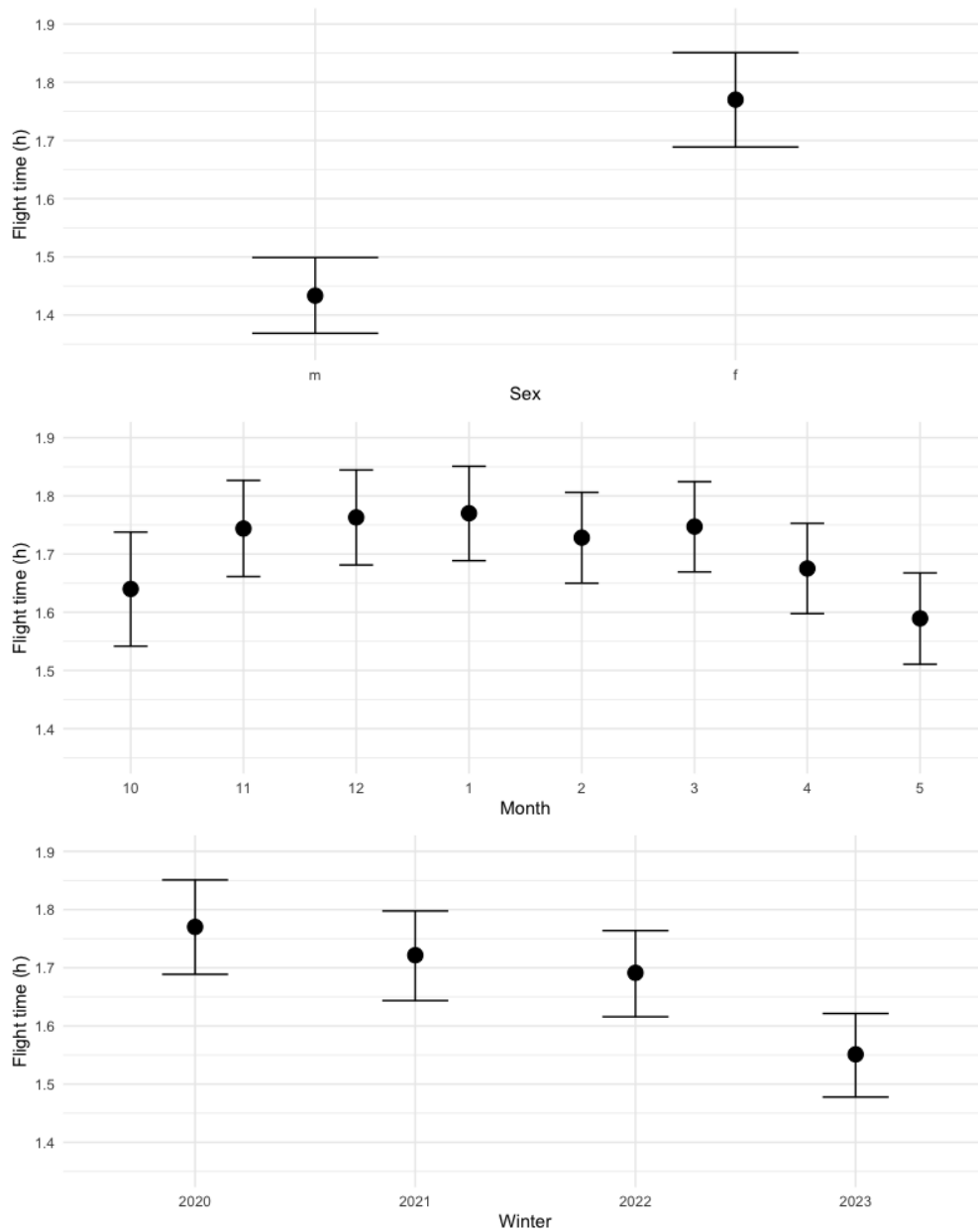


Figure 2.3 Model-predicted conditional effects showing mean differences and 80% credible intervals in flight time (h) between sexes and among months and years for 204 Brant in New Jersey and New York across 21,500 total Brant-days from 2020–23.

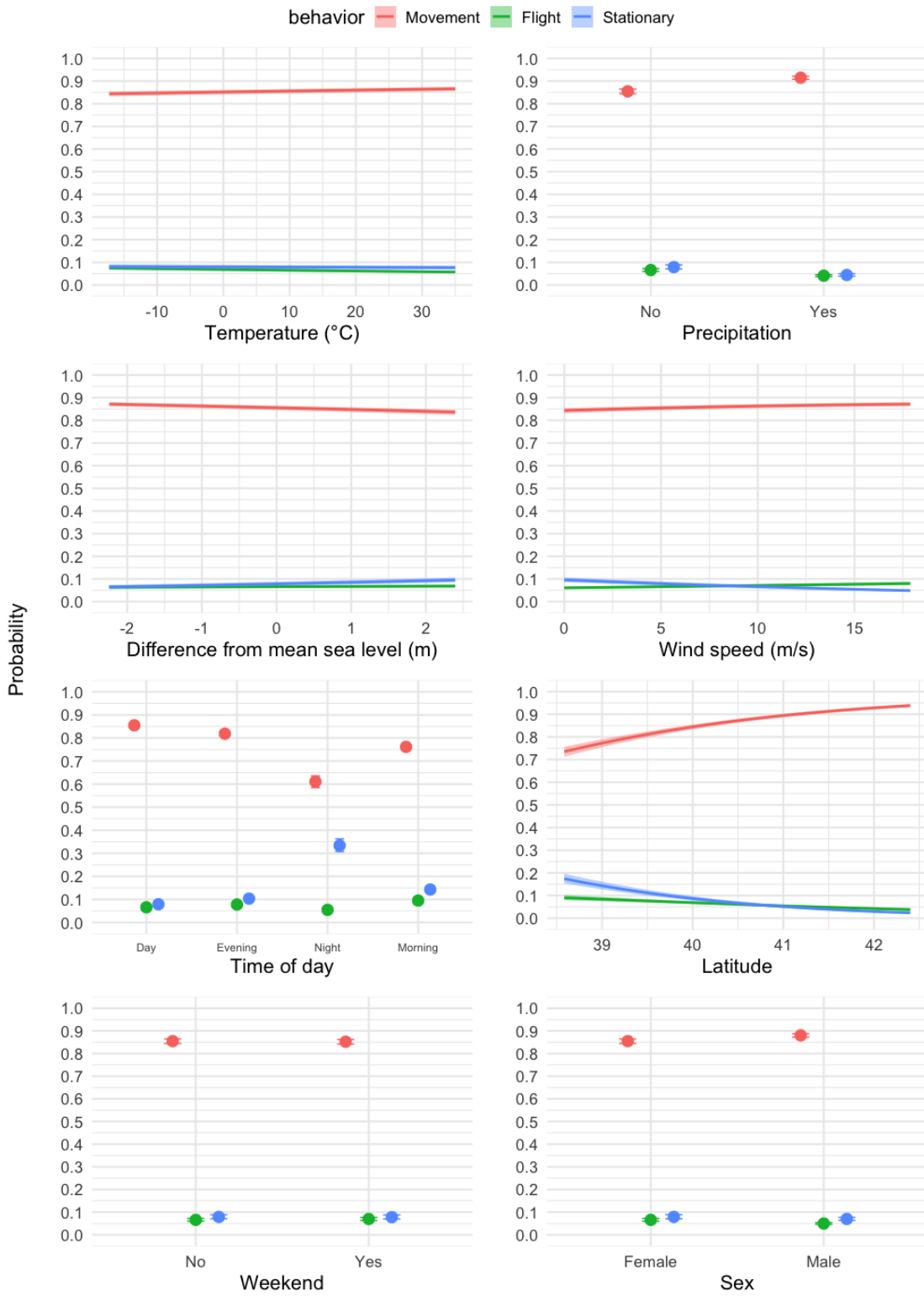


Figure 2.4 Conditional effects plots for the behavioral proportion model showing how the probability of being in each behavior responds to changes in environmental and temporal variables for 204 Brant in New Jersey and New York from 2020–23 using 515,883 accelerometry bursts.

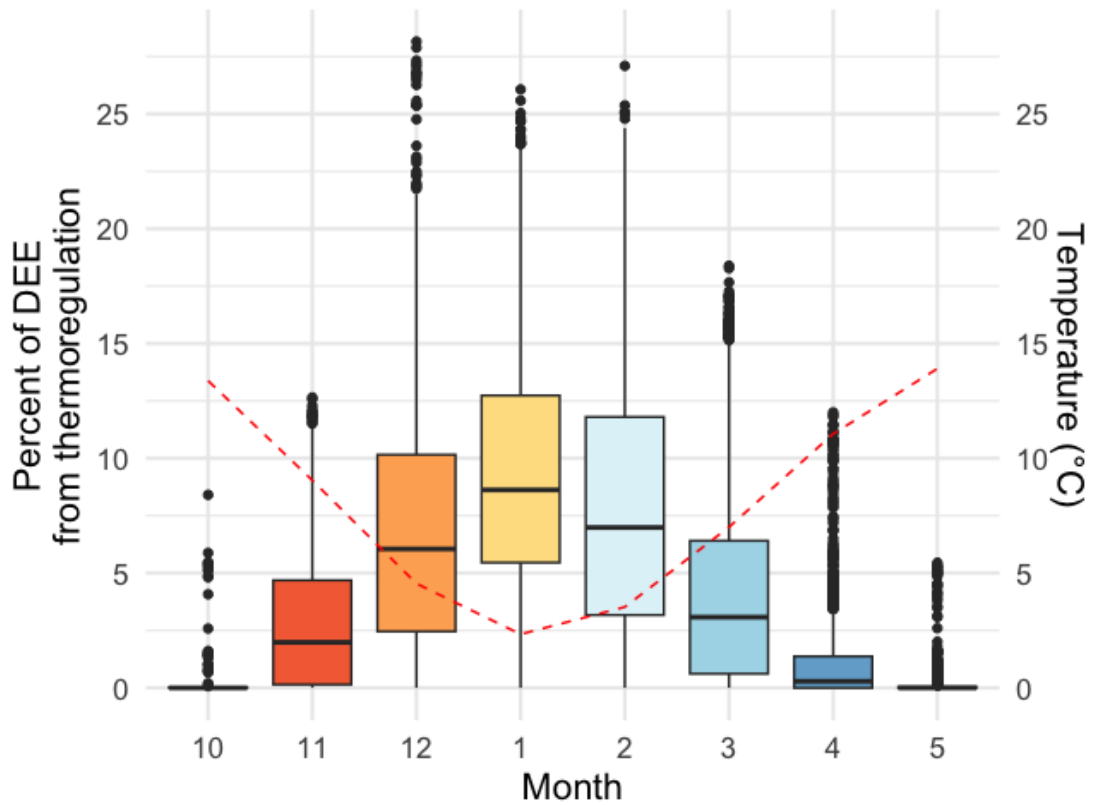


Figure 2.5 Boxplot illustrating differences in the percentage of daily energy expenditure (DEE) attributed to thermoregulatory costs by month for 204 Brant in New Jersey and New York across 21,500 total Brant-days from 2020–23. Red dashed line indicates average temperature experienced by Brant for that month.

