ECOLOGY OF MID-CONTINENT MIGRATORY SHOREBIRDS, PERFORMANCE OF TRACKING DEVICES, AND MODELLING ANIMAL SOCIAL STRUCTURE AND DEMOGRAPHY

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By

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The undersigned, appointed by the dean of the Graduate School, have examined the dissertation entitled

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DISSERTATION ABSTRACT

Migratory birds are threatened by landscape and climate change, and shorebirds are particularly imperiled. Shorebirds undertake some of the most impressive migrations in the world, but in every season, there are threats such as habitat loss, limited prey abundance, overhunting, and climate change contributing to their declines. New technologies and analytical techniques offer opportunities to improve our ability to disentangle drivers of shorebird declines to inform conservation investments. However, it is important to test and evaluate new technologies and methods to move toward the most cost-effective and least invasive ways to gather necessary information. The chapters of my dissertation were: (1) studying environmental drivers of migration decision-making and reproductive success in black-bellied plovers (*Pluvialis squatarola*); (2) examining spatial and temporal habitat characteristics that influence energy expenditure and behavior in American avocets (*Recurvirostra americana*); (3) characterizing and comparing migration strategies among three species with contrasting life histories: American avocets, black-bellied plovers, and Hudsonian godwits (*Limosa haemastica*); (4) testing performance of tracking devices for bird research; and (5) developing and evaluating a modelling approach to combine social structure and survival information. In chapter 1, we found that winter and spring weather conditions influenced migration duration and number of stopovers in black-bellied plovers, and these metrics explained substantial variation in reproductive success, while breeding season weather did not. In chapter 2, we found that in two study areas with contrasting habitat compositions, landcover type, time of day, and tide all explained substantial variation in energy expenditure (i.e., activity) in American avocets, but that relationships were different between the two sites. In chapter 3, we showed that shorebirds with different migration distances varied in both their migration strategies and in their plasticity in

strategy. In chapter 4, we found that tracking devices performed well enough to meet most research objectives in standardized tests, however we caution that device performance is likely reduced when deployed on wild birds. We split chapter 5 in two parts: (a) we present current literature and techniques for studying animal social structure and demography, and (b) we developed a simulation study that evaluated performance of a model linking social network analysis and Cormack-Jolly-Seber survival models and found that models performed with minimal bias and good precision, but precision was influenced by data resolution.

Chapters 4 and 5 are submitted versions of manuscripts that have been published or accepted for publication. Chapter 4 is published in *Journal of Field Ornithology* and chapter 5 is accepted for publication in *Animal Behaviour*. The citations for the published articles are as follows:

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CHAPTER 1

Fitness consequences of weather and migration characteristics in black-bellied plovers

Abstract

Weather conditions experienced by birds can influence their migration decision-making and strategy both within and across seasons. Additionally, decision-making during migration may influence subsequent fitness (reproductive success and/or survival). Examining the effects of fine-scale weather variables on individuals throughout the year could help identify stages of the annual cycle when species may be most affected by climate change. In this study, we captured 24 black-bellied plovers (*Pluvialis squatarola*) on wintering areas along the western Gulf of Mexico coast and tracked their locations once every 2 hours through their breeding season in the Alaskan and Canadian arctic. We quantified migration strategies and weather conditions experienced by each individual throughout the winter, spring, and summer seasons. We analyzed these data using a Bayesian hierarchical model which connected regressions linking weather with migration metrics, and migration metrics and breeding season weather with reproductive success. We found negative relationships between two migration metrics, migration duration and number of stopovers, and reproductive success, but not substantial relationships between breeding season weather variables and reproductive success. We found negative relationships between winter temperature, migration temperature, and migration NDVI and both migration duration and number of stopovers, in addition to positive relationships between the number of stopovers and storms during migration, migration duration, and winter precipitation. These results suggest that reproductive success is influenced by

weather throughout the annual cycle and migration strategy is a key mechanism through which these effects operate. This knowledge is useful for future studies examining individual responses to climate change and suggests that factors influencing migration strategy may also be important for fitness.

Introduction

Migratory shorebirds are threatened globally (Wauchope et al. 2017). In North America, shorebirds that migrate though the mid-continent are at greater risk of decline compared to coastal populations (Thomas et al. 2006). Shorebird decline has been linked to climate change (Piersma & Lindström 2004; Galbraith et al. 2014). Despite this, evidence of changes in weather causing phenological mismatch or reduced reproductive success in shorebirds has been difficult to disentangle. For example, in a 7-year study of 7 species of arctic-nesting shorebirds, Weiser et al. (2017) found no evidence of effects of environmental variables or predator abundance at nest sites on reproductive traits. Smith et al. (2010) found that snowmelt and predators affected breeding chronology, while weather variables did not. In other cases, conditions brought about by climate change have resulted in improved conditions for shorebirds, at least in the short term (Piersma & Lindström 2004, van de Pol et al. 2010). However, climate change is expected to negatively affect shorebirds and their habitats in all stages of the annual cycle (Piersma & Lindström 2004, Galbraith, et al. 2014), so environmental pressures from all seasons could be influencing shorebirds presently and should be studied.

Although it takes up only a small part of the year, migration is an energetically costly and risky stage of the annual cycle (Wilcove & Wikelski 2008, Piersma et al.

2016). Many studies of the effects of climate on shorebird reproductive success have focused on interannual variation at the population level and during the breeding season, but there may be carry-over effects accumulating throughout the year which influence the fitness (i.e., survival and reproductive success) of individuals, and, therefore, the population. Carry-over effects are events and processes occurring in one season that bring about sub-lethal effects on individual fitness in a subsequent season (Harrison et al. 2011). Theoretical models and empirical studies have demonstrated that carry-over effects can cascade to influence population dynamics (Norris 2005, Inger et al. 2010). In the context of our study, sub-lethal effects refer to any consequence of sub-optimal conditions or decision-making that can reduce fitness. Examining the effects of fine-scale variation in weather variables on individuals throughout the year provides a different perspective than an assessment of weather on demography. Unique yet complementary information can be provided by individual- and population- level studies. While population-level studies often involve long-term data sets with which we can observe changes in demographic rates across years and allow researchers quantify environmental factors that are affecting population dynamics (e.g., Cunningham et al. 2021), individual-level studies can result in detailed information about movement, behavior, and decision-making, often over a relatively short period of time. Using individual-based data, we can identify drivers of individual decisions related to habitat use and migration strategy and relate these decisions to weather and landscape variables (e.g., Senner et al. 2018, Efrat et al. 2019). Individual tracking data can provide information about consequences of environmental characteristics on fitness through behavior and movement.

Weather conditions can influence many components of migration strategy, migration duration, route, and stopover decisions (Shamoun-Baranes et al. 2010). European robins (*Erithacus rubecula*) were more likely to depart stopover sites when wind speed and precipitation were both low (Schaub et al. 2004). Season-specific influences of wind and barometric pressure have been linked with golden eagles in Alaska taking a northern or southern route across mountains (Eisaguirre et al. 2018). However, for species with long and risky migrations, characteristics related to migration phenology or strategy may not strongly influence fitness; Senner et al. (2014) suggested that the lack of carry-over effects on timing of migration and reproductive success observed in Hudsonian godwits may be due to their extreme life-history strategies causing mortality before carry-over effects can take effect. Studying carry-over effects of weather on migration strategy and fitness could help to identify stages of the annual cycle at which a changing climate is most likely to influence shorebird fitness.

The black-bellied plover (grey plover; *Pluvialis squatarola*) is a relatively large, arctic-nesting migratory shorebird that is distributed worldwide, and its association with mixed assemblages of shorebird species makes it a good model species for studies of shorebird ecology (Poole et al. 2020). After rapid decline between the 1970s and 1990s, populations in the western hemisphere appear to be more stable, but still declining or unknown in some locations (Andres et al. 2012). In North America, most research on the species has focused on breeding ecology (Poole et al. 2020), so studying the winter and spring migration ecology, in addition to the breeding ecology, adds to our understanding of black-bellied plover ecology and more broadly, carry-over effects on migratory shorebirds. It is also a very widespread species so individuals are likely to take different migration routes and choose different stopover and breeding locations (Figure 1.1). This variation, along with their associations with other species, makes them an appropriate species to study migration traits because findings from this species can also be considered for other shorebird species that are too small to carry tracking devices that collect detailed GPS data.

Our objectives were to test for effects of winter and spring weather conditions on reproductive success through migration decision-making in black-bellied plovers, and compare effects of weather conditions during winter, migration and breeding seasons on reproductive success to identify critical stages of the annual cycle and inform targeted monitoring and conservation.

Methods

Bird Capture and Deployment of Tracking Devices

We captured black-bellied plovers in coastal Texas and Louisiana, USA, using rocket nets and cannon nets. All captures took place during winter and spring 2019-2021. Birds captured in Louisiana were wintering individuals and captured between early January and early March each year. Birds captured in Texas were captured in late March to early May and were presumed wintering birds, however, the few birds captured very late in the season could possibly have begun migration previously. All birds captured were fitted with a USGS Bird Banding Laboratory metal band, under permit to BMB (permit #21314). We aged birds according to molt and plumage characteristics (Meissner & Cofta 2014). We collected morphometric data from each bird and a blood sample for molecular sexing (van der Velde et al. 2017).

We deployed 2 models of tracking devices on black-bellied plovers and ensured that the weight of the device was ~3% of bird body weight, but for this study we used only data from 6.6-g Pinpoint Argos Solar S (heareafter 6-g; *n*=33) devices manufactured by Lotek (Newmarket, ON, Canada) due to their increased duty cycle capacity. We attached all devices using leg-loop harnesses (Sanzenbacher et al. 2000) comprised of silicone ("Stretch Magic") or elastic shock cord. The devices collected GPS data and uploaded it via the Argos satellite system. Devices were programmed to collect a GPS fix every 2 hours (12 locations per day) and the GPS data they collect is precise to ±10 m (Clements et al. 2022). Devices were expected to last from deployment through the breeding season, and only devices which collected data consistently through 15 July of the year they were deployed were included in analyses to ensure that data were collected through expected end of incubation in mid-July. 24 of 33 6-g devices collected data at least through 15 July, and two of these appeared to have recorded a mortality event or detached from bird. The remaining nine devices which did not collect data through 15 July appeared to be abrupt device failures, so we were not able to determine fate of birds. Therefore, we used data from 24 of 33 6-g devices for analyses in this study.

Tracking Data Storage and Processing

Data from devices were stored in Movebank (Kranstauber et al. 2011). We used Movebank to filter location quality based on Lotek Cyclic Redundancy Check status for Lotek tags. Then, we used the SDLFilter package (Shimada et al. 2012) in Program R to remove duplicate points and outliers based on a speed threshold of 150 km/hour. The SDLFilter package calculates speed based on GPS locations and timestamps and can also detect duplicate points in space and time. Finally, we visually identified and removed several remaining outlier points, most of which showed erroneous future times or were located at 0 degrees latitude and longitude.