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Chapter 3

EXPLORING HOME RANGE, DAILY MOVEMENT, AND HABITAT USE OF WINTERING ATLANTIC BRANT

Introduction

Understanding waterfowl home ranges and habitat use on the wintering grounds is of high priority for managing waterfowl populations (Williams et al. 2014). Shifts in habitat use could negatively affect waterfowl populations through increased energy expenditure and cross-seasonal effects (Kaminski and Gluesing 1987, Anteau and Afton 2009, Sedinger and Alisauskas 2014). Recent advances in technology, such as Global Positioning System–Global System for Mobile Communications (GPS–GSM) transmitters, have allowed for greater precision in quantifying habitat use (e.g., Sur et al. 2021, Luukkonen et al. 2022, Overton and Casazza 2023, VonBank et al. 2023), which has provided a better understanding of individual-level and regional variation, larger sample sizes, and increased coverage of inaccessible locations (Wilson et al. 2006, Brown et al. 2013). This technology can provide scientists and managers with useful insights into the habitat and space use of their target species.

Atlantic Brant (*Branta bernicla hrota*; hereafter “Brant”), which winter in the coastal saltmarsh regions of the eastern US and breed in the eastern Arctic, have a relatively small total population (~150,000) that has fluctuated greatly in the past due to both severe winters and the loss of their preferred submerged aquatic food source

(Phillips 1932, Kirby and Obrecht 1982, Castelli et al. 2010). These major events led to an increase in feeding on upland cultivated grass on golf courses, athletic fields, and lawns (Cottam et al. 1944, Ward et al. 2005, Ladin et al. 2011). As these sources of food vary in energy density and nutritional quality (Ladin et al. 2011), this habitat shift may directly impact energy budgets of Brant and therefore population numbers, increasing the need to better understand the habitat use of Brant, an objective of the Atlantic Brant management plan (Castelli et al. 2011).

The majority of studies investigating habitat use by Atlantic Brant have examined foregut contents, rather than using observational or tracking data. Smith et al. (1985) noted that Brant wintering on Long Island consume a greater amount of cultivated grasses than those in New Jersey, potentially due to social tradition. Ladin et al. (2014) found an overall Brant diet of 52% macroalgae, 22% salt marsh cordgrass, 18% eelgrass, and 8% terrestrial grass and clover, with significant differences in composition among months and regions and a more stable diet throughout the winter for birds in New Jersey and New York. In the only tracking study of Atlantic Brant, they were found to spend most of their time in open water habitats, with an increasing amount of time spent in emergent herbaceous wetlands and a decreasing amount of time spent in developed areas (i.e., cultivated grass fields) as the winter progressed (Castelli et al. 2010). This trend of switching to feeding on emergent saltmarsh vegetation later in the winter has also been observed in other populations of Brant worldwide (St. Joseph 1979, Vickery et al. 1995, Ward et al. 2005, Tinkler et al. 2009). However, due to low location accuracy, Castelli et al.

(2010) were unable to determine the home range sizes of Brant, and they caution against drawing conclusions from their summary of habitat use due to a lack of statistical significance.

I used a robust dataset of high-accuracy (~10 m) GPS–GSM transmitters deployed on Atlantic Brant to further refine our understanding of their wintering habitat use in New Jersey and New York, their primary wintering area (Castelli et al. 2011). I report home range size and daily distance traveled, which has never been determined for Brant, and explore differences within the population. I further summarize habitat use per GPS location for direct comparison with previous reports of Brant habitat use and examine differences within the population and over the wintering period.

Study Area

The study area was restricted to coastal New Jersey and the southern coast of Long Island, New York, which contains about 85% of the Atlantic Brant population during the winter (Castelli et al. 2011). Wintering Brant primarily use barrier islands and the bays that separate those islands from the mainland and rarely travel inland more than a few kilometers from saltmarsh (Figure 3.1). There were three primary wetland habitat types in the study area: open water, estuarine marsh, and saltmarsh (Cowardin et al. 1979). The open water habitat consisted of shallow subtidal embayments, while the estuarine habitat consisted of intertidal streambeds, rocky shores, unconsolidated shores, and mudflats. The saltmarsh habitat contained both

irregularly and regularly flooded intertidal emergent wetland dominated by *Spartina* spp. Additionally, upland habitat adjacent to these wetland habitats in urban and suburban areas was primarily turfgrass lawns, golf courses, and athletic fields covered by terrestrial grass (*Poa* spp.) and clover (*Trifolium* spp.). The average winter low temperature in New Jersey (Atlantic City) was 0.1 °C, and the average high was 6.6 °C, with an average of 26.7 cm of winter rain. The average winter low temperature on Long Island (Wantagh Cedar Creek) was -1.3 °C, and the average high was 6.7 °C, with an average of 26.6 cm of winter rain (National Centers for Environmental Information 2021).

Methods

Capture and telemetry

The New Jersey Division of Fish and Wildlife and New York Department of Environmental Conservation captured Brant between January and March 2020–23 using rocket nets, typically on upland athletic fields or at freshwater inlets, with decoys and an electronic calling device. All captured birds were banded, and ~60 birds/year received Ornitela OrniTrack 25 solar-powered GPS–GSM backpacks. Backpacks were attached via an over-wing harness. Most instrumented birds were also marked with individually numbered tarsal bands to allow for individual identification in the field. Additional units were deployed opportunistically on the breeding grounds in Canada by Environment and Climate Change Canada during the breeding season.

Telemetry units were <3% of body weight, per Bird Banding Laboratory recommendations. GPS data were recorded by the telemetry units every 30 min throughout the wintering period when battery power was sufficient.

Analyses

All analyses were conducted in R (R Core Team 2021). Since my goal was to determine home ranges and movements for the wintering period, I censored each individual bird down to its core range for each winter. Despite Brant wintering throughout the entire study area, many Brant exhibited stopover behavior and moved locations multiple times on the “wintering grounds.” For example, many birds spent 1–30 days in Jamaica Bay, New York, after arriving in October or November and before moving farther south or east to their core wintering area. Then, they moved back north, typically in March or April, to another stopover location, where they remained until departing for the breeding grounds in Canada (unpublished data). Thus, the core wintering area was typically defined as the southernmost or easternmost wintering location where a bird spent the majority of the winter (typically 2–3 months or more), which always overlapped the December–February period, which is the coldest part of the winter. Thus, I allowed an individual Brant’s behavior to determine the length of its wintering period rather than using a fixed wintering period that may have included non-wintering behavior. I used a changepoint analysis using the “changepoint” package in R (Killick et al. 2022) to assist with identifying these stopover sites, although the final date ranges were verified from manual inspection of

the GPS data. Birds were assumed to still be in their core wintering area at the time of capture. The data were further censored by removing one additional day after the banding date and one day prior to death or departure from the core wintering area. Only birds with ≥ 28 days of GPS data were included in home range analyses.

Home ranges (95% utilization distribution) were calculated using the “amt” package (Signer et al. 2019), which uses the “ctmm” package (Calabrese et al. 2016) to calculate an autocorrelated kernel density estimate (AKDE). Unlike many home range estimates, an AKDE does not assume the data are independent and identically distributed and fits multiple continuous time movement models to determine the best fit for the autocorrelation structure of the data (Fleming and Calabrese 2017, Noonan et al. 2019). Home ranges were fit for the core wintering area of each Brant each winter.

Two home range estimates were many times larger than all others; these two outliers were removed from analyses under the assumption that I missed non-wintering (i.e., stopover or spring) movements during the date selection process described above. Before modeling, I used a linear model to check for a relationship between the number of days used to construct the home range (range 28–204) and the size of the home range and found no relationship ($p = 0.679$, $R^2 = 0.0007$, $n = 244$, $t = 0.414$). To determine differences between sexes and among years and geographic regions while accounting for individual variation, I fit a Bayesian generalized linear mixed-effect model using the “brms” package in R (Bürkner 2017). To examine differences in home range size, I constructed a Gaussian model with wide priors of

Normal(0, 10) for the intercept and Normal(0, 5) for the slopes using the formula $area \sim 1 + sex + winter + region + (1 / individual)$, where *area* is the log of the home range size in ha and *region* is one of four regions: southern New Jersey, northern New Jersey, western Long Island, and eastern Long Island. I used this model for both 95% and 50% AKDE home range estimates.

I calculated step lengths in m between all consecutive GPS locations for each individual bird using the “amt” package. I then grouped these data by date and summed the step lengths to obtain the total daily distance moved in km. There was a clear divide between days with daily travel distance <78 km ($n = 21,362$) and >92 km ($n = 7$); days with >92 km were considered outliers due to erroneous GPS fixes and/or non-wintering movements and were removed. The smallest outlier (0.05 km) was likewise removed, as it was 6.9 times smaller than the next smallest data point and may reflect an inactive GPS unit that was accidentally not removed from analyses. To determine differences between sexes and among months, years, and geographic regions while accounting for individual variation in total daily distance traveled each day, I constructed a Gaussian model with wide priors of Normal(0, 10) for the intercept and Normal(0, 5) for the slopes using the formula $dist \sim 1 + sex + winter + month + region + (1 / individual)$, where *dist* is the log of the distance traveled in a day in km.

For analysis of habitat use, raw GPS locations were used and their underlying habitat type extracted from a raster layer of the 2021 National Land Cover Database (Dewitz 2023) using the “terra” package in R. Habitat types were grouped following

Castelli et al. (2010), merging all developed land types together to compare with open water and emergent herbaceous wetlands, the primary habitats used by Brant. I also combined all remaining habitat types into an “other” category and marked any points with a recorded ground speed of >5 m/s and/or with an altitude >100 m or <-100 m below mean sea level as flight points, which were not to be used for determining habitat proportions. Locations with a horizontal dilution of precision (HDOP; a measure of location accuracy that should be around 1) >2 were marked as error points and added to the “other” category, as their underlying habitat types could be unreliable. I then calculated proportions of points assigned to each land cover type used per bird per day. I removed any days that had >49 and <45 total points to minimize odd sampling errors and missed relocations; with a rate of one point every 30 m, each day should have had 48 locations total.

I used three Bayesian zero-inflated beta regressions to determine the effects of sex, winter, month, and region on the proportion of a day spent in each primary habitat type—developed, emergent herbaceous wetland, and open water—using the formula $habitat\ type \sim 1 + sex + winter + month + region + (1 | individual)$ and assuming a constant (intercept-only) zero-inflation probability across all observations (the default in “brms”). I used default uninformative “brms” priors and a random effect of the individual Brant. I removed 21 days for which the use proportion of a habitat type was 1, as the beta distribution cannot model 1s and it is likely that these days amount to sampling errors or abnormal behavior.

For each fixed effect, I considered an effect to explain substantial variation in the response variable if its 80% credible interval (CI) did not overlap 0. All averages are reported with their standard error (SE).

Results

There were 244 Brant-winters included across 183 individuals (109 male, 74 female) and four winters. For the first winter of the study, 2019–20, only data from males from February–May were collected. All other winters had a mix of sexes and contained data from all months October–May. October data were removed from habitat use analyses due to a low sample size. All model R -hat values were <1.01 , which indicates model convergence. Home ranges were calculated for all 244 Brant-winters, and daily distances were calculated for 21,361 Brant-days.

Home ranges

The average size (\pm SE) of a Brant 95% AKDE winter home range was 1,797.7 \pm 166.7 ha, while the median was 835.5 ha (range 81.0–22,817.0 ha; including removal of the two highest outliers). The average size of a Brant 50% AKDE home range was 324.6 ha \pm 34.3, while the median was 131.0 ha (range 14.0–4,860.0 ha).

There was no effect of sex on 95% home range size or 50% home range size (Table A11). There was a small effect of winter on home range size, with winter 2023 showing no notable difference from the reference winter of 2020 in either model, while 2021 was notably lower in both models (95%: 338.9 [80% CI 14.7–573.4] ha

less; 50%: 69.0 [80% CI 12.3–109.6] ha less) and 2022 was notably higher in the 95% home range model (498.0 [80% CI 45.1–1085.4] ha more) than 2020. Region of the study area had the strongest effect on home range sizes in the model, with birds from western Long Island predicted to have 66% (80% CI 57–73%) smaller 95% (977.6 [80% CI 847.6–1084.9] ha smaller) and 69% (80% CI 61–76%) smaller 50% (174.7 [80% CI 152.7–191.2] ha smaller) home ranges and birds from eastern Long Island predicted to have 42% (80% CI 1–99%) larger 95% home ranges (620.3 [80% CI 14.9–1471.0] ha larger) than the reference category of northern New Jersey. Southern New Jersey had a mostly negative but non-notable effect in comparison to northern New Jersey in both models (Figure 3.2). For full model results, see Table A11.

Daily distance

The average total daily distance moved was 11.35 ± 0.08 km, with a median of 9.98 km and a range of 0.38–77.35 km. Females were predicted to move 0.64 (80% CI 0.0–1.2) km more than males on average each day, a 5% (80% CI 1–10%) increase in movement. There was a weak negative effect of winters 2021 (0.85 [80% CI 0.1–1.4] km lower) and 2023 (0.95 [80% CI 0.3–1.5] km lower) in comparison to winter 2020 (Figure 3.3). There was very little effect of month, with only April having a very weak positive effect (3–6 % higher) and May having a very weak negative effect (1–5 % lower) on daily distance compared to January. Region had a stronger effect on daily distance in the model, with birds from northern New Jersey and southern New Jersey predicted to travel 2.04 (80% CI 1.28–2.85) km and 1.53 (80% CI 0.80–2.17) km

more each day, respectively, than those from eastern Long Island, while birds from western Long Island were predicted to travel 1.91 (80% CI 1.34–2.35) km less each day. For full model results, see Table A12.

Habitat use

On average, Brant spent $31.1\% \pm 0.2\%$ of the day on open water, $22.9\% \pm 0.2\%$ on developed land, and $38.9\% \pm 0.3\%$ in emergent herbaceous wetland. Other habitats were used rarely throughout the winter (mean $1.1\% \pm 0.0001\%$), and $6.1\% \pm 0.04\%$ of each day was spent in flight on average. Use of developed land increased from 16.4% in November to 31.8% in May, while use of open water declined from 42.4% in November to 24.2% in May (Figure 3.4). Use of emergent herbaceous wetlands peaked at 43.1% in March.

The zero-inflated beta regression models of habitat use predicted that females spent 3.3% (80% CI 1.9–4.6%) less time in a day in developed habitats (a 23% [80% CI 13–32%] decrease), 2.2% (80% CI 0.0–4.5%) more time on open water (a 3% [80% CI 0–7%] increase), and an equal amount of time in emergent herbaceous wetlands compared to males (Tables A13–15). Compared to the reference winter of 2020, all subsequent winters were predicted to show weakly increased use of developed land (Figure 3.5a) and weakly reduced use of open water (Figure 3.5b), while only 2021 differed weakly from 2020 for emergent herbaceous wetland (Figure 3.5c). Monthly differences in the use of developed land exhibited a positive linear relationship in reference to November (Figure 3.5a), with each subsequent month

increasing the mean effect size until reaching the highest estimate in May. Conversely, use of open water was predicted to decline throughout the winter (Figure 3.5b), with May showing the strongest negative effect. Use of emergent herbaceous wetlands was weakly lower than November until a notable increase in February, with a peak in March and a slight decrease in April and May.

Regional differences in habitat use had the strongest effect in the models (Figure 3.5). All regions were predicted to have much less use of open water than northern New Jersey, with western Long Island having the strongest negative effect, being 34% (80% CI 32–35%) lower (a 51% [80% CI 48–53%] decrease). Conversely, all regions were predicted to have much more use of emergent herbaceous wetlands than northern New Jersey, with western Long Island having the strongest positive effect, being 22% (80% CI 19–25%) higher (a 105% [80% CI 92–118%] increase). Southern New Jersey differed most notably from the reference category of northern New Jersey regarding use of developed land, being 4.7% (80% CI 3.8–5.7%) lower (a 33% [80% CI 26–40%] decrease), while the other regions had a smaller 20–22% increase in developed use compared to northern New Jersey. For full model results, see Appendix Tables A13–15.

Discussion

Atlantic Brant display regional differences throughout their wintering range. It was thought that only 5% of the Brant population fed on upland cultivated fields (Ward et al. 2005), and birds in New York are well documented to consume more

upland grasses than those in any other region (Smith et al. 1985, Ladin et al. 2014). These regional differences within the population may be attributed to assortative mating by necklace type (Vangilder and Smith 1985), which is reflected in small genetic differences among regions (Novak et al. 1989). This lack of complete random mating, together with the wintering site fidelity and social behavior of Brant, as well as the inter-year consistency of upland cultivated grass availability, may have led to differential learning and the transmission of traditions among regions, potentially explaining why upland field feeding is not consistent within the population (Smith et al. 1985).

My results reflect the importance of these regional differences, particularly regarding birds in western Long Island, who displayed reduced home ranges and daily movements, as well as an increased use of developed habitats and emergent herbaceous wetlands compared to birds from New Jersey. I hypothesize that these differences in movement and habitat use are due to the greater abundance of large golf courses adjacent to the saltmarsh in western Long Island compared to the rest of my study area. These golf courses provide a nearly unlimited supply of cultivated grasses, which are more energy dense than other Brant foods (Ladin et al. 2011), throughout the entire winter. Thus, Brant in this region may have reduced energy expenditure and a greater supply of available food, thereby altering their movements and space use relative to the rest of the population. Further research is required to explore variation in habitat availability among regions and to link habitat use and energetics to further our understanding of these differences.

While only a 5% difference, the increased amount of daily movement found for females compared to males agrees with data obtained from the accelerometers, which recorded movement every 6 min to allow for the classification of behaviors and found that females were in flight more often than males (Chapter 2). This did not alter home range size, however, although it may increase energy expenditure due to the high energetic cost of flight (Ladin et al. 2011). Differences in home range sizes and daily movement among years, while detectable, were often small and are likely explained by changes in food availability, temperature, and/or disturbance among years (Ladin et al. 2014).

Habitat use determined in this study differed from previously published estimates. I found ~14% less usage of open water habitats by Brant, similar amounts of developed land use, and ~21% more usage of emergent herbaceous habitats than Castelli et al. (2010). These differences are likely due to increased sample size and location accuracy of modern GPS–GSM telemetry units. Furthermore, I found differing temporal trends in open water use, which decreased as the winter progressed, and developed habitat use, which increased throughout the winter. A decline in open water use may be caused by reduced food in that habitat, as the *Ulva* spp. that Brant primarily eat are depleted and destroyed by wind and waves over the course of the winter (Kirby and Obrecht 1982). Additionally, availability of eelgrass may decline as Brant consume it. The spike in usage of both emergent herbaceous wetland and developed habitats beginning in February and March can likely be attributed to the beginning of the growing season for terrestrial and saltmarsh grasses as temperatures

rise. Depletion of *Ulva* and eelgrass by that point of the winter may also require Brant to meet their energy requirements by switching to consuming upland grasses.

Some caution in interpreting these habitat use results may be warranted. In particular, the National Land Cover Database (NLCD) layer used to determine habitat use has a coarser resolution (30×30 m) than the telemetry units (~ 10 m), which could lead to incorrectly assigned habitats, particularly at boundaries of habitat types (e.g., a shoreline), which Brant frequent. Additionally, the NLCD has rather coarse habitat types, which may overestimate upland field use in particular. While I generally assumed that being on developed land was equivalent to upland field use in this study, a cursory look the raw data indicates that this assumption is not always met. Therefore, using habitat data with a finer resolution and a greater number of habitat types may allow for a more detailed and nuanced look at Brant habitat use, particularly at habitat edges. Furthermore, without knowing the habitat available to each Brant, it is less certain if they avoided certain habitats more or if those habitats were simply not available to them. This information would be the next step in further solidifying regional differences among Brant.

Regional differences were the more prominent aspect of Brant movement and habitat use in New Jersey and New York. These differences suggest that different regions, even within the same state, may require different management strategies. Movement and habitat use differences may have arisen during past population declines caused by a loss of eelgrass and severe winters (Phillips 1932, Kirby and Obrecht 1982) and persisted or increased differently among regions (Smith et al. 1985). My

results deepen our understanding of these regional differences and support a need to further combine habitat use and energetic requirements to allow for a finer-scale understanding of Brant subpopulations for future management strategies.