Identifying reproductive success

We used full-term incubation (24 days) as a proxy for reproductive success because it was most identifiable using GPS data. A full-term incubation for black-bellied plovers is 24-26 days (Poole et al. 2020). Males and females share incubation duties and switch every few hours. Incubation time is expected to vary slightly by sex (male incubates more toward the beginning, female more toward the end). All black-bellied plovers used in this analysis were identified as male via molecular sexing. Thus, we expected birds incubating nests to have successive points in a relatively small area for the full term of incubation. Our criteria for ascribing full-term incubation were based on average daily displacement and patterns of return to a potential nest site. If a bird showed daily average displacement of <500 m for the duration of the incubation period (i.e., average displacement between points each day remained below 500m), a stationary site was visually identifiable, and the individual consistently returned to the area within a 30-m buffer around a potential nest site for 24 days, that bird was ascribed as having a successful nest that year (Figure A1.1).

Data post-incubation period (i.e., from August) was also used for devices presumed dropped or on dead individuals (devices remaining stationary for an extended period of time) to ensure we would not incorrectly ascribe breeding status to these individuals. Two individuals were assigned NA (i.e., unknown) for breeding because they were stationary during and after the incubation period. This indicated a dropped device or mortality sometime after incubation had started, so we were not able to discern breeding status. We resighted black-bellied plovers with their leg bands (presumed to have been banded as part of our study) during the subsequent fall and winter after spring tagging, but did not see devices on some individuals in both Texas and Louisiana (J. Loghry & S. Clements, personal observation). Thus, there is evidence that devices were dropped during the study period. Therefore, we chose to assign these two individuals as NA rather than unsuccessful nesters.

We hypothesized that more efficient migration, with either fewer stopovers or shorter stopover durations, would increase the chances of reproductive success because black-bellied plovers often migrate with long flights between stopovers, suggesting that these birds have evolved such that a fast migration is beneficial (Hedenström & Alerstam 1997). We present hypotheses for each set of covariates below in the weather data section.

Identifying stopover sites

We first identified points within the breeding range using a 50% kernel density estimate on all points above 65 degrees latitude because all migrations led to breeding sites north of this latitude (Figure 1.1). We defined the last point of migration as the last point collected before the bird crossed into the breeding area. We then identified stopover sites as points <30 km from a previous point. A threshold of 30 km was chosen based on the distribution of step lengths between points and visual inspection of point clusters. Exo et al. (2019) used a similar displacement-based approach to identify black-bellied plover stopover sites in the East Atlantic Flyway using a 20-km distance threshold, however we chose 30 km because it resulted in fewer subdivisions of stopover sites by a single long movement. Note that the distance threshold can be expected to be different depending on movement patterns of species being studied and duty cycle of data collection. After identifying whether or not each point was less than 30 km in distance from the subsequent point, we used run length encoding to identify clusters. We applied the following criteria to identify stopover sites: (1) ≥3 consecutive points within 30 km of one another or at least 6 hours within the area, and (2) not within wintering or breeding areas. We chose to classify short stopping periods as stopovers because birds may stop over for a variety of purposes that may influence their decision-making and fitness (Linscott & Senner 2021), and our high data resolution allowed us to identify stopover events that would not be detectable with less data. We then visually identified stopover sites and in a few cases where a bird left a stopover site briefly (one point) and later returned we ascribed that area as one stopover site. Each stopover site was assigned a unique label. We ascribed the wintering area as the first such cluster of points in the data set, such that that the first point of migration was the first movement over 30 km from the wintering area that led to the eventual crossing into the breeding area (Soriano-Redondo et al. 2020). We used the first cluster of points for wintering areas because unlike breeding areas in which birds are moving and searching for foraging and nesting habitat, our black-bellied plovers remained at the same site throughout the winter (i.e., the wintering area would be classified as a stopover site under our framework for stopover identification). Therefore, a Kernel Density Estimate was not needed.

We calculated two migration metrics to characterize individual decision-making. First, we counted all unique stopover sites used by each bird (NSTOP) and then calculated migration duration as the amount of time between the first and last GPS locations classified as migration points (MGDR). We chose these metrics because number of stopovers can be thought of as related to energy acquisition, while migration duration may be more related to the balance between energy acquisition and expenditure. Number of stopovers and duration of migration are expected to influence fitness because of the importance of balancing energy acquisition and expenditure during migration (e.g., Gómez et al. 2017; Prop et al. 2003). These terms were not strongly correlated ($r = 0.14$).

Weather data

We acquired temperature and precipitation data for the winter, migration, and breeding seasons; barometric pressure for the migration and breeding seasons; and Normalized Difference Vegetation Index (NDVI; a proxy for food availability) for the migration season to test hypotheses about drivers of migration metrics. Using data from all seasons will help to understand the relative effects of conditions throughout the winter when birds are preparing for migration and conditions during the migration period. We extracted weather separately for each season because weather metrics may influence birds differently in each season. Additionally, local weather conditions can be more important than broad-scale climate patterns for migration decisions (Tøttrup et al. 2010), so we aimed to summarize each variable in ways that took advantage of the spatial variation we were able to capture with spatial data, while providing an index of overall conditions throughout each season.

NDVI –NDVI indicates net primary productivity, which influences availability of insects (Sanz et al. 2003, Buchan et al. 2021). Black-bellied plovers primarily feed on invertebrates (Poole et al. 2020). We downloaded 16-day, 1-km resolution NDVI data and used data collected in May and June of 2019-2021 (ordinal days 129, 145, 161, and 177). We extracted the average NDVI within a 30 km buffer around each point within a stopover for the point in time closest to the time at which the GPS location was collected. We then summarized NDVI for the entire migration by calculating the mean NDVI for all locations at times each bird was there. We anticipated that higher NDVI at stopover sites around the time a bird was present would be associated with fewer or shorter stopovers because better conditions for invertebrates may increase foraging efficiency, as well as a shorter migration duration because if less energy is expended foraging during stopovers, birds may have more energy for migration.

Temperature – We acquired surface temperature data from the National Centers for Environmental Prediction using the RNCEP package (Kemp et al. 2012). We downloaded temperature data from the NCEP Reanalysis 1 interpolated to each bird's set of locations in space and time using RNCEP. We then calculated mean temperature across all migration points and breeding points identified (see above). Because we had variable amounts of winter tracking data among birds and our captures were concentrated at two specific wintering sites in Louisiana and Texas, we extracted winter temperature data from the months of January through April from the grid cells in which the sites were located for 2019-2021. We anticipated that higher breeding season temperatures would be associated with increased probability of reproductive success because overall warmer breeding sites may have earlier snowmelt which has been associated with increased clutch sizes (Weiser et al. 2018). Although our analysis did not include migration timing and snowmelt, there is evidence from other studies that shorebirds are resilient to variation in the timing of snowmelt and prey emergence. For example, many shorebirds show plasticity in nest initiation in response to weather conditions in breeding areas (McGuire et al. 2020) and are not strongly limited by phenological mismatch between hatching and peak invertebrate abundance (Reneerkens et al. 2016; Weiser et al. 2018). We expected higher winter and migration temperatures would be associated with shorter migrations and fewer stopovers because, similarly to NDVI, warmer temperatures could create favorable conditions for food availability.

Wind - Similarly, we downloaded wind data using RNCEP for all migration points which were categorized as flight (i.e., not a stopover, breeding, or wintering point). We used RNCEP to calculate flow assistance (i.e., tailwind; Kemp et al. 2012) and used the mean flow assistance at flight points to represent wind experienced by birds during migration. We expected that higher tailwind would be associated with shorter migration duration and fewer stopovers.

Severe Weather - We also downloaded barometric pressure from RNCEP as an indicator of severe weather. We used rasters of barometric pressure data from January-July of 2019-2021 based on a polygon encompassing the entire range of the black-bellied plovers in our study during this time period. We then summarized barometric pressure for each day in each location the bird was in during the migration and breeding seasons. We calculated daily barometric pressure and change in barometric pressure since the previous day. Then, we classified the lowest 10% of barometric pressure as low pressure and the lowest 10% of change in barometric pressure as a large drop in pressure. If the day a bird was located at a point was classified as both low pressure and a large drop, we assume the bird experienced severe weather. We counted the number of unique days a bird experienced severe weather during migration and breeding. Extreme weather events may decrease prey density (Corte et al. 2017) and during the migration season extreme weather is known to result in in-flight mortality for birds (Newton 2006), so it is reasonable to suspect that some sub-lethal effects such as forced stopovers or re-routing of movements may occur. During the breeding season, extreme weather can also affect productivity in birds (Martin et al. 2017). We expected that more extreme weather events during the breeding season would reduce the probability of reproductive success, and that extreme weather during the migration season would be associated with more stopovers and a longer migration duration.

Precipitation - We downloaded precipitation data from the NOAA Climate Prediction Center (CPC) for the years of 2019-2021. For precipitation in breeding areas, we calculated mean daily precipitation across grid cells in which breeding season GPS locations for each bird were located between the first day of the year and the end of July during the year the bird nested. For winter precipitation, we calculated mean daily precipitation across grid cells in which the bird's wintering site was located January through April of the year the bird was captured. For migration, we calculated cumulative mean daily precipitation from early winter until mid-May across all stopover sites, as the effect of spring precipitation on the presence of shorebirds can be influenced by previous precipitation (J. Jorgensen, R. Penner & M. Hanan, personal observation). We also calculated precipitation rate at each point collected for a bird in the 5 days leading up to the day it was at each location, because available water at stopover sites in the Great

Plains can be dynamic and vary quickly in time and birds may opportunistically select stopover habitat.

Building the hierarchical model

We hierarchically modeled the effects of winter and migration weather on migration metrics and the effects of migration metrics and breeding season weather on reproductive success (i.e., full-term incubation). The hierarchical model allowed for uncertainty to propagate though all levels of the model. We used a single model comprised of variables based on our ecological questions rather than a model selection approach because we wanted to compare the effects of individual variables to one another within the model rather than comparing the fit of competing combinations of variables. We ran the model in Jags (Plummer 2003) through Program R version 4.1.2 (R Core Team 2021) using the JagsUI package (Kellner 2015). We determined convergence based on R-hat <1.05 (Brooks & Gelman 1998) and visual inspection of chains. We also calculated pairwise correlations between all weather covariates and did not include any two with r>0.50 within the same level of the model (Table A1.1). Model code is provided in Appendix 1.

Our hierarchical model was comprised of two linear regressions and one logistic regression,

$$NSTOP_i = \beta_0^{[NSTOP]} + \beta_1 STm_i + \beta_2 NDVIm_i + \beta_3 TPw_i + \beta_4 TPm_i + \beta_5 PRCm_i + \beta_6 PRRm_i$$

$$MGDR_i = \beta_0^{[MGDR]} + \beta_7 TWDm_i + \beta_8 NDVIm_i + \beta_9 TPw_i + \beta_{10} TPm_i + \beta_{11} PRCw_i$$

$$logit(BREED_i) = \beta_0^{[BREED]} + \beta_{12}NSTOP_i + \beta_{13}MGDR_i + \beta_{14}TPb_i + \beta_{15}STb_i + \beta_{16}PRCb_i$$

where α is the intercept in each regression, and for each individual bird *i*, *NSTOP* is the number of stopover sites, *MGDR* is the migration duration in days, *BREED* is a binary variable with 1 for successful full-term incubation, 0 for failed incubation or deferral of reproductive attempt, and NA if breeding status was not able to be determined. *STm* and *STb* were the number of days during migration and breeding, respectively, that the bird experienced extreme weather (i.e., strong storms). *NDVIm* was the mean NDVI across all migration points. *TPw*, *TPm*, and *TPb* were the mean temperatures across the winter, migration, and breeding seasons, respectively. *PRRm* was the mean precipitation rate within the 5 days leading up to each migration point. *PRCw* was the cumulative precipitation for each year in wintering locations, and *PRCm* and *PRCb* were cumulative precipitation for each year in migration and breeding locations, respectively. *TWDm* was the mean flow assistance (tailwind) for flight points during migration. We report the posterior mean for each β and 95% credible interval, as well as the proportion of posterior samples that were >0 or <0 on the same side as the mean as evidence that the β was positive or negative, for each regression. We plotted predicted values of the relationship between a response and an effect when the proportion of posterior samples above or below 0 was >0.80.