Figures

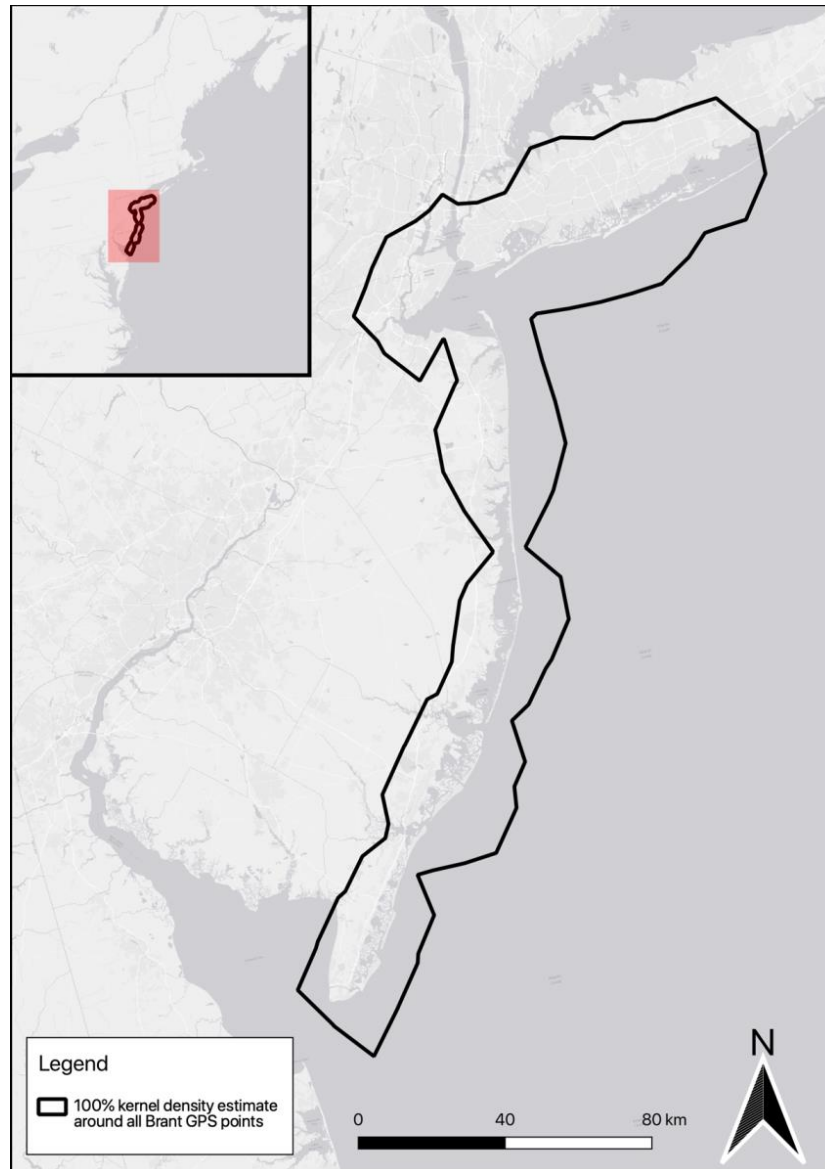


Figure 3.1 Study area represented as a 100% kernel density estimate around all GPS points obtained from telemetered Brant in New Jersey and New York from 2020–23.

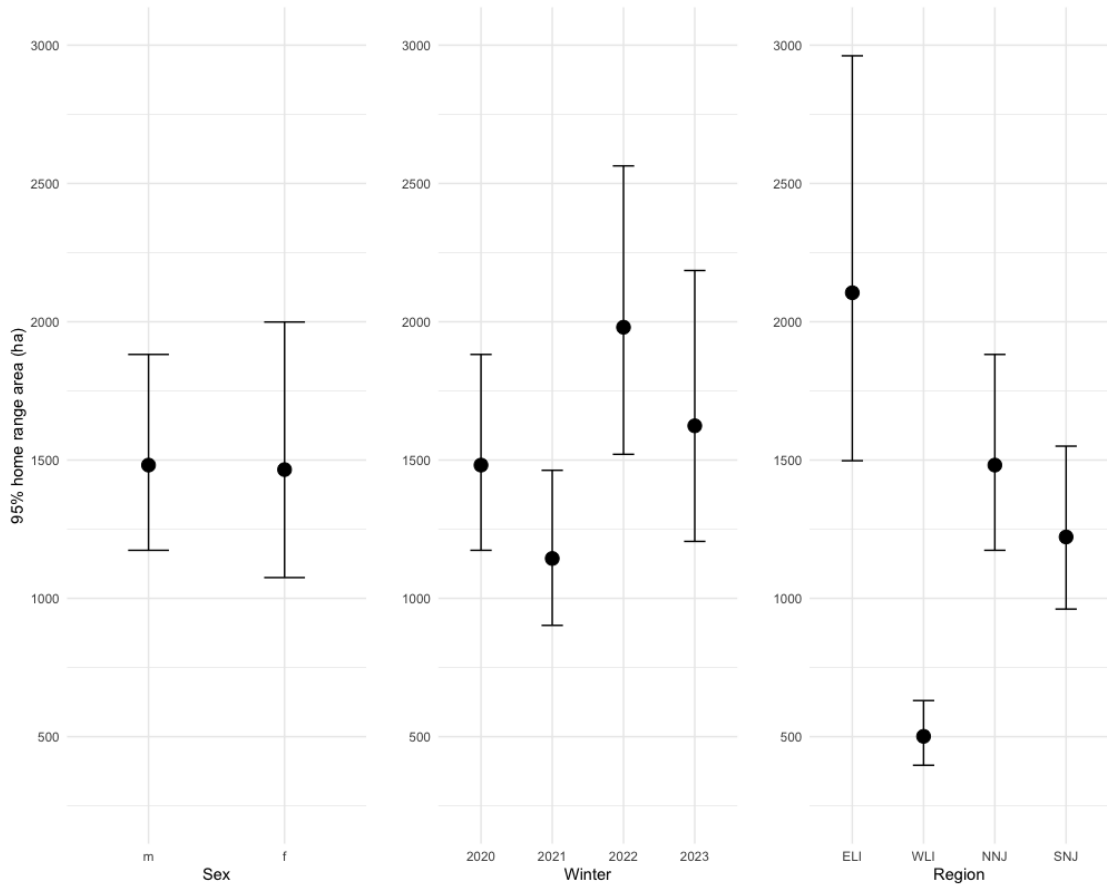


Figure 3.2 Conditional effects (mean and 80% credible interval) of covariates in the Bayesian regression model of the core winter 95% autocorrelated kernel density estimate home range size (ha) of Brant in New Jersey and New York from 2020–23.

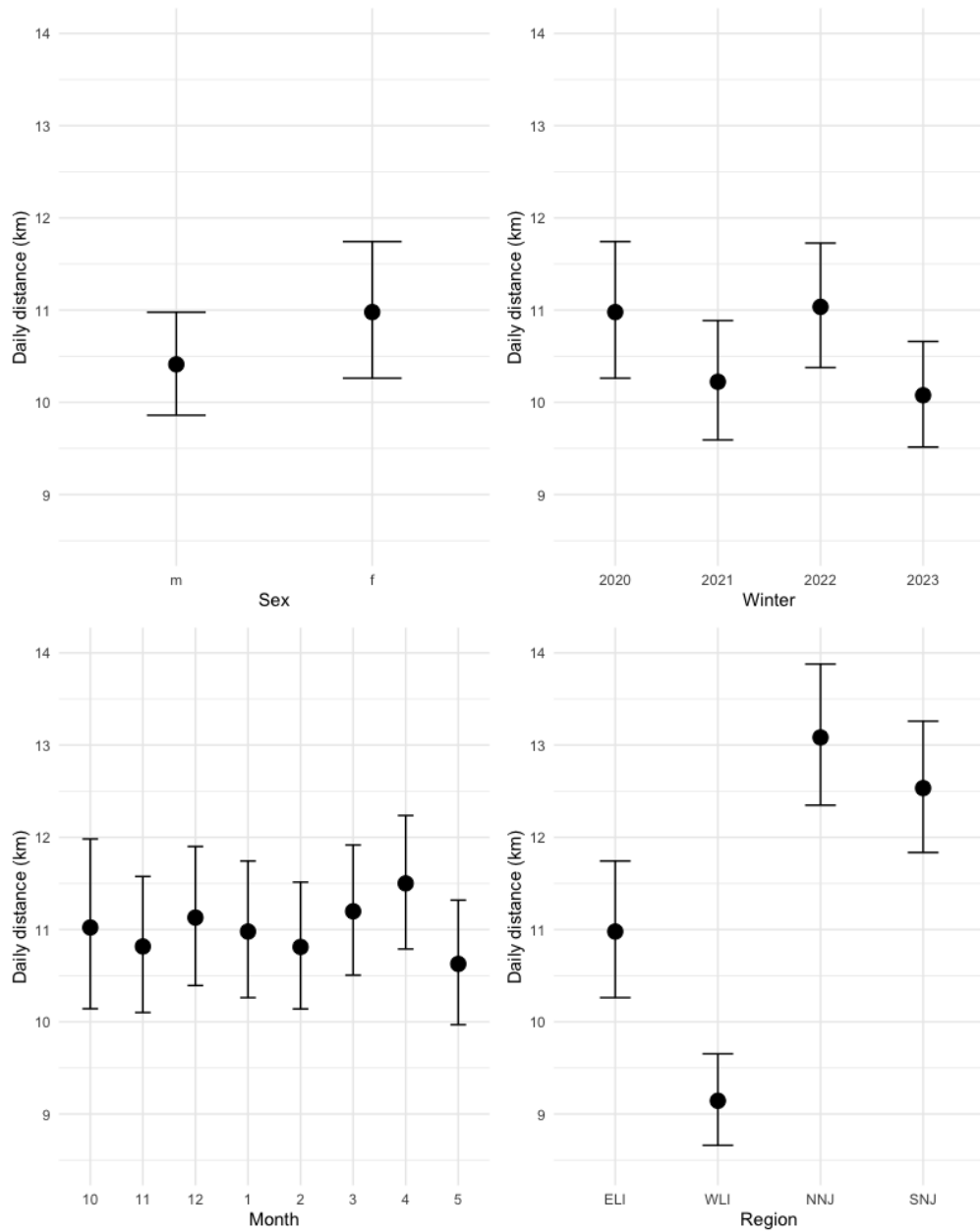


Figure 3.3 Conditional effects (mean and 80% credible interval) of covariates in the model of daily distance traveled (km) of Brant in New Jersey and New York from 2020–23.

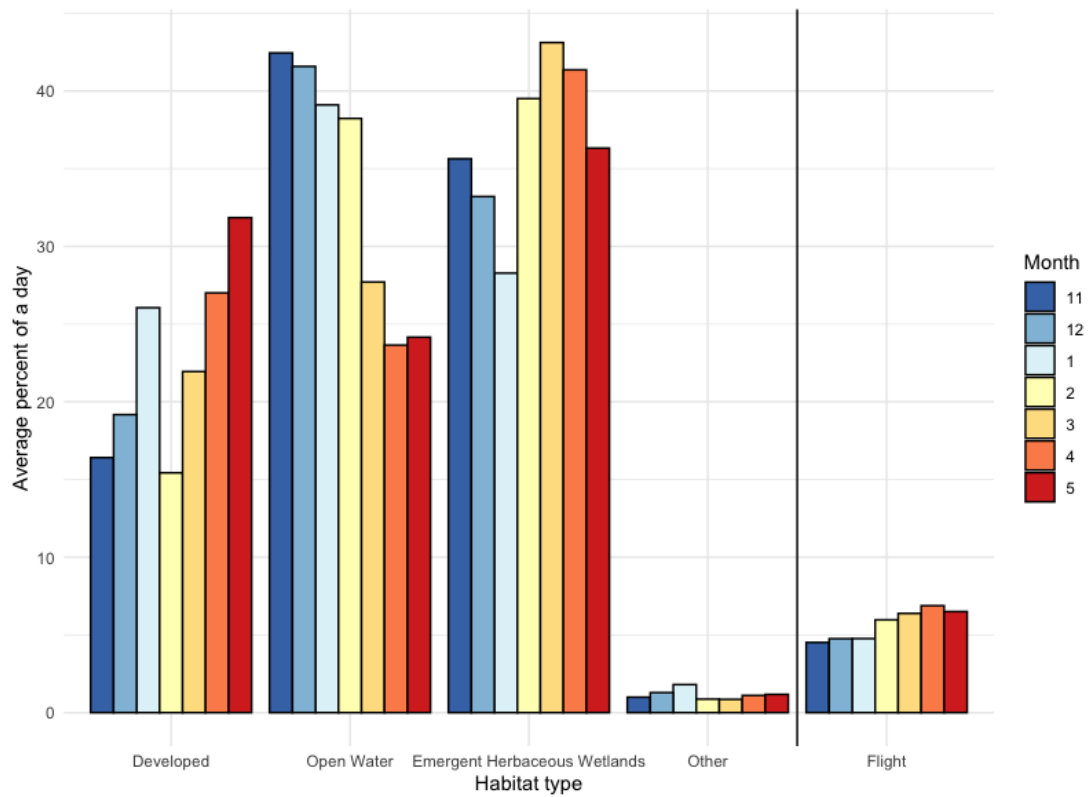


Figure 3.4 Bar chart showing the variability in average daily habitat use across months of Brant in New Jersey and New York from 2020–23. Flight data represent GPS points marked as flight and not given a habitat type.

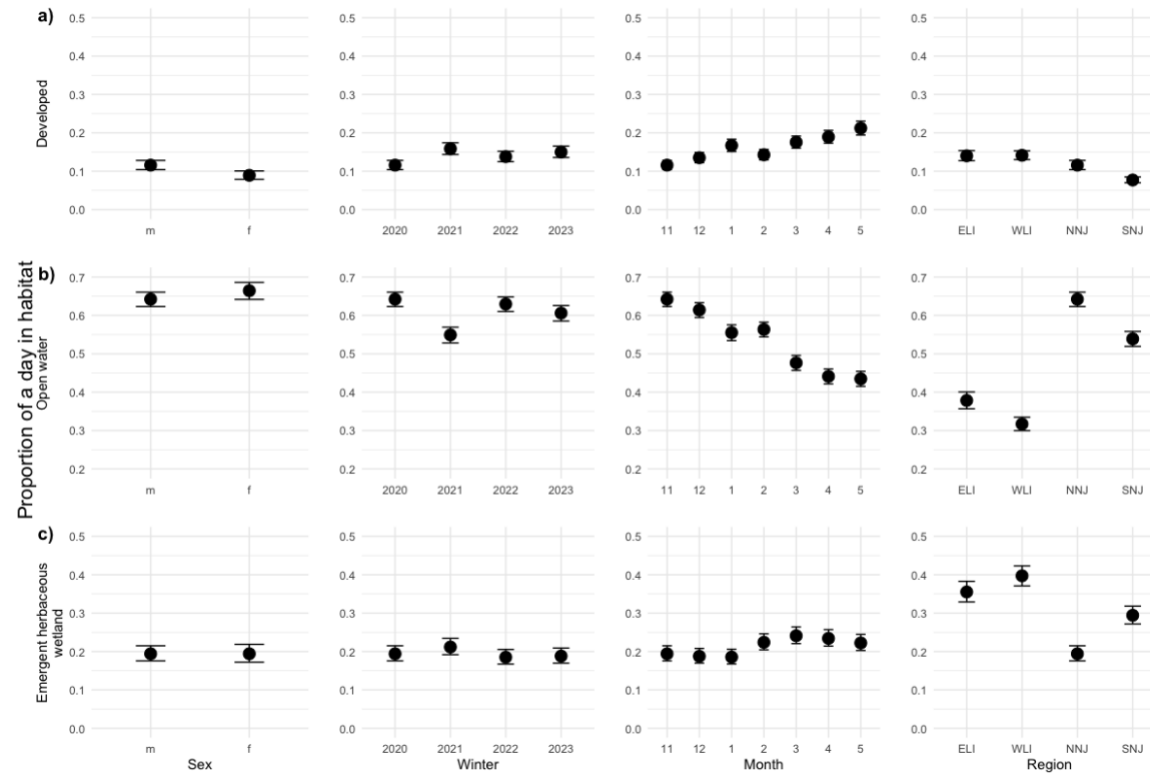


Figure 3.5 Conditional effects of covariates in each model of habitat use of Brant in New Jersey and New York from 2020–23. A) depicts the predicted daily proportion of use for the developed land category. B) depicts the predicted daily proportion of use for the open water category. C) depicts the predicted daily proportion of use for the emergent herbaceous wetland category.

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Appendix

FULL MODEL RESULTS

Table A.1 Full model results for the global field use model ($R^2 = 0.31$) for 69 pairs of used and unused fields for Brant in New Jersey and New York from 2020–23. Estimate is the mean response value; Est. Error is the estimated error; l-80% CI and u-80% CI are the lower and upper 80% credible intervals, respectively; Rhat is a model convergence diagnostic; and Bulk_ESS and Tail_ESS show effective sample sizes (20,000 draws) and sampling efficiency for the posterior distribution.

| Variable | Estimate | Est.Error | l-80% CI | u-80% CI | Rhat | Bulk_ESS | Tail_ESS |
|---------------------|----------|-----------|----------|----------|------|----------|----------|
| Month sd(Intercept) | 0.5 | 0.44 | 0.07 | 1.06 | 1 | 6534.05 | 8818.99 |
| SID sd(Intercept) | 0.22 | 0.17 | 0.03 | 0.45 | 1 | 13613.37 | 9508 |
| Intercept | 0.69 | 0.44 | 0.17 | 1.24 | 1 | 14114.11 | 11877.15 |
| Avg_height | -0.71 | 0.36 | -1.17 | -0.26 | 1 | 17983.48 | 15149.45 |
| Grass | 0.34 | 0.3 | -0.04 | 0.72 | 1 | 20952.13 | 15502.63 |
| Clover | -0.16 | 0.22 | -0.44 | 0.12 | 1 | 23213.14 | 15645.95 |
| Other | -0.06 | 0.27 | -0.42 | 0.28 | 1 | 19275.75 | 15809.19 |
| Dead | 0.11 | 0.25 | -0.21 | 0.43 | 1 | 18804.56 | 14797.72 |
| CN_Ratio | -0.24 | 0.26 | -0.57 | 0.08 | 1 | 19099.32 | 15422.81 |
| Energy | -0.08 | 0.28 | -0.45 | 0.28 | 1 | 19434.38 | 13760.85 |
| Roost_Distance_m | -0.07 | 0.22 | -0.36 | 0.21 | 1 | 29639.83 | 14224.99 |
| Field_area_m2 | 3.47 | 0.97 | 2.28 | 4.75 | 1 | 19354.31 | 13524.95 |
| Water_Distance_m | -0.37 | 0.27 | -0.72 | -0.03 | 1 | 23200.82 | 16160.98 |

Table A.2 Full model results for the intrinsic field use model ($R^2 = 0.12$) for 69 pairs of used and unused fields for Brant in New Jersey and New York from 2020–23. Estimate is the mean response value; Est. Error is the estimated error; l-80% CI and u-80% CI are the lower and upper 80% credible intervals, respectively; Rhat is a model convergence diagnostic that should be 1 at convergence; and Bulk_ESS and Tail_ESS show effective sample sizes (20,000 draws) and sampling efficiency for the posterior distribution.

| Variable | Estimate | Est.Error | l-80% CI | u-80% CI | Rhat | Bulk_ESS | Tail_ESS |
|---------------------|----------|-----------|----------|----------|------|----------|----------|
| Month sd(Intercept) | 0.33 | 0.32 | 0.04 | 0.72 | 1 | 6656.6 | 8084.36 |
| SID sd(Intercept) | 0.17 | 0.13 | 0.03 | 0.35 | 1 | 15133.55 | 9412.2 |
| Intercept | -0.01 | 0.27 | -0.32 | 0.31 | 1 | 11776.06 | 9294.92 |
| Avg_height | -0.77 | 0.29 | -1.15 | -0.41 | 1 | 16749.7 | 13818.17 |
| Grass | 0.32 | 0.26 | -0.01 | 0.66 | 1 | 18305.58 | 13877.67 |
| Clover | -0.29 | 0.21 | -0.56 | -0.03 | 1 | 24546.6 | 15041.26 |
| Other | 0.05 | 0.22 | -0.24 | 0.33 | 1 | 20174.23 | 14609.95 |
| Dead | 0.09 | 0.21 | -0.18 | 0.36 | 1 | 23003.42 | 15617.08 |
| CN_Ratio | -0.13 | 0.21 | -0.4 | 0.14 | 1 | 21399.29 | 16301 |
| Energy | 0.09 | 0.23 | -0.2 | 0.38 | 1 | 22134.17 | 16350.52 |

Table A.3 Full model results for the extrinsic field use model ($R^2 = 0.24$) for 69 pairs of used and unused fields for Brant in New Jersey and New York from 2020–23. Estimate is the mean response value; Est. Error is the estimated error; l-80% CI and u-80% CI are the lower and upper 80% credible intervals, respectively; Rhat is a model convergence diagnostic that should be 1 at convergence; and Bulk_ESS and Tail_ESS show effective sample sizes (20,000 draws) and sampling efficiency for the posterior distribution.

| Variable | Estimate | Est.Error | l-80% CI | u-80% CI | Rhat | Bulk_ESS | Tail_ESS |
|---------------------|----------|-----------|----------|----------|------|----------|----------|
| Month sd(Intercept) | 0.28 | 0.26 | 0.04 | 0.6 | 1 | 12656.11 | 11975.93 |
| SID sd(Intercept) | 0.19 | 0.15 | 0.03 | 0.4 | 1 | 15968.64 | 10826.11 |
| Intercept | 0.64 | 0.37 | 0.19 | 1.12 | 1 | 21837.99 | 14481.46 |
| Roost_Distance_m | -0.06 | 0.2 | -0.31 | 0.18 | 1 | 39669.62 | 14127.34 |
| Field_area_m2 | 3.15 | 0.94 | 1.99 | 4.37 | 1 | 25701.58 | 13267.58 |
| Water_Distance_m | -0.51 | 0.25 | -0.83 | -0.2 | 1 | 36403.23 | 14393.29 |