Results

Eleven black-bellied plovers were classified as successful in full-term incubation, 11 were unsuccessful, and 2 were unknown. Therefore, the model was run on information for 24 birds. The number of stopovers for an individual ranged from 2 to 10 (mean = 6.17, standard deviation [SD] = 1.73). Migration duration ranged from 17.08 to 32.91 days (mean = 23.39, SD = 4.46). Summaries of each weather variable are presented in Table A1.2, and box plots of the effect sizes for each covariate in the model are presented in Figure 1.2.

Migration duration was a stronger predictor of reproductive success (β=-0.77, 95% CRI -1.56, -0.25; P=1.00) than the number of stopovers (β=-0.85, 95% CRI -3.31, 0.83; P=0.85), but both effects were negative and explained substantial variation in reproductive success (Figure 1.3). Of the breeding season weather metrics we tested, temperature (β=0.02, 95% CRI -0.19, 0.26; P=0.60), cumulative precipitation (β=0.00, 95% CRI -0.06, 0.06; P=0.51), and number of storm days (β=-0.04, 95% CRI -2.09, 2.13; P=0.53) did not explain substantial variation in breeding success.

Most weather metrics we tested explained substantial variation in migration duration except tailwind (β=0.06, 95% CRI -0.34, 0.48; P=0.60). Strong relationships between migration environmental variables and migration duration included NDVI (β=-0.63, 95% CRI -1.04, -0.20; P=1.00), and migration temperature (β=-1.19, 95% CRI -1.62, -0.76; P=1.00). NDVI and migration temperature had negative relationships with migration duration (Figure 1.3). Strong winter weather effects on migration duration included temperature (β=-0.78, 95% CRI -1.22, -0.34; P=1.00) and cumulative precipitation (β=0.22, 95% CRI -0.18, 0.67; P=0.85). Winter temperature had a negative relationship with migration duration while winter precipitation had a positive relationship with migration duration (Figure 1.4).

Most weather metrics we tested also explained substantial variation in the number of stopovers. Migration weather variables for which $P>0.8$ included number of storm days ($\beta=0.33$, 95% CRI -0.14, 0.81; $P=0.91$), NDVI ($\beta=-0.25$, 95% CRI -0.70, 0.20; $P=0.87$), temperature ($\beta=-0.55$, 95% CRI -0.10, -0.09; $P=0.99$), and cumulative precipitation ($\beta=-0.30$, 95% CRI -0.77, 0.16; $P=0.91$). Winter temperature ($\beta=-0.38$, 95% CRI -0.89, 0.14; $P=0.93$) also explained variation in the number of stopovers. The relationship between number of stopovers and migration precipitation rate was weak ($\beta=0.12$, 95% CRI -0.32, 0.57; $P=0.81$). The number of storms had a positive relationship with the number of stopovers, while NDVI, migration temperature, migration cumulative precipitation, and winter temperature had negative relationships with the number of stopovers (Figure 1.5).

Discussion

We found that migration duration and the number of stopovers explained variation in reproductive success, and that weather variables during both the migration and winter seasons influenced these two migration metrics. These results suggest that decision-making during migration is important for reproductive success and is also a mechanism through which environmental conditions throughout the winter and spring can influence breeding season performance. With the climate changing rapidly, weather conditions will likely become influential in the future and these results add to current understanding of the influence of behavior and abiotic factors on reproductive success.

Contrary to our hypothesis, the breeding season weather terms we examined did not explain substantial variation in reproductive success. Breeding season storms, temperature, and precipitation were not strong predictors of reproductive success. This is consistent with findings by Finch et al. (2014), suggesting that carry-over effects of temperature and precipitation in winter and summer influenced breeding phenology and brood size more than breeding season weather in 3 migratory passerines. However, Ockendon et al. (2013) observed that breeding season temperature and precipitation were more important predictors of breeding phenology than wintering temperature and precipitation. In the case of black-bellied plovers, breeding season weather may have limited impact on reproductive success because weather conditions in the arctic are not always directly related to food availability (Saalfeld et al. 2019).

Consistent with our hypotheses, we found that migration duration and to a lesser extent number of stopovers were moderate predictors of reproductive success. This suggests that the effects of individual decisions pertaining to migration strategy that accumulate to determine the migration duration and number of stopovers are more influential toward reproductive success than breeding season weather conditions, at least among our tagged sample. Based on our model, a shorter migration with fewer stopovers resulted in increased probability of reproductive success. This makes sense from the perspective of efficiency; ideally, birds would minimize time and energy spent on migration, and they have evolved strategies to balance energy expenditure and acquisition (Alerstam & Lindström,1990). Faster migration has been linked to stopover quality and subsequent reproductive success (Gómez et al. 2017), and our results are consistent with this. A longer migration with more stopovers may mean that birds are less able to accumulate the energy they need at each step of the migration (Prop et al. 2003). In addition to the balance of energy expenditure and acquisition, fewer stopovers and a shorter migration duration may indicate that fewer problems (such as storms, disturbances) were encountered during migration, or that the stopover sites chosen were of high quality (Roques et al. 2020). However, the influence of migration metrics on reproductive success can be expected to be different in some systems that are different than migratory shorebirds; for example, birds with shorter migrations or migrations not constrained by wetland habitat requirements (e.g., Buchan et al. 2021).

The strong influence of weather during both migration and winter on our migration metrics suggests the presence of sub-lethal fitness consequences of weather within and across seasons. These consequences appear in migration decision-making which results at least partially from weather conditions birds experienced, and propagated to explain variation in reproductive success. Migration duration results from the accumulation of decisions related to migration phenology, and phenology can often be explained by winter and spring weather conditions (Cotton, 2003, Haest et al. 2020, van Buskirk et al. 2009), so it is not surprising that NDVI, winter temperature, winter precipitation, and migration temperature all explained substantial variation in it. Although migration duration and the number of stopovers were not strongly correlated with one another, they were affected similarly by winter temperature, migration temperature, and NDVI. Higher temperatures may increase food availability and allow birds to refuel more efficiently before and during migration (Evans 1976). NDVI can influence migration phenology (Tøttrup et al. 2008), so also likely influences the decisions resulting in phenology. If we assume that NDVI is a proxy for invertebrate availability (Pettorelli et al. 2005, Buchan et al. 2021) for black-bellied plovers, higher NDVI during migration may reduce the amount of time needed to acquire necessary energy, reducing the duration of migration. Together, these features could mean the quality of stopovers were generally higher and less stops were needed. Additionally, as we predicted, an increase in extreme weather increased the number of stopovers, which we believe is because birds experienced increased energy requirements or less ability to move in poor weather. Migration during extreme weather is physically and physiologically challenging (Gardener et al. 2017, Van Den Broeke & Gunkel, 2021) and therefore likely to increase the energy requirement of migration. Cumulative precipitation in the months preceding the migration period influenced the number of stopovers more than precipitation in the days leading up to stopover site use. Surface water is very dynamic and causes shorebird distribution and use to also be dynamic (Skagen & Knopf 1994, Steen et al. 2018). Although the connection between precipitation rate and surface water is complicated, it may be that short-term variation in precipitation causes less variation in water on the landscape than long-term precipitation conditions do. Increased precipitation at stopovers can be expected to increase fitness through survival; Halupka et al. (2017) found that precipitation increased survival of reed warblers (*Acrocephalus scirpaceus*) at stopover sites, likely due to increases in food availability, and similarly, variation in shorebird abundance at stopovers have been linked to precipitation and drought (Anderson et al. 2021, Steen et al. 2018), suggesting that food abundance brought about by precipitation could also influence shorebird survival. In our study, more cumulative precipitation resulted in fewer stopovers, so this may mean that birds stopping in areas with more moisture already in the soil do not need as many stops to obtain the necessary energy due to moist-soil conditions leading to more productive temporary wetlands resulting from spring precipitation.

Broad-scale migration metrics, especially migration duration, are the product of decisions made related to migration timing. Detailed studies of phenology would be beneficial better understanding carry-over effects of weather on productivity though individual decision-making. It is also important to note that all of our tagged birds were male, and there are known differences between male and female behavior in black-bellied plovers. Males arrive earlier to breeding areas and depart later than females (Poole et al. 2020). Males are expected to be less physiologically constrained at the beginning of the breeding season because they do not lay eggs, but more physiologically constrained at the end of the breeding season because the female leaves immediately after hatching and leaves all care of the young to the male (Poole et al. 2020). Our estimate of 50% of individuals reaching full-term incubation using location data is similar to the estimate by Hussel and Page (1976) who found that 54.7% of black-bellied plover nests reached a full-term incubation using on-the-ground observations. Assuming that reproductive success rates have not changed significantly over time, this suggests that our approach worked well for identifying successful incubation. The tracking devices we used limited our inference on reproductive success to a full-term incubation. However, it is possible using a tracking device integrating both GPS and acceleration to identify successful breeding attempts, failed breeding attempts, and breeding deferrals (Cunningham 2019, Schreven et al. 2021). The ability to identify deferrals would allow the decision to breed, which is likely the result of physiological constraints, to be linked with conditions in previous seasons. Additionally, stopover habitat quality is undoubtably important for black-bellied plover migration, so subsequent investigations on the influence of landscape characteristics on stopover habitat selection would provide a more complete understanding of the influence of both weather and habitat quality on migration metrics.

The influence of carry-over and cross-seasonal effects of weather and landscape conditions on fitness and phenology in birds has been well-established in the literature (e.g., Duriez et al. 2012, Rockwell et al. 2012, Sedinger & Alisauskas, 2014, Sutton et al. 2021). However, without detailed individual-level data, it is difficult to disentangle the mechanisms through which weather is influencing phenology or fitness. Our study aimed to determine whether duration of migration and number of stopovers influence reproductive success in black-bellied plovers and quantify the influence weather variables within and among seasons on these two mechanisms. We found evidence of effects of winter and spring weather on spring migration duration and number of stopovers, and effects of these metrics on reproductive success in a migratory shorebird. This reveals complex linkages between weather, migration strategy, and reproductive success in black-bellied plovers. Extreme weather and droughts are likely to become worse in the future, as is sea level rise, resulting in loss and degradation of habitat (Piersma & Lindström, 2004). These changes are likely to further constrain birds and make individual decision-making during migration more important. Increased monitoring of winter and stopover conditions, which are currently under-studied, could be critical for shorebird conservation planning as the climate and landscape change.