Table A.4 Full model results for the field use model that allowed the variable effects to vary by month ($R^2 = 0.38$) for 69 pairs of used and unused fields for Brant in New Jersey and New York from 2020–23. Estimate is the mean response value; Est. Error is the estimated error; l-80% CI and u-80% CI are the lower and upper 80% credible intervals, respectively; Rhat is a model convergence diagnostic that should be 1 at convergence; and Bulk_ESS and Tail_ESS show effective sample sizes (20,000 draws) and sampling efficiency for the posterior distribution.

| Variable | Estimate | Est.Error | l-80% CI | u-80% CI | Rhat | Bulk_ESS | Tail_ESS |
|---------------------|----------|-----------|----------|----------|------|----------|----------|
| Month sd(Intercept) | 0.72 | 0.62 | 0.11 | 1.53 | 1 | 9571.75 | 11258.04 |
| SID sd(Intercept) | 0.29 | 0.23 | 0.05 | 0.61 | 1 | 13669.97 | 10840.53 |
| Intercept | 0.73 | 0.6 | 0.02 | 1.46 | 1 | 14368.29 | 12839.61 |
| Avg_height | -1.13 | 0.67 | -1.95 | -0.37 | 1 | 13596.39 | 12066.48 |
| Grass | 0.47 | 0.5 | -0.11 | 1.08 | 1 | 15637.84 | 12470.24 |
| Clover | -0.19 | 0.42 | -0.67 | 0.29 | 1 | 14673.9 | 11734.65 |
| Other | -0.02 | 0.47 | -0.57 | 0.52 | 1 | 14470.64 | 11045.09 |
| Dead | 0.09 | 0.46 | -0.44 | 0.62 | 1 | 13479.63 | 12105.81 |
| CN_Ratio | -0.45 | 0.52 | -1.03 | 0.13 | 1 | 13107.75 | 10149.35 |
| Energy | -0.04 | 0.47 | -0.6 | 0.52 | 1 | 16935.03 | 13364 |
| Roost_Distance_m | -0.2 | 0.47 | -0.7 | 0.3 | 1 | 13235.98 | 10772.11 |
| Field_area_m2 | 4.54 | 1.38 | 2.89 | 6.31 | 1 | 17073.4 | 13329.47 |
| Water_Distance_m | -0.53 | 0.57 | -1.21 | 0.11 | 1 | 14903.46 | 10788.91 |

Table A.5 Full model results for the null (intercept-only) field use model ($R^2 = 0.01$) for 69 pairs of used and unused fields for Brant in New Jersey and New York from 2020–23. Estimate is the mean response value; Est. Error is the estimated error; l-80% CI and u-80% CI are the lower and upper 80% credible intervals, respectively; Rhat is a model convergence diagnostic that should be 1 at convergence; and Bulk_ESS and Tail_ESS show effective sample sizes (20,000 draws) and sampling efficiency for the posterior distribution.

| Variable | Estimate | Est.Error | l-80% CI | u-80% CI | Rhat | Bulk_ESS | Tail_ESS |
|---------------------|----------|-----------|----------|----------|------|----------|----------|
| Month sd(Intercept) | 0.21 | 0.2 | 0.03 | 0.45 | 1 | 12876.17 | 10902.9 |
| SID sd(Intercept) | 0.14 | 0.11 | 0.02 | 0.3 | 1 | 18368.3 | 8949.57 |
| Intercept | 0 | 0.21 | -0.26 | 0.25 | 1 | 21444.26 | 13012.07 |

Table A.6 Full model results for the upland field use intensity model ($R^2 = 0.70$) for 69 pairs of used and unused fields for Brant in New Jersey and New York from 2020–23. Estimate is the mean response value; Est. Error is the estimated error; l-80% CI and u-80% CI are the lower and upper 80% credible intervals, respectively; Rhat is a model convergence diagnostic that should be 1 at convergence; and Bulk_ESS and Tail_ESS show effective sample sizes (20,000 draws) and sampling efficiency for the posterior distribution.

| Variable | Estimate | Est.Error | l-80% CI | u-80% CI | Rhat | Bulk_ESS | Tail_ESS |
|---------------------|----------|-----------|----------|----------|------|----------|----------|
| Month sd(Intercept) | 0.82 | 0.36 | 0.49 | 1.26 | 1 | 6025.63 | 8703.4 |
| Intercept | 2.84 | 0.36 | 2.43 | 3.26 | 1 | 4830.73 | 7135.4 |
| Avg_height | 0.55 | 0.04 | 0.5 | 0.6 | 1 | 14511.42 | 15260.56 |
| Grass | -0.31 | 0.03 | -0.34 | -0.27 | 1 | 18168.08 | 14897.68 |
| Clover | -0.1 | 0.04 | -0.15 | -0.06 | 1 | 22283.16 | 14768.09 |
| Other | 0.02 | 0.03 | -0.01 | 0.06 | 1 | 19861.33 | 15726.18 |
| Dead | 0.19 | 0.03 | 0.15 | 0.23 | 1 | 15548.58 | 14626.11 |
| CN_Ratio | 0.07 | 0.02 | 0.04 | 0.1 | 1 | 17411.45 | 15403.59 |
| Energy | -0.23 | 0.03 | -0.28 | -0.19 | 1 | 16629.22 | 14567.14 |
| Roost_Distance_m | -0.23 | 0.03 | -0.27 | -0.19 | 1 | 18584.6 | 15771.51 |
| Field_area_m2 | 0.36 | 0.01 | 0.34 | 0.38 | 1 | 15806.86 | 15354.98 |
| Water_Distance_m | -0.85 | 0.07 | -0.94 | -0.76 | 1 | 18976.5 | 15264.82 |

Table A.7 Full model results for the daily energy expenditure model ($R^2 = 0.13$) for 21,500 Brant-days in New Jersey and New York from 2020–23. Estimate is the mean response value; Est. Error is the estimated error; l-80% CI and u-80% CI are the lower and upper 80% credible intervals, respectively; Rhat is a model convergence diagnostic that should be 1 at convergence; and Bulk_ESS and Tail_ESS show effective sample sizes (80,000 draws) and sampling efficiency for the posterior distribution. The reference category for sex is female, for month 1 (January), and for winter 2020.

| Variable | Estimate | Est.Error | l-80% CI | u-80% CI | Rhat | Bulk_ESS | Tail_ESS |
|--------------|----------|-----------|----------|----------|------|----------|----------|
| Intercept | 1342.76 | 15.31 | 1323.15 | 1362.43 | 1 | 1864.36 | 3835.86 |
| Sex: male | -21.65 | 16.92 | -43.32 | -0.25 | 1 | 1287.42 | 2660.27 |
| February | -17.84 | 4.04 | -23.02 | -12.66 | 1 | 12830.94 | 28392.71 |
| March | -52.93 | 3.92 | -57.95 | -47.9 | 1 | 11803.35 | 25449.03 |
| April | -91.55 | 3.98 | -96.65 | -86.46 | 1 | 11622.99 | 25081.83 |
| May | -115.17 | 4.55 | -120.99 | -109.31 | 1 | 13487.53 | 29175.56 |
| October | -108.64 | 11.03 | -122.89 | -94.61 | 1 | 37169.82 | 51709.4 |
| November | -68.14 | 4.55 | -73.99 | -62.3 | 1 | 19059.28 | 37406.78 |
| December | -28.47 | 4.16 | -33.8 | -23.14 | 1 | 18576.11 | 35047.23 |
| Winter: 2021 | 6.27 | 4.45 | 0.6 | 12 | 1 | 14160.33 | 30894 |
| Winter: 2022 | -4.61 | 5.6 | -11.74 | 2.61 | 1 | 11137.19 | 23238.33 |
| Winter: 2023 | -43.57 | 7.53 | -53.22 | -33.89 | 1 | 9224.73 | 19313.23 |

Table A.8 Full model results for the daily flight time model ($R^2 = 0.09$) for 21,500 Brant-days in New Jersey and New York from 2020–23. Estimate is the mean response value; Est. Error is the estimated error; l-80% CI and u-80% CI are the lower and upper 80% credible intervals, respectively; Rhat is a model convergence diagnostic that should be 1 at convergence; and Bulk_ESS and Tail_ESS show effective sample sizes (80,000 draws) and sampling efficiency for the posterior distribution. The reference category for sex is female, for month 1 (January), and for winter 2020.

| Variable | Estimate | Est.Error | l-80% CI | u-80% CI | Rhat | Bulk_ESS | Tail_ESS |
|--------------------------|----------|-----------|----------|----------|------|----------|----------|
| individual sd(Intercept) | 0.49 | 0.03 | 0.46 | 0.53 | 1 | 3893.92 | 8331.72 |
| Intercept | 1.77 | 0.06 | 1.69 | 1.85 | 1 | 1545.32 | 3948.6 |
| Sex: male | -0.33 | 0.07 | -0.43 | -0.24 | 1 | 934.25 | 2301.29 |
| February | -0.04 | 0.02 | -0.06 | -0.02 | 1 | 13221.21 | 26812.18 |
| March | -0.02 | 0.02 | -0.04 | 0 | 1 | 12009.83 | 24322.12 |
| April | -0.09 | 0.02 | -0.11 | -0.07 | 1 | 12251.72 | 24963.08 |
| May | -0.18 | 0.02 | -0.2 | -0.16 | 1 | 14416.4 | 29798.91 |
| October | -0.13 | 0.04 | -0.19 | -0.07 | 1 | 37046.69 | 48367.4 |
| November | -0.03 | 0.02 | -0.05 | 0 | 1 | 18685.17 | 36562.76 |
| December | -0.01 | 0.02 | -0.03 | 0.01 | 1 | 17701.72 | 35890.5 |
| Winter: 2021 | -0.05 | 0.02 | -0.07 | -0.03 | 1 | 14540.71 | 29424.01 |
| Winter: 2022 | -0.08 | 0.02 | -0.11 | -0.05 | 1 | 11767.42 | 25059.92 |
| Winter: 2023 | -0.22 | 0.03 | -0.26 | -0.18 | 1 | 10311.35 | 21215.33 |

Table A.9 Full model results for the daily stationary time model ($R^2 = 0.53$) for 21,500 Brant-days in New Jersey and New York from 2020–23. Estimate is the mean response value; Est. Error is the estimated error; l-80% CI and u-80% CI are the lower and upper 80% credible intervals, respectively; Rhat is a model convergence diagnostic that should be 1 at convergence; and Bulk_ESS and Tail_ESS show effective sample sizes (80,000 draws) and sampling efficiency for the posterior distribution. The reference category for sex is female, for month 1 (January), and for winter 2020.

| Variable | Estimate | Est.Error | l-80% CI | u-80% CI | Rhat | Bulk_ESS | Tail_ESS |
|--------------------------|----------|-----------|----------|----------|------|----------|----------|
| individual sd(Intercept) | 1.96 | 0.1 | 1.83 | 2.09 | 1 | 1906.06 | 3644.38 |
| Intercept | 5.53 | 0.25 | 5.22 | 5.85 | 1 | 1342.24 | 3235.74 |
| Sex: male | -0.88 | 0.28 | -1.24 | -0.53 | 1 | 967.14 | 2086.45 |
| February | 0.24 | 0.06 | 0.16 | 0.32 | 1 | 12083.75 | 25911.93 |
| March | 0.17 | 0.06 | 0.1 | 0.25 | 1 | 11130.95 | 23043.54 |
| April | -0.42 | 0.06 | -0.5 | -0.34 | 1 | 11386.73 | 23620.97 |
| May | -0.55 | 0.07 | -0.64 | -0.46 | 1 | 12926.78 | 28038 |
| October | 0.87 | 0.17 | 0.65 | 1.08 | 1 | 39373.91 | 51946.7 |
| November | 0.22 | 0.07 | 0.13 | 0.31 | 1 | 19641.34 | 37307.31 |
| December | -0.09 | 0.06 | -0.17 | -0.01 | 1 | 18094.36 | 34854.11 |
| Winter: 2021 | 0.56 | 0.07 | 0.47 | 0.65 | 1 | 12766.64 | 27082.79 |
| Winter: 2022 | -0.1 | 0.09 | -0.22 | 0.01 | 1 | 10244.66 | 22138.55 |
| Winter: 2023 | -0.62 | 0.11 | -0.76 | -0.47 | 1 | 9670.51 | 20146.8 |

Table A.10 Full model results for the behavioral proportion (categorical) regression model for 515,883 Brant accelerometry bursts in New Jersey and New York from 2020–23. Estimate is the mean response value; Est. Error is the estimated error; l-80% CI and u-80% CI are the lower and upper 80% credible intervals, respectively; Rhat is a model convergence diagnostic; and Bulk_ESS and Tail_ESS show effective sample sizes (60,000 iterations). Fly and stationary values are relative to the reference category, movement. The reference category for sex is female, for weekend being the weekend, and for time of day (“tod”) day.

| Variable | Estimate | Est.Error | l-80% CI | u-80% CI | Rhat | Bulk_ESS | Tail_ESS |
|--------------------------------|----------|-----------|----------|----------|------|-----------|----------|
| bird sd(Fly: Intercept) | 0.70 | 0.04 | 0.65 | 0.75 | 1 | 3903.17 | 8275.75 |
| bird sd(Stationary: Intercept) | 0.86 | 0.05 | 0.8 | 0.92 | 1 | 2325.67 | 5739.32 |
| Fly: Intercept | -2.56 | 0.08 | -2.66 | -2.46 | 1 | 2127.28 | 4645.66 |
| Stationary: Intercept | -2.38 | 0.1 | -2.5 | -2.26 | 1 | 1132.94 | 2423.59 |
| Fly: temperature | -0.03 | 0.01 | -0.04 | -0.03 | 1 | 69904.48 | 48560.73 |
| Fly: precipitation | -0.54 | 0.03 | -0.58 | -0.51 | 1 | 80840.56 | 46599.54 |
| Fly: water height | 0.02 | 0.01 | 0.01 | 0.03 | 1 | 85009.13 | 46824.13 |
| Fly: wind speed | 0.04 | 0.01 | 0.03 | 0.05 | 1 | 79092.7 | 46233.24 |
| Fly: tod: evening | 0.21 | 0.03 | 0.17 | 0.25 | 1 | 77912.69 | 46502.37 |
| Fly: tod: night | 0.15 | 0.01 | 0.13 | 0.17 | 1 | 60103.46 | 47521.28 |
| Fly: tod: morning | 0.48 | 0.03 | 0.45 | 0.52 | 1 | 66414.21 | 45687.98 |
| Fly: latitude | -0.16 | 0.03 | -0.2 | -0.13 | 1 | 5827.94 | 12124.82 |
| Fly: weekend | 0.06 | 0.01 | 0.04 | 0.08 | 1 | 78900.75 | 44902.34 |
| Fly: sex: male | -0.31 | 0.1 | -0.44 | -0.18 | 1 | 1904.58 | 4307.33 |
| Stationary: temperature | -0.01 | 0 | -0.02 | 0 | 1 | 80640.2 | 45255.22 |
| Stationary: precipitation | -0.65 | 0.02 | -0.67 | -0.63 | 1 | 73520.59 | 47313.35 |
| Stationary: water height | 0.06 | 0 | 0.06 | 0.07 | 1 | 104023.59 | 46234.17 |
| Stationary: wind speed | -0.12 | 0 | -0.12 | -0.11 | 1 | 92284.16 | 45109.37 |
| Stationary: tod: evening | 0.31 | 0.03 | 0.28 | 0.34 | 1 | 70522.4 | 46960.79 |

Table A.10 continued

| | | | | | | | |
|--------------------------|-------|------|-------|------|------|----------|----------|
| Stationary: tod: night | 1.78 | 0.01 | 1.77 | 1.79 | 1 | 56882.25 | 46709.51 |
| Stationary: tod: morning | 0.71 | 0.02 | 0.68 | 0.74 | 1 | 63197.33 | 45772.79 |
| Stationary: latitude | -0.33 | 0.02 | -0.36 | -0.3 | 1 | 8221.14 | 15276.79 |
| Stationary: weekend | -0.01 | 0.01 | -0.02 | 0 | 1 | 79683.26 | 46228.75 |
| Stationary: sex: male | -0.15 | 0.12 | -0.31 | 0.01 | 1.01 | 959.84 | 2008.32 |

Table A.11 Full model results for both 95% ($R^2 = 0.42$) and 50% ($R^2 = 0.42$) autocorrelated kernel density estimate home ranges for 244 Brant-winters in New Jersey and New York from 2020–23. Estimate is the mean response value; Est. Error is the estimated error; l-80% CI and u-80% CI are the lower and upper 80% credible intervals, respectively; Rhat is a model convergence diagnostic that should be 1 at convergence; and Bulk_ESS and Tail_ESS show effective sample sizes (20,000 iterations) and sampling efficiency for the posterior distribution. The reference category for sex is male, for winter 2020, and for region northern New Jersey.

| Size | Variable | Estimate | Est.Error | l-80% CI | u-80% CI | Rhat | Bulk_ESS | Tail_ESS |
|------|-----------------------------|----------|-----------|----------|----------|-------|-----------|-----------|
| 50% | individual sd(Intercept) | 0.482 | 0.172 | 0.234 | 0.683 | 1.001 | 1511.263 | 2975.432 |
| | Intercept | 5.534 | 0.196 | 5.283 | 5.787 | 1 | 14505.212 | 14295.637 |
| | Sex: female | -0.077 | 0.183 | -0.312 | 0.156 | 1 | 10813.107 | 14381.931 |
| | Winter: 2021 | -0.32 | 0.204 | -0.582 | -0.058 | 1 | 13302.184 | 15359.412 |
| | Winter: 2022 | 0.275 | 0.221 | -0.008 | 0.557 | 1 | 9895.824 | 13527.292 |
| | Winter: 2023 | 0.17 | 0.242 | -0.141 | 0.479 | 1 | 10458.809 | 12550.358 |
| | Region: southern NJ | -0.141 | 0.207 | -0.405 | 0.124 | 1 | 12761.076 | 14567.981 |
| | Region: western Long Island | -1.182 | 0.194 | -1.431 | -0.935 | 1 | 10086.423 | 12621.641 |
| | Region: eastern Long Island | 0.292 | 0.284 | -0.076 | 0.652 | 1 | 8231.611 | 13690.472 |
| | sigma | 0.904 | 0.084 | 0.795 | 1.016 | 1.001 | 1836.778 | 4666.697 |
| 95% | individual sd(Intercept) | 0.44 | 0.167 | 0.19 | 0.633 | 1.001 | 1409.088 | 2290.201 |
| | Intercept | 7.302 | 0.184 | 7.068 | 7.54 | 1 | 19531.303 | 14607.779 |
| | Sex: female | -0.011 | 0.172 | -0.232 | 0.208 | 1 | 10345.378 | 13783.45 |
| | Winter: 2021 | -0.257 | 0.191 | -0.5 | -0.013 | 1 | 14604.298 | 15494.911 |
| | Winter: 2022 | 0.289 | 0.208 | 0.021 | 0.556 | 1 | 11457.592 | 14423.702 |
| | Winter: 2023 | 0.09 | 0.232 | -0.206 | 0.392 | 1.001 | 9525.797 | 13654.986 |
| | Region: southern NJ | -0.194 | 0.191 | -0.44 | 0.049 | 1 | 13055.736 | 14836.131 |
| | Region: western Long Island | -1.086 | 0.182 | -1.319 | -0.852 | 1 | 11235.421 | 12403.089 |
| | Region: eastern Long Island | 0.35 | 0.268 | 0.005 | 0.691 | 1 | 9002.345 | 11034.364 |
| | sigma | 0.839 | 0.079 | 0.737 | 0.944 | 1.001 | 1794.317 | 5507.154 |

Table A.12 Full results for the model of daily distance traveled ($R^2 = 0.24$) for 21,369 Brant-days in New Jersey and New York from 2020–23. Estimate is the mean response value; Est. Error is the estimated error; l-80% CI and u-80% CI are the lower and upper 80% credible intervals, respectively; Rhat is a model convergence diagnostic that should be 1 at convergence; and Bulk_ESS and Tail_ESS show effective sample sizes (40,000 draws) and sampling efficiency for the posterior distribution. The reference category for sex is female, for winter 2020, for month 1 (January), and for region eastern Long Island.