Figures

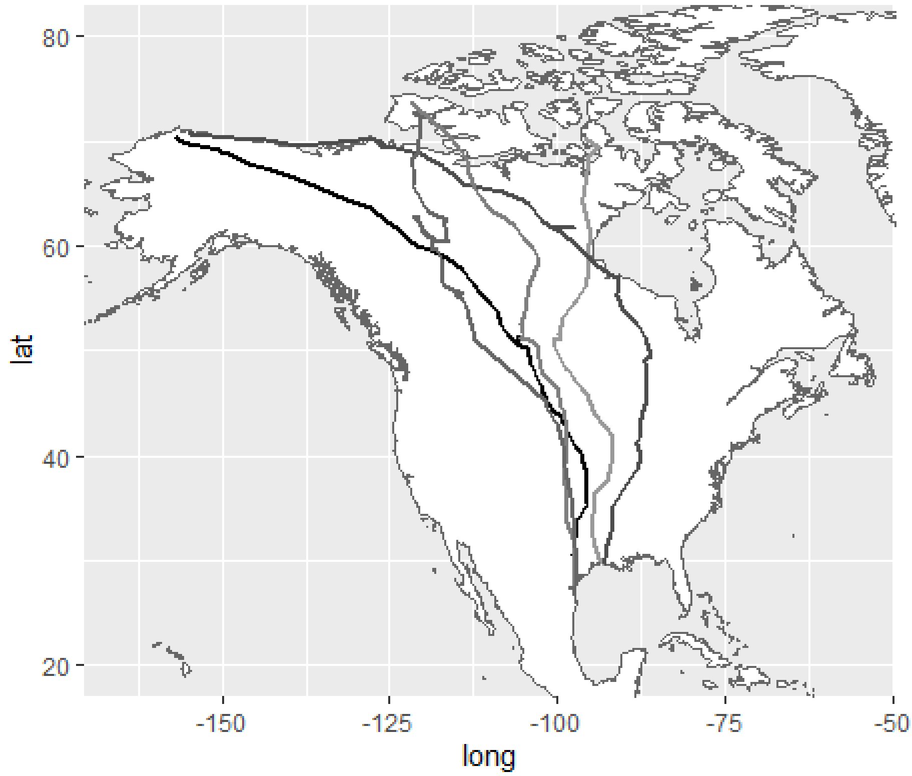

Figure 1.1. Five examples of black-bellied plover spring migration tracks from our study; each track is represented in gray. Individuals migrated though the mid-continent of North America to breeding areas often in the North Slope of Alaska or Banks Island in the Canadian Arctic, but some breeding areas were farther east in Nunavut.

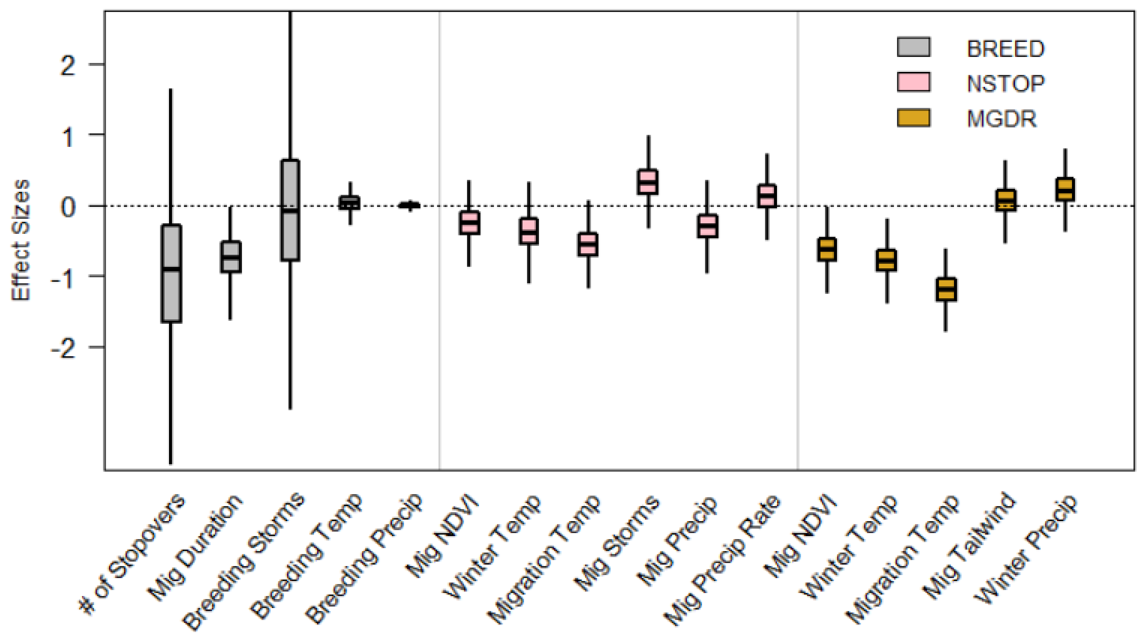

Figure 1.2. Effect sizes for each covariate from a hierarchical model on the probability of reproductive success (BREED), number of stopovers (NSTOP) and migration duration (MGDR; each response indicated by a color and separated by vertical gray lines) for black-bellied plovers. The horizontal line indicates 0 (no effect).

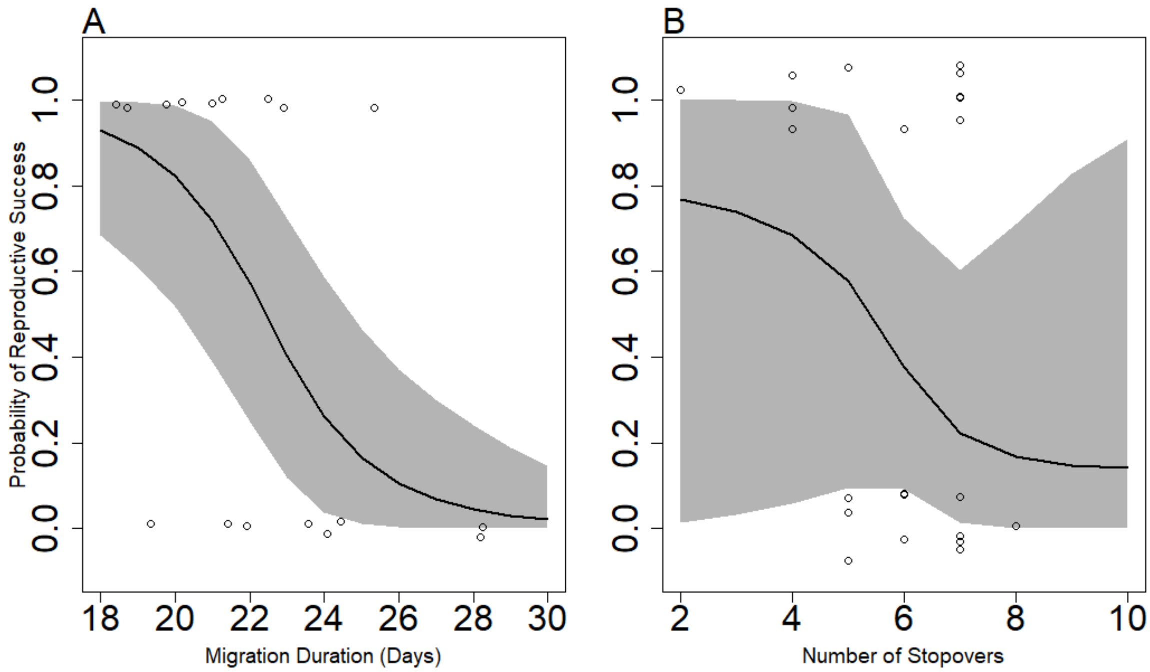

Figure 1.3. Predicted effect of (A) migration duration and (B) number of stopovers on black-bellied plover breeding success. The line represents the mean and the gray ribbon represents the 95% credible interval, and the points represent raw data.

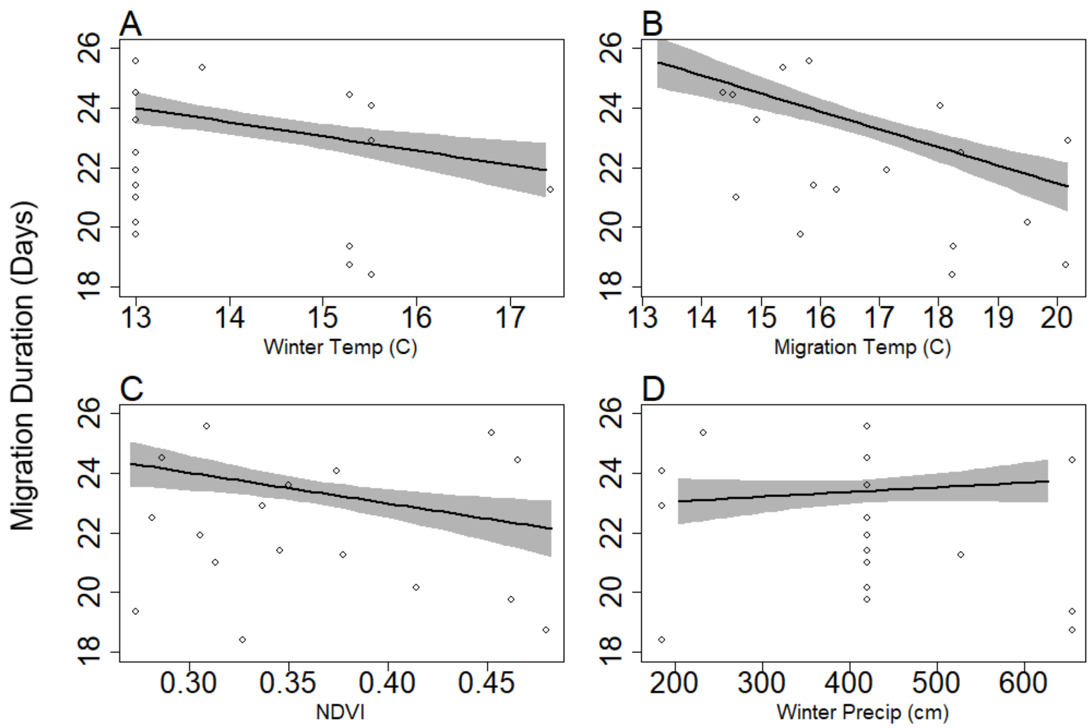

Figure 1.4. Predicted effect of (A) winter temperature, (B) migration temperature, (C) NDVI, and (D) winter cumulative precipitation on spring migration duration (days) in black-bellied plovers. The lines represent the mean, the gray ribbons represent the 95% credible interval, and the points represent raw data.