| Variable | Estimate | Est.Error | l-80% CI | u-80% CI | Rhat | Bulk_ESS | Tail_ESS |
|-----------------------------|----------|-----------|----------|----------|-------|-----------|-----------|
| individual sd(Intercept) | 0.231 | 0.013 | 0.214 | 0.248 | 1.001 | 4166.34 | 6422.839 |
| Intercept | 2.396 | 0.052 | 2.328 | 2.463 | 1.001 | 5204.724 | 9580.856 |
| Sex: male | -0.053 | 0.038 | -0.101 | -0.005 | 1 | 3157.596 | 6735.813 |
| Winter: 2021 | -0.072 | 0.016 | -0.093 | -0.051 | 1 | 12645.525 | 20794.82 |
| Winter: 2022 | 0.005 | 0.02 | -0.021 | 0.031 | 1 | 10392.049 | 17828.03 |
| Winter: 2023 | -0.086 | 0.026 | -0.119 | -0.053 | 1 | 9317.878 | 14938.224 |
| February | -0.016 | 0.014 | -0.033 | 0.002 | 1 | 12366.529 | 20198.368 |
| March | 0.019 | 0.014 | 0.002 | 0.037 | 1 | 11590.325 | 18553.312 |
| April | 0.046 | 0.014 | 0.028 | 0.064 | 1 | 11541.895 | 18476.855 |
| May | -0.033 | 0.016 | -0.053 | -0.012 | 1 | 13404.953 | 21833.199 |
| October | 0.004 | 0.04 | -0.047 | 0.055 | 1 | 35233.094 | 29194.306 |
| November | -0.015 | 0.016 | -0.036 | 0.006 | 1 | 19027.706 | 26735.046 |
| December | 0.013 | 0.015 | -0.005 | 0.032 | 1 | 17551.804 | 24276.771 |
| Region: northern NJ | 0.176 | 0.046 | 0.118 | 0.235 | 1.001 | 4842.516 | 7906.025 |
| Region: southern NJ | 0.132 | 0.036 | 0.086 | 0.178 | 1.001 | 6460.419 | 11569.809 |
| Region: western Long Island | -0.183 | 0.038 | -0.232 | -0.133 | 1.001 | 4772.928 | 8463.045 |
| sigma | 0.421 | 0.002 | 0.419 | 0.424 | 1.001 | 49366.606 | 28697.117 |

Table A.13 Full model results for the developed habitat use model ($R^2 = 0.29$) using a default “brms” zero-inflated beta distribution for 18,501 Brant-days in New Jersey and New York from 2020–23. Estimate is the mean response value; Est. Error is the estimated error; l-80% CI and u-80% CI are the lower and upper 80% credible intervals, respectively; phi is the spread of data around the mean; zi is the intercept for the zero process; Rhat is a model convergence diagnostic that should be 1 at convergence; and Bulk_ESS and Tail_ESS show effective sample sizes (40,000 draws) and sampling efficiency for the posterior distribution. The reference category for winter is 2020, for month 11 (November), and for region northern New Jersey.

| Variable | Estimate | Est.Error | l-80% CI | u-80% CI | Rhat | Bulk_ESS | Tail_ESS |
|-----------------------------|----------|-----------|----------|----------|-------|-----------|-----------|
| individual sd(Intercept) | 0.514 | 0.031 | 0.475 | 0.555 | 1.001 | 2640.358 | 6579.116 |
| Intercept | -1.791 | 0.094 | -1.913 | -1.671 | 1.002 | 2059.556 | 4412.789 |
| Sex: female | -0.297 | 0.086 | -0.407 | -0.187 | 1.002 | 1424.177 | 3042.445 |
| Winter: 2021 | 0.378 | 0.028 | 0.342 | 0.414 | 1 | 9288.267 | 17003.425 |
| Winter: 2022 | 0.208 | 0.037 | 0.161 | 0.255 | 1 | 7785.028 | 14429.32 |
| Winter: 2023 | 0.31 | 0.047 | 0.25 | 0.371 | 1 | 6742.004 | 12326.643 |
| December | 0.183 | 0.028 | 0.146 | 0.219 | 1 | 10760.192 | 18780.608 |
| January | 0.442 | 0.03 | 0.404 | 0.48 | 1 | 10327.297 | 20224.906 |
| February | 0.249 | 0.03 | 0.211 | 0.289 | 1 | 7627.602 | 15758.13 |
| March | 0.505 | 0.028 | 0.469 | 0.541 | 1 | 6654.011 | 12610.249 |
| April | 0.604 | 0.028 | 0.568 | 0.64 | 1.001 | 6554.053 | 12780.706 |
| May | 0.754 | 0.031 | 0.715 | 0.793 | 1 | 7238.067 | 15232.92 |
| Region: southern NJ | -0.46 | 0.107 | -0.596 | -0.322 | 1.002 | 1927.685 | 3289.377 |
| Region: western Long Island | 0.238 | 0.087 | 0.127 | 0.35 | 1.002 | 2078.925 | 3817.979 |
| Region: eastern Long Island | 0.227 | 0.11 | 0.087 | 0.371 | 1.001 | 2277.077 | 4633.451 |
| phi | 10.62 | 0.121 | 10.465 | 10.775 | 1 | 34583.319 | 28796.767 |
| zi | 0.191 | 0.003 | 0.187 | 0.194 | 1 | 38278.552 | 30237.091 |

Table A.14 Full model results for the open water habitat use model ($R^2 = 0.53$) using a default “brms” zero-inflated beta distribution for 18,501 Brant-days in New Jersey and New York from 2020–23. Estimate is the mean response value; Est. Error is the estimated error; l-80% CI and u-80% CI are the lower and upper 80% credible intervals, respectively; phi is the spread of data around the mean; zi is the intercept for the zero process; Rhat is a model convergence diagnostic that should be 1 at convergence; and Bulk_ESS and Tail_ESS show effective sample sizes (40,000 draws) and sampling efficiency for the posterior distribution. The reference category for winter is 2020, for month 11 (November), and for region northern New Jersey.

| Variable | Estimate | Est.Error | l-80% CI | u-80% CI | Rhat | Bulk_ESS | Tail_ESS |
|-----------------------------|----------|-----------|----------|----------|-------|-----------|-----------|
| individual sd(Intercept) | 0.394 | 0.024 | 0.364 | 0.425 | 1.001 | 4942.572 | 10282.779 |
| Intercept | 0.678 | 0.068 | 0.591 | 0.764 | 1.001 | 3609.118 | 7194.126 |
| Sex: female | 0.104 | 0.065 | 0.022 | 0.187 | 1.002 | 2712.569 | 6184.029 |
| Winter: 2021 | -0.408 | 0.03 | -0.447 | -0.369 | 1 | 12650.799 | 21796.88 |
| Winter: 2022 | -0.058 | 0.037 | -0.105 | -0.011 | 1 | 10267.227 | 18229.743 |
| Winter: 2023 | -0.164 | 0.046 | -0.223 | -0.104 | 1 | 9138.533 | 16095.884 |
| December | -0.127 | 0.025 | -0.16 | -0.095 | 1 | 19157.228 | 27574.955 |
| January | -0.383 | 0.028 | -0.419 | -0.346 | 1 | 18583.233 | 27017.905 |
| February | -0.347 | 0.027 | -0.382 | -0.313 | 1 | 12040.827 | 21830.387 |
| March | -0.71 | 0.026 | -0.743 | -0.677 | 1 | 11191.354 | 20451.523 |
| April | -0.856 | 0.026 | -0.889 | -0.823 | 1 | 11068.333 | 19819.037 |
| May | -0.883 | 0.03 | -0.921 | -0.844 | 1 | 12995.123 | 22362.991 |
| Region: southern NJ | -0.45 | 0.069 | -0.538 | -0.361 | 1 | 4020.301 | 7272.48 |
| Region: western Long Island | -1.397 | 0.067 | -1.483 | -1.31 | 1.001 | 3752.19 | 7722.335 |
| Region: eastern Long Island | -1.121 | 0.08 | -1.223 | -1.02 | 1 | 4543.17 | 9100.616 |
| phi | 8.317 | 0.086 | 8.207 | 8.428 | 1 | 58784.58 | 30170.737 |
| zi | 0.032 | 0.001 | 0.03 | 0.034 | 1 | 66521.893 | 28542.877 |

Table A.15 Full model results for the emergent herbaceous wetland habitat use model ($R^2 = 0.50$) using a default “brms” zero-inflated beta distribution for 18,501 Brant-days in New Jersey and New York from 2020–23. Estimate is the mean response value; Est. Error is the estimated error; l-80% CI and u-80% CI are the lower and upper 80% credible intervals, respectively; phi is the spread of data around the mean; zi is the intercept for the zero process; Rhat is a model convergence diagnostic that should be 1 at convergence; and Bulk_ESS and Tail_ESS show effective sample sizes (40,000 draws) and sampling efficiency for the posterior distribution. The reference category for winter is 2020, for month 11 (November), and for region northern New Jersey.

| Variable | Estimate | Est.Error | l-80% CI | u-80% CI | Rhat | Bulk_ESS | Tail_ESS |
|-----------------------------|----------|-----------|----------|----------|-------|-----------|-----------|
| individual sd(Intercept) | 0.689 | 0.042 | 0.637 | 0.743 | 1.002 | 1416.092 | 3054.534 |
| Intercept | -1.316 | 0.1 | -1.443 | -1.187 | 1.005 | 1301.106 | 2825.742 |
| Sex: female | 0 | 0.107 | -0.138 | 0.137 | 1.005 | 677.717 | 1493.268 |
| Winter 2021 | 0.112 | 0.032 | 0.071 | 0.153 | 1.001 | 5336.943 | 12477.766 |
| Winter 2022 | -0.059 | 0.04 | -0.11 | -0.009 | 1.001 | 4422.242 | 9307.448 |
| Winter 2023 | -0.039 | 0.052 | -0.106 | 0.028 | 1.001 | 3973.848 | 8366.023 |
| December | -0.042 | 0.027 | -0.076 | -0.008 | 1.001 | 8163.687 | 16257.747 |
| January | -0.057 | 0.03 | -0.095 | -0.018 | 1.001 | 7778.363 | 16554.558 |
| February | 0.186 | 0.028 | 0.149 | 0.222 | 1.002 | 4845.776 | 10178.655 |
| March | 0.284 | 0.027 | 0.249 | 0.319 | 1.002 | 4426.727 | 9149.374 |
| April | 0.245 | 0.027 | 0.21 | 0.28 | 1.002 | 4481.005 | 9518.365 |
| May | 0.175 | 0.031 | 0.136 | 0.215 | 1.002 | 5116.603 | 11609.238 |
| Region: southern NJ | 0.563 | 0.095 | 0.442 | 0.685 | 1.001 | 2278.749 | 5324.208 |
| Region: western Long Island | 1.042 | 0.091 | 0.925 | 1.16 | 1.002 | 1449.772 | 4086.313 |
| Region: eastern Long Island | 0.855 | 0.102 | 0.724 | 0.986 | 1.002 | 2249.939 | 4663.092 |
| phi | 8.42 | 0.087 | 8.309 | 8.532 | 1 | 22204.32 | 26598.042 |
| zi | 0.081 | 0.002 | 0.078 | 0.084 | 1 | 23587.956 | 26387.976 |