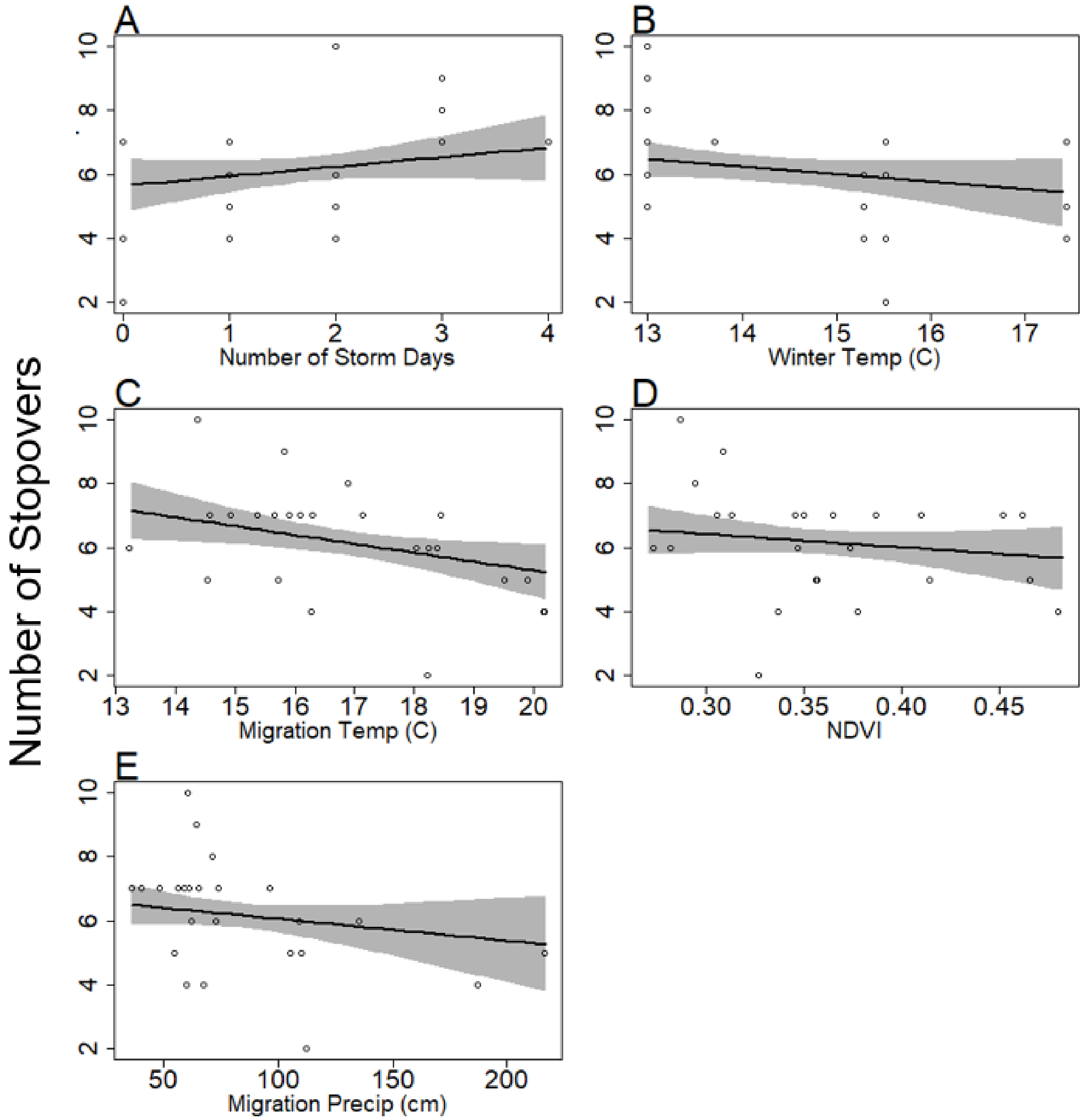

Figure 1.5. Predicted effect of (A) number of days with a storm, (B) winter temperature, (C) migration temperature, (D) NDVI, and (E) migration cumulative precipitation on number of stopovers during spring migration in black-bellied plovers. The lines represent the mean, the gray ribbons represent the 95% credible intervals, and the points represent raw data.

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CHAPTER 2

Shorebird energy expenditure at two wintering sites is driven by different habitat and environmental relationships

Abstract

Migratory shorebirds spend much of the year in their non-breeding habitats. There are increasing examples that conditions experienced by birds in the non-breeding season are important throughout the annual cycle, necessitating more detailed explorations about habitat use and drivers of habitat quality in wintering areas. We focused on two sites in wintering areas for American avocets (*Recurvirostra americana*) in coastal Texas and Louisiana that differ in habitat composition, Mustang Island in Texas and Rockefeller Wildlife Refuge in Louisiana. We used GPS-acceleration (ACC) data to explore drivers of avocet energy expenditure in space and time to evaluate patterns of habitat use based on location and behavior. We analyzed data using a Bayesian linear mixed model with overall dynamic body acceleration (ODBA; a proxy for energy expenditure) as a response variable and tide, time of day, day of year, and landcover as hypothesized drivers. To examine patterns of behavior and habitat use, we also used k-means clustering to classify points into two behavioral categories, active and stationary, based on ODBA. We found that landcover type, tide amplitude, and time of day all explained substantial variation in energy expenditure, but that patterns in these effects differed between Louisiana and Texas sites. For example, the interaction of landcover and tide was more influential in Louisiana than Texas, and Texas birds showed a substantial dichotomy in energy expenditure between day and night, while Louisiana birds did not. We also found that habitat use differed between the two sites; most notably, avocets used much more shore habitat in the Texas site. Additionally, we found that habitat use was similar between

active and inactive GPS points across both sites. Our results suggest that for American avocets and similar shorebirds, the utility of the same habitat for foraging, roosting, or other activities changes with temporal factors, and that these types of temporal factors in addition to differences in habitat use across the wintering range of species should be taken into consideration for conservation planning.

Introduction

Wintering ecology of migratory birds is generally less studied than breeding ecology, yet there is increasing evidence that decisions by birds in one season can cascade to influence productivity or survival in a subsequent season (Marra et al. 2015, Norris et al. 2004). Habitat quality during winter is a particularly interesting facet of non-breeding ecology and can explain variation in productivity and survival. Habitat quality is defined by its capacity to provide resources and conditions for individual and population persistence (Hall et al. 1997). Often, researchers and practitioners use habitat use as a measure of quality, however, heavily used habitats are not always of the best quality from fitness or population viability perspectives (Van Horne et al. 1983, Weegman et al. 2016). Factors such as disturbance, food availability, and environmental conditions all influence habitat quality, but without detailed demographic measurements or individual behavioral data the attributes of an area that influence its quality as habitat can be difficult to disentangle (Johnson 2007). Tracking individual birds can provide detailed information about how birds are using the habitats they are in, which can contribute to a better understanding of habitat quality. In this study, we used GPS-acceleration (ACC) data to understand the behavioral implications of winter habitat, time of day, and tide for the American avocet

(*Recurvirostra americana*; hereafter avocet), a wetland dependent migratory shorebird, in two different wintering sites on the coast of the Gulf of Mexico.

American avocets winter throughout both the Atlantic and Pacific coasts of Mexico and the southern United States, and breed in wetlands over a large part of midcontinent North America, from Texas to southern Alberta and Saskatchewan. They feed on invertebrates as well as occasional small fish and seeds (Ackerman et al. 2020). In the 1800s, before extensive hunting occurred, the avocet's breeding range extended much farther north and east than it does currently (Godfrey 1986, Leck 1984). The American avocet is considered an indicator of environmental quality in its breeding areas, as contaminants have been a significant conservation issue in breeding areas for the species (Ackerman et al. 2007, 2008). Most research focused on American avocets has been related to ecotoxicology and breeding ecology, but migratory behavior and routes are mostly unknown (Ackerman et al. 2020) and the winter season has received much less research attention than the breeding season (Ackerman et al. 2020, Molina et al. 2018). American avocet winter habitat use and behavior has been best studied on the Pacific and Atlantic coasts of the United States and Mexico (e.g., Ackerman et al. 2007, Boettcher et al. 1995, Evans & Harris 1994, Molina et al. 2018). Studies on avocets in the Gulf Coast include Dinsmore (1977), who observed foraging and roosting behavior of avocets and black-necked stilts (*Himantopus mexicanus*) on the Gulf Coast of Florida, and Bolduc and Afton (2004), who conducted a multi-species analysis to study relationships between sediment characteristics, hydrologic variables, and invertebrates and density of 15 waterbird species including avocets. There is substantial variation in habitat type across the wintering range of avocets, so more detailed information about their habitat use and behavior on Gulf Coast wintering sites would fill a key information gap for conservation and monitoring efforts for avocets and similar shorebirds.

Presently, habitat requirements for avocets and many other shorebirds are uniformly defined across the Gulf Coastal Prairie Bird Conservation Region (J Olszak, Pers. Comm, North American Bird Conservation Initiative 2014). However, habitat composition and configuration are highly variable within the Gulf Coastal Prairie. There is evidence that avocets behave and use habitat differently among different habitat types within the Gulf Coastal Prairie (W. Vermillion, unpublished data). We focused on two areas of the Gulf Coast with ecosystems that are characterized differently, with unique conservation and management challenges, Mustang Island in Texas and Rockefeller Wildlife Refuge in Louisiana.

The Mustang Island area contains substantially developed areas including Corpus Christi and Port Aransas, but also some protected areas. Rockefeller Wildlife Refuge is a state refuge in an area with minimal development. Avocet behavioral associations with habitat use are not well known in either location, and local differences in habitat requirements are not currently reflected in Gulf Coast shorebird conservation plans (J. Olszak & W. Vermillion, Pers. Comm.). With consideration to differences in the ecology of species, information about avocet habitat use can also provide broader information about shorebirds and waterbirds using similar habitats on the Gulf Coast. However, presence or abundance of a species in a habitat is only one part of understanding the role of the habitat to the species, so adding information about behavior and energy expenditure in specific habitats improves opportunities for impactful conservation plans. For example, understanding the dynamics of foraging behavior can be used to strengthen predictions of population responses to environmental change (van der Kolk et al. 2020), and understanding how birds are using the landscape (e.g., foraging, roosting) can be useful for holistically defining habitat suitability and prioritizing key areas for conservation (Rogers et al. 2006).

The ability to balance energy expenditure and acquisition has strong effects on survival and reproduction (Brown et al. 2004, Illius et al. 1995, Wilson et al. 2013), and is linked to the ecological characteristics of species, likely influencing factors such as home range size, timing of migration and reproduction, and ultimately population trends (Mosser et al. 2014). The energetic cost of foraging and moving through the landscape is a strong selective pressure and driver of fine-scale decision making (Shepard et al. 2013). Spatial variation in energy expenditure is an important consideration for understanding patterns of land use and population dynamics (Mosser et al. 2014). For migratory birds, the composition and configuration of the landscape and environmental conditions both influence their ability to balance energy gains and losses throughout the annual cycle (Farmer & Parent 1997, O'Reilly and Wingfeld 1995, Wiersma and Piersma 1994). The influence of winter habitat on patterns of activity and energy expenditure is likely important for the condition of the bird for migration and breeding seasons. Shorebirds, including avocets, spend the majority of time they are awake on foraging (Davis & Smith 1998, Morrier & McNiel 1991), so energy expenditure can provide information about where and when shorebirds are likely foraging or stationary.

Energy acquisition is difficult to measure, but we are able to measure energy expenditure, and this may be informative for understanding space use within a season and landscape effects on energy expenditure and behavior. Advances in tracking technology allow researchers to quantify energy expenditure and activity levels, which has many applications including studying constraints brought about by environmental or habitat conditions (Wikelski and Cook 2006). GPS-acceleration (ACC) tracking devices allow spatial patterns of energy expenditure to be assessed because they collect ACC data which can be associated with animal locations. ACC data can be used to calculate overall dynamic body acceleration (ODBA; Wilson et al. 2006, Shepard et al. 2008), which is a proxy for energy expenditure (Gleiss et al. 2011). Approximating energy expenditure via GPS and acceleration data (i.e., developing an energy landscape; Shepard et al. 2013) allows researchers to study spatial patterns and drivers of energy expenditure in a variety of terrestrial and aquatic animals. For example, Wilson et al. (2013) quantified the energy landscape around a colony of imperial cormorants (*Phalocrocorax atriceps*) and observed a variety of foraging techniques with regard to diving depth and distance from the colony, but found a strong trend toward minimally costly locations and depths. Mosser et al. (2014) used acceleration data to quantify energetic demands for caribou (*Rangifer tarandus*) in relation to landscape characteristics. Scharf et al. (2016) recorded ODBA of fishers (*Pekania pennanti)* within their home ranges to try to find variables impacting spatial variation in energy expenditure, and observed high individual variation in the influence of habitat characteristics on energy expenditure. Brownscombe et al. (2017) found that energy expenditure of reef fish was explained by interactions between habitat, tide, and season. Similar data for avocets could reveal patterns of behavior and energy expenditure useful for investigating habitat quality.

By quantifying energy expenditure in avocets and relating it to specific site characteristics, the information can be used to inform local conservation efforts focused on important habitat types used by birds throughout the day and throughout winter. Additionally, describing differences in habitat use among sites could improve conservation plans for avocets and similar species. The objectives of this study were to (1) determine landscape and temporal drivers of energy expenditure for American avocets in two wintering areas with different habitat types on the western Gulf Coast and (2) summarize landcover in each study site according to avocet location and behavioral information.

We predicted that both landcover and tide would influence energy expenditure in both areas, with shore habitat expected to be associated the lowest energy expenditure and higher tides to be associated with lower energy expenditure. We also expected that energy expenditure would be higher during the day, morning, and evening than at night. Based on preliminary summaries of expert opinion and observations, we predicted that avocets would use unconsolidated shore landcover more in Texas than Louisiana. We also expected that activity patterns would vary across landcover types.

Methods

Study Sites

Rockefeller Wildlife Refuge in southwest Louisiana, USA (Figure 2.1; hereafter Louisiana), is part of the Chenier Plain region spanning the coast of southwest Louisiana and east Texas (between Vermillion Bay, Louisiana and East Bay, Texas). The Chenier Plain is dominated by emergent wetlands, and also contains inland pastures and rice fields (Gosselink 1979). It is characterized by heavy rainfall and humidity (Gosselink 1979). Our study area was in Rockefeller Wildlife Refuge, and this area of the Chenier

Plain is comprised of freshwater marsh, in addition to brackish marsh, salt marsh, and open water habitat (Perry et al., 2011). Shoreline has receded ~10 m per year (Byrnes et al. 1995), and Rockefeller Wildlife Refuge has lost ~150 acres per year since it was established in 1920. Southwest Louisiana is sparsely populated, but severe erosion is a concern in addition to oil and gas development. Oil and gas exploration and sea level rise exacerbate shoreline and marsh loss (Ko & Day 2004, Sasser et al. 1986).

Mustang Island, Texas (Figure 2.1; hereafter Texas) is a barrier island between the Gulf of Mexico and Corpus Christi Bay located north of Laguna Madre. The habitat in the area is different from the Chenier Plain ecosystem in that tidal flats are the dominant shorebird habitat. Unlike the coastal wetlands of the Chenier Plain which consist of emergent marsh interspersed with small pools, there is less vegetation in tidal flats, (Coastal Bend Bays & Estuaries Program 2020). Additionally, there is extensive unconsolidated shore habitat along the sides of barrier islands and channels in our Texas study area around Mustang Island, while there is less unconsolidated shore in Louisiana (NOAA 2016). In general, the lower Texas coast experiences higher temperatures and less precipitation than the Louisiana site (NOAA 2022). In addition, our capture site was in Corpus Christi, TX, and 84% of points collected by our birds were north of the city limit of Corpus Christi, while 16% were south of the city limit in the Laguna Madre area. Based on the locations of most birds, we also expect birds at our Texas site to experience more anthropogenic disturbance than those at our Louisiana site. Erosion is also a concern on the lower Texas coast.

Bird Movement Data

We captured and placed GPS-acceleration (ACC) tracking devices on avocets at two main sites near Grand Chenier, Louisiana and Corpus Christi, Texas. We used 10-gram Ornitrack-10 tracking devices (Ornitela; Vinius, Lithuania) and attached them with a leg loop harness made of elastic shock cord (Rappole & Tipton 1991, Sanzenbacher et al. 2000). These devices were solar-rechargeable, collected location data via the GPS satellite system, contained a tri-axial accelerometer, and transmitted data through the Global System for Mobile Communication (GSM) network. We aged and sexed birds in the field according to color and wear of coverts and primaries for age and bill morphology for sex (Pyle 1997) and later confirmed the sex of most birds using molecular methods (van der Velde et al. 2017). We randomly selected second year and older birds, ensuring that they were at least 300 g so that the device would be <3% of body weight (mean bird mass was 368.8 g, SD 43.1). In Louisiana, we captured birds by hand and using dip nets and deployed 27 devices over 13 occasions in January and February 2020 and 2021. In Texas, we captured birds using cannon nets and deployed 9 devices in April 2021. We deployed a total of 36 devices between the two sites, but excluded 4 birds that were transmitting data for less than 28 days and 2 others that transmitted data throughout the season but for which device battery level was too low to collect ACC data. In total, data from 31 birds were used in this analysis (8 from Texas and 23 from Louisiana).

All tracking devices in 2020, along with the 9 deployed in Texas in 2021, were initially deployed to collect one GPS fix per hour (24 per day) and one ACC fix for 3 seconds at 10 Hz every 6 minutes. For those in Louisiana in 2020, the GPS duty cycles were reduced to once every 4 hours (6 per day) temporarily due to excessive battery drainage, and later increased to once every 2 hours (12 per day). ACC duty cycles were unchanged except during times when device battery fell below 25% capacity, in which case the devices were programmed to stop collecting ACC data. In 2021, tracking devices in Louisiana were programmed to collect one GPS fix every 2 hours and one ACC fix every 20 minutes. The changes in duty cycle were due to differences in battery capacity given differences in specific device model (some were newer versions with greater memory capacity) and differences in GSM coverage between sites.

We determined ODBA by subtracting the average acceleration due to gravity over each 3-second burst from the total acceleration (i.e., gravity plus animal movement). Static acceleration is subtracted from total acceleration, resulting in dynamic acceleration, that is only animal movement (Shepard et al. 2008). The dynamic acceleration of each axis is then summed (i.e., ODBA = $|A_x| + |A_y| + |A_z|$, where A_x, A_y, and A_z represent the dynamic acceleration of each axis (Wilson et al. 2006, Shepard et al. 2008). We used the mean ODBA of each 3-second burst to represent the burst. Then, we used the ACC fix collected closest in time to each GPS fix to assign an ODBA value to the location of the GPS fix and discarded other ODBA values.

For molecular sexing, we extracted DNA using DNEasy Blood & Tissue Kits (Qiagen, Valencia, California) following the manufacturer's protocol. We amplified the CHD gene using the primer set 2602F/2669R, which was developed and tested specifically for shorebirds (van der Velde et al. 2017). We followed the PCR protocol described by van der Velde et al. (2017). We separated samples through a 3% agarose gel in TBE buffer and visualized PCR products by ethidium bromide staining. We sexed each bird according to the number of bands in the gel (Fridolfsson and Ellegren 1999).

Covariate Data: Landscape, Tide, and Time

We collated data on landcover type, tide amplitude, time of day, and day of year to use as covariates in our models for objective 1. We assigned each GPS point to one of 4 categories (morning, day, evening, and night) to describe the time of day based on the time stamp from the GPS fix. We chose to divide time of day into categories to account for changes in activity levels at dawn and dusk in addition to day and night. Morning was considered 11:00–13:59 UTC, (3 hours surrounding sunrise), day was considered 14:00–21:59 UTC, evening was considered 22:01–1:59 UTC (3 hours surrounding sunset) on the next day and night was considered 2:00–10:59 UTC. This was based on the approximate time of sunrise and sunset in Grand Chenier, Louisiana in late March. We also assigned the ordinal date to each GPS point as a measure of time to account for variation over the course of the season.

For each bird location, we extracted 30-m resolution landcover data from the Coastal Change Analysis Program (C-CAP; NOAA 2016). The C-CAP data set is the coastal equivalent of the National Land Cover Database, and contains similar landcover types, but makes more distinctions between wetland categories, including differentiating between freshwater and saltwater wetlands (NOAA 2016). It is also consistent across our Louisiana and Texas study sites. We extracted only the 30-m grid cell in which each GPS point occurred; we did not summarize the surrounding cells because points were often very close together and a test of precision among our tracking devices showed that when a device is stationary, points collected are within 20 m of one another 98% of the time (Clements et al. 2022). We reclassified the C-CAP rasters into 6 categories: developed, agriculture, estuarine emergent wetlands, palustrine emergent wetlands, open water, and unconsolidated shore. We excluded developed areas from analysis of Louisiana birds because there were very few points (0.0006%) in developed areas. We retained points in developed areas for analyses of Texas birds. For our energy expenditure models, we combined estuarine and palustrine emergent wetlands into one category to simplify the model because there is evidence that avocets do not have a preference for foraging in saline or non-saline wetlands (Boettcher et al. 1995). However, we retained them as separate categories in our summary of habitat use because the spatial distribution of estuarine and palustrine emergent wetlands may be different across sites and while salinity may not substantially influence foraging behavior, understanding differences in use between these wetland types could be valuable for conservation planning.

Tide data for Vermillion and Cameron parishes, Louisiana, was collected from station #8766072 in Vermillion parish. This tide station was the closest in location to where Louisiana birds were located throughout most of the study period. There were more tide stations in Texas, so we downloaded data from 4 stations in Nueces, Kleberg, and Kennedy counties depending on bird location (Station #8776604, #8775237, #8775792, #8777812). We used tide data from the closest tide station in space to each location for Texas birds. All tide data were collected at 6 minute intervals and each GPS point was assigned the tide amplitude value closest to it in time.

Model

To address objective 1, we used a Bayesian linear mixed model to model the effects of habitat, tide, and time of day on energy expenditure. The model can be written mathematically as:

$$Y_{i,j,k} \sim \beta_0 + \beta_j L_i + \beta_k M_i + \beta_1 T_i + \beta_2 D_i + \beta_j L_i T_i + \epsilon_i$$

where *Y* was ODBA for GPS point *i*, landcover type *j*, time of day *k*. β_0 is the intercept. *L* is landcover, *M* is time of day assigned to a category (morning, day, evening, or night), *T* is tide height and *D* is ordinal date at point *i*. ε_i is an individual random effect. We ran models in Jags (Plummer 2003) through Program R (version 4.1.2; R Core Team 2021) using the jagsUI package (Kellner 2015). We monitored convergence based on R-hat < 1.1 (Brooks & Gelman 1998) and visually inspected chains. For landcover, we used shore as a reference condition to compare effect sizes of all other levels of landcover. Therefore, the effect size of shore was set to 0. We chose shore as a reference condition because avocets are often observed roosting on the shore at both study sites. However, when tide conditions provide optimal water depth, they may also forage on shore. This means that shore habitat is intuitive to interpret in relation to emergent wetlands, open water, and agriculture. We included an interaction between tide and landcover because avocets usually forage in water and do not prefer to probe in the mud (Ackerman et al. 2020). Similarly, most shore and emergent wetland areas are tidal so foraging habitat availability will change with tide, and it is expected based on other shorebird studies that habitat availability will change with tide (Fasola & Biddau 1997; McKonkey & Bell, 2005). We represented time as ordinal day to account for variation between the beginning and end of season in case there is, for example, an increase in foraging activity or a shift in habitat use pre-migration. Finally, we included time of day in the model behavior and movement are expected to change with time of day (Jourdan et al. 2021, Kuwae 2007). We ran the model two separate times, once for Louisiana data from February, March, and April 2020 and 2021 (*N* = 23 birds, 12,414 data points) and once for Texas data from April 2021 (*N* = 8 birds, 4686 data points) because we expected different relationships between the two study sites and had differing amounts of data and time periods over which data were collected.

For categorical covariates, we summarized effect sizes as positive or negative relative to the reference condition and present the evidence that an effect was positive or negative as proportion of posterior samples above or below 0 (*P*). For both categorical and continuous covariates, if at least 80% of posterior samples were above or below zero, we interpret that an effect explained substantial variation in the response.

Landcover Use

To address objective 2, we summarized data for each individual bird. We first calculated the total percentage of GPS points collected in each landcover class and reported it with a box plot which compared results between Louisiana and Texas. Additionally, we used k-means clustering to classify points into two categories, inactive and active, based on ODBA using the factoextra package (Kassambara & Mundt 2017) in Program R (R Core Team 2021). We ascribed the lower energy expenditure class as inactive and the higher energy expenditure class as active, as flight points were excluded from this analysis.

While in many cases it is possible to use a training dataset of known behaviors to identify specific behaviors in ACC data using machine learning algorithms, we were not able to obtain enough training data to use this method. We constructed box plots to summarize the percent of points categorized as inactive and active collected in each landcover class. We summarized this information separately for Louisiana and Texas.

Results

Energy Expenditure

We captured 36 avocets total, and we used 17,100 GPS fixes from 31 birds during February, March, and April 2020 and 2021. Based on the results of molecular sexing, the avocets we captured and tagged with tracking devices in Louisiana were 75% female and 25% male, while in Texas all captured and tagged birds were male. Energy expenditure varied in space and time (Figures 2.2, 2.3, A1.2).

When using data from Louisiana birds during February, March, and April 2020 and 2021, interactions between tide and agriculture (β = 0.45, 95% CRI 0.32, 0.58; P = 1.00), tide and emergent wetlands (β = 0.20, 95% CRI 0.16, 0.28; P = 1.00), and tide and open water (β = 0.13, 95% CRI 0.05, 0.21; P = 1.00) all had positive relationships with ODBA relative to unconsolidated shore (Figure 2.4; note that although effect sizes for interactions are positive, trend is negative due to the strong effect of tide being considered). Ordinal date had a small positive relationship with ODBA (β = 0.16, 95% CRI 0.11, 0.21; P = 1.00; Figure 2.5). Relative to day, ODBA was lower in the morning (β = -0.10, 95% CRI -0.18, -0.03; P = 1.00), substantially higher in the evening (β = 0.37, 95% CRI 0.28, 0.45; *P* = 0.97), and slightly higher at night (*β* = 0.06, 95% CRI 0.01, 0.10; *P* = 0.97; Figure 2.6).

When using data from Texas birds from April 2021, the interaction between tide and any landcover type was not strong, except for developed landcover (*β* = 0.48, 95% CRI 0.16, 0.90; *P* = 1.00); however, tide (*β* = -0.11, 95% CRI -0.16, -0.06; *P* = 1.00; Figure 2.7) and landcover type as individual effects explained substantial variation in ODBA. Among the landcover types emergent wetlands (*β* = 0.05, 95% CRI -0.05, 0.14; *P* = 0.82) and open water (*β* = -0.11, 95% CRI -0.16, -0.06; *P* = 1.00) had positive relationships with ODBA relative to unconsolidated shore (Figure 2.8). ODBA in agriculture was similar to that for unconsolidated shore (*β* = 0.046, 95% CRI -0.05, 0.14; *P* = 0.63). Ordinal date did not explain variation in ODBA (*β* = 0.00, 95% CRI -0.03, 0.04; *P* = 0.57). Relative to day, ODBA was lower in the morning (*β* = -0.12, 95% CRI -0.16, -0.06; *P* = 0.97) and higher in the evening (*β* = 0.32, 95% CRI 0.20, 0.44; *P* = 1.00) and night (*β* = 0.71, 95% CRI 0.61, 0.80; *P* = 1.00; Figure 2.9).

Landcover Use

Use of landcover types varied between Louisiana and Texas (Figure 2.10), most notably, the proportion of points in unconsolidated shore was much greater for Texas (mean = 0.60, SD = 0.07) than Louisiana (mean = 0.16, SD = 0.10). Further, the proportion of points collected in each landcover type was not substantially different between active and inactive points in Louisiana or Texas (Figure 2.11).

Discussion

We found different patterns in landscape drivers of energy expenditure between our two study sites (Mustang Island, Texas and Rockefeller Wildlife Refuge, Louisiana) as well as different patterns of habitat use, however, temporal factors, including time of day and tide amplitude often had stronger effects than landcover variables at both sites. Habitat composition is quite different between our two study sites, but other environmental conditions could cause differences in behavior and energy expenditure between sites. We consider our Louisiana site at Rockefeller Wildlife Refuge to be representative of the Chenier Plain ecosystem but do not consider our Mustang Island site to be representative of undeveloped areas of the lower Texas coast because most of our data was collected in areas with substantial human development. Because these two sites differ in both habitat composition and amount of human activity they may not be directly comparable but do provide insight into differences in avocet activity among other areas sharing characteristics with our focal areas. Our results highlight the utility of incorporating region-specific and time-varying environmental and behavioral information in assessments of energy expenditure as an indicator of habitat quality for conservation and monitoring plans

We found that tide had a negative relationship with ODBA in Texas and in Louisiana across most landcover types and that landcover explained substantial variation in ODBA. The interaction of tide and landcover was important only for developed landcover in Texas while the interaction was important for all landcover types in Louisiana. However, note that although the interactions all have a positive effect sizes for Louisiana, in predictions, all terms involved in the interaction are used, meaning that trends in ODBA as tide changes in each landcover type are still expected to be negative due to the much stronger effect of tide than landcover. We anticipated that because avocets often forage in the water column, energy expenditure due to feeding would change with tide (Basso et al. 2018, Dinsmore et al. 1977). Given avocets prefer an intermediate water depth (10-17 cm; Boettcher et al. 1995), the negative relationship between tide and energy expenditure in Texas means that, assuming most energy expenditure is due to foraging activity (Davis & Smith 1998, Morrier & McNiel 1991), more foraging habitat for them is available at lower tides. In Louisiana, interactions between tide and agriculture, emergent wetlands, and open water all showed positive relationships with ODBA relative to shore, meaning that in general, birds were more active in these habitats, but activity level was also strongly influenced by tide. The largest positive effect size was for agriculture, which was the only non-tidal habitat in the model for Louisiana. The positive effect was likely because in general, tide increased later in the study period, as did use of agricultural areas. Based on GPS movement data, the avocets were not being pushed out of other habitats into agricultural areas, but rather a small subset of individuals moved north for periods of days or weeks. In Louisiana, rice fields are abundant, and avocets are known to use flooded agricultural fields (Colwell et al. 2001). However, agriculture made up only a small proportion of habitats used. Tide had a positive relationship with ODBA for both open water and emergent wetlands. (Ackerman et al. 2020), and avocets were usually roosting when observed on shore at our Louisiana study site. In Texas, although the interaction of landcover and tide did not explain substantial variation in ODBA except in the case of developed landcover, tide was negatively associated with ODBA and open water and emergent wetlands had positive effects on ODBA relative to unconsolidated shore, similarly to Louisiana. However, in Texas, agriculture did not explain substantial variation in ODBA. The positive interaction of tide and ODBA for developed landcover could mean that foraging habitat in developed areas expands as water level increases. Our results for avocets are likely different than those from other shorebird species with different morphology and foraging strategies because tide and landcover could affect habitat quality and availability differently for each species (Baker & Baker, 1973). For example, in a study of tidal habitat dynamics on shorebird use of shrimp farms, Basso et al. (2018) showed that several species of shorebirds with varying foraging strategies, including avocets, behaved differently.

In Louisiana, ODBA increased slightly during the period February to April. This could indicate an increase in foraging activity before migration (Lindström 2003). It could also be contributed to by the longer day length (Evans 1976), because the effect of night on ODBA relative to day was small for Louisiana and the difference may not have been enough to eliminate within-season variation.

Time of day explained substantial variation in ODBA, and, unexpectedly, ODBA was higher at night than during the day, and this effect was strong in Texas. Shorebirds may forage at night either because foraging opportunities are less restricted at night, or to compensate for not acquiring enough energy during the day (Colwell 2010). Especially during the day, human activity is substantial at our Mustang Island, Texas site. It is known that bird presence and foraging activity is often decreased by human disturbance. For example, Cestari (2015) found negative associations between the number of people on a beach in a populated area and presence of mixed flocks of shorebirds in coastal Brazil. Navedo et al. (2019) found significantly lower Hudsonian godwit abundance and foraging activity at sites with human disturbance compared to sites without disturbance. In the Mustang Island area, birds may often be spatially and temporally displaced from foraging areas by human disturbance (Foster et al. 2009). It is possible that birds in this area forage more at night to avoid disturbance from human activities such as fishing and birdwatching, in addition to traffic from small and large boats, as many of them were located in areas near roads or channels where these disturbances were taking place frequently. In Louisiana, there is very little development at the site so human development and activity are not expected to influence bird activity levels. Additionally, artificial light sources can increase visibility for nocturnally foraging shorebirds (Dwyer et al. 2013), which may also allow the Texas birds to increase foraging activity at night, whereas Louisiana birds without artificial light may maintain a more constant rate of foraging between day and night. This could explain the much smaller positive effect of night on ODBA in Louisiana.

Texas birds had proportionally more locations in unconsolidated shore habitat than Louisiana birds. Based on eBird (ebird.org) records and expert opinion, there is high variation and uncertainty in avocet use of shore habitat, and avocets were thought to use shore more in Texas than Louisiana (W. Vermillion/GCJV, unpublished data). Our results suggest that this uncertainty could be due to differences in habitat composition and bird behavior in the Texas coast and Louisiana chenier plain ecosystems that characterize our study sites, in addition to different anthropogenic pressures between the Mustang Island and Rockefeller Wildlife Refuge sites, both of which are representative of different combinations of factors that could influence shorebird activity in many areas of the Gulf coast. In the case of shore, the differences in behavior are likely because shore habitat in Louisiana is less suitable for avocets, and because there is extensive marsh habitat but little shore habitat in Louisiana. Avocets prefer foraging in areas with fine substrate and within the water column (Boettcher et al. 1995, Ackerman et al. 2020). At our sites in Louisiana, much of the shore habitat is not optimal for foraging, with coarse substrate, and along the coastline and channels the water becomes deep quickly, but at our Texas sites, substrate is much finer and there is more shore available with more optimal water depths for foraging. Additionally, in a study of shorebird foraging behavior in a wetland complex in coastal Texas, Rowell-Garvon and Withers (2009) found that avocets most often foraged in tidal ponds and saltmarshes with emergent vegetation when these habitats were available. Emergent wetlands were the most commonly used habitat type used in Louisiana, but use was more limited at our study site in Texas. For both Louisiana and Texas birds, there was little difference between the proportion of points classified as active and inactive within each landcover type. This is likely because foraging conditions in the same place changed with tide for avocets and other shorebirds (Dinsmore 1977). Tide was an important predictor of ODBA in both states either on its own or through interaction with landcover.

Our results show differences between avocet energy expenditure, behavior, and habitat use between Mustang Island in Texas and Rockefeller Wildlife Refuge in Louisiana, and more broadly, provide a detailed understanding of avocet activity during the wintering season. This study shows that avocets exhibit plasticity to take advantage of available habitat and tide conditions, as well as adjust to disturbance or other sub-optimal conditions. Not all habitats of the same type are equal in environmental conditions, so it is important to account for both spatial and temporal factors when prioritizing areas for conservation. We found substantial variation in habitat and behavior for avocets within the Gulf Coastal Prairie bird conservation region, and we anticipate that there is similar variation for other species within the region, and that many bird conservation regions have ecologically different areas that could influence the behavior of species within them. Individual variation and general patterns in energy expenditure could explain effects of landscape in wintering and staging areas on fitness throughout the year, so targeted monitoring and conservation of birds and their wintering habitats could benefit species throughout the annual cycle. Mapping high- and low-activity areas in space and time could be used to prioritize likely foraging and roosting areas and this information could also be used for further efforts to confirm behavioral patterns in greater detail. For example, measures could be taken to decrease human disturbance at daytime roosting sites, or habitats with heavy foraging activity could be further examined to study food availability or other fine-scale characteristics that may be driving high activity levels. In the case of Mustang Island in Texas and Rockefeller Wildlife Refuge in Louisiana, differences in habitat use and patterns of energy expenditure mean that the two regions should identify priority habitat for conservation and monitoring differently according to their unique landscape configurations and conservation challenges.

In conclusion, we used energy expenditure data as a measure to investigate potential habitat quality and location data and summarize habitat use in American avocets across two different wintering sites. We found that energy expenditure, much of which should be due to foraging, is driven by tide, landcover, and time of day in both sites, but the patterns of energy expenditure in relation to these factors varied between the two sites. We also found that landcover use differed between the two sites but did not differ between active and inactive behavioral states. In the future, with climate change and sea level rise, hydrology of coastal ecosystems is expected to change, and human development is expected to increase. We know that winter habitat quality is very important for fitness outcomes for birds throughout the annual cycle (Marra et al. 2015), so future work could focus on evaluating the fitness consequences of winter energy expenditure and behavior. Our findings suggest that birds use the same habitat differently depending on conditions the area is experiencing, so both temporal and spatial attributes of habitats should be taken into consideration for conservation planning.

Figures

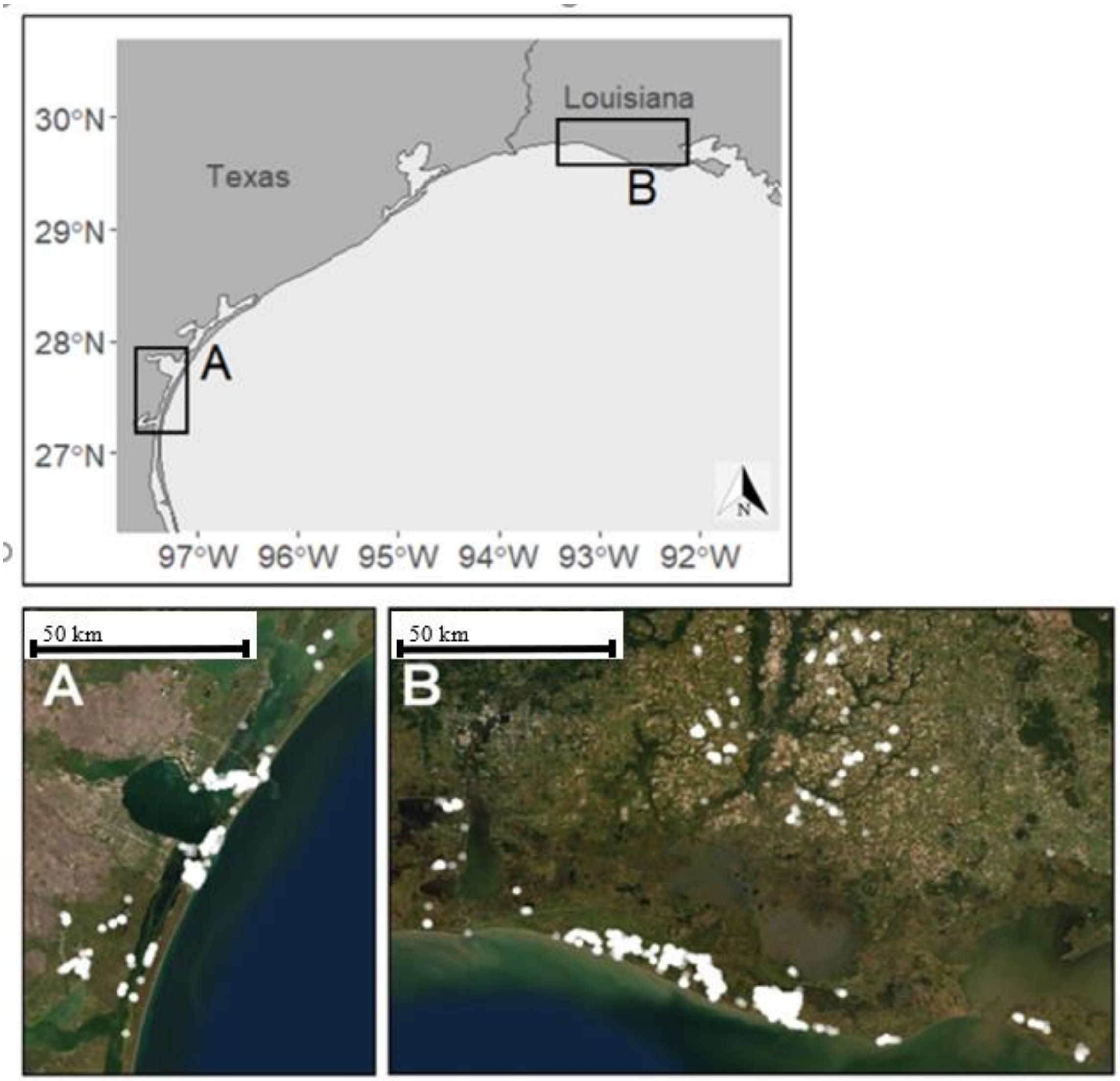

Figure 2.1. Map of study locations and aerial imagery for each study site in (A) Texas and (B) Louisiana with American avocet locations as white points. Points in Texas are from 8 birds in April 2021 and points in Louisiana are from 27 birds between February and April 2020 and 2021. Most points collected in Louisiana were within Rockefeller Wildlife Refuge and most points collected in Texas were on and around Mustang Island, Texas.

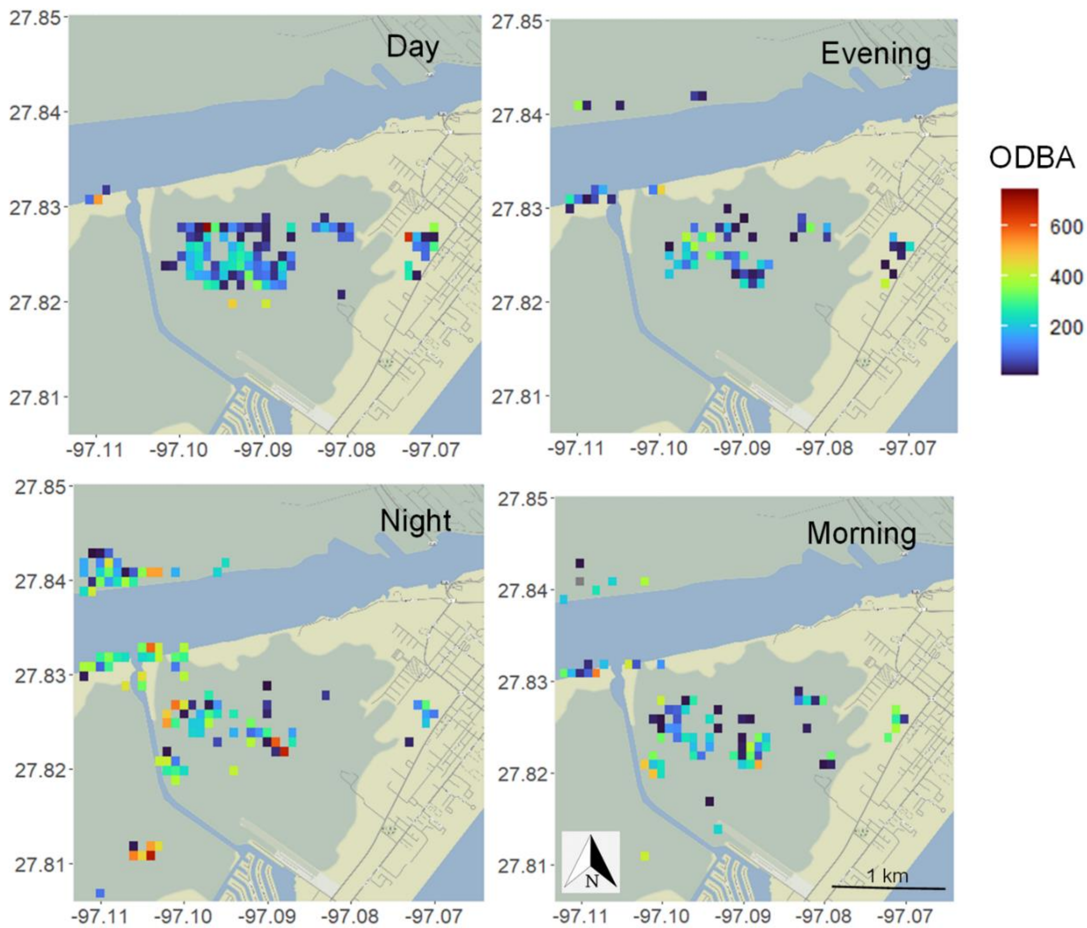

Figure 2.2. Map of one example subset of the study area in Port Aransas, Texas to show temporal variation in bird location and ODBA using a 100-m square grid cell. The 100-m grid cells show temporal variation in American avocet location and ODBA. Each panel represents one time of day and the color of grid cells represents mean ODBA of all points collected within the cell. Data came from 5 individuals using the area in 2021.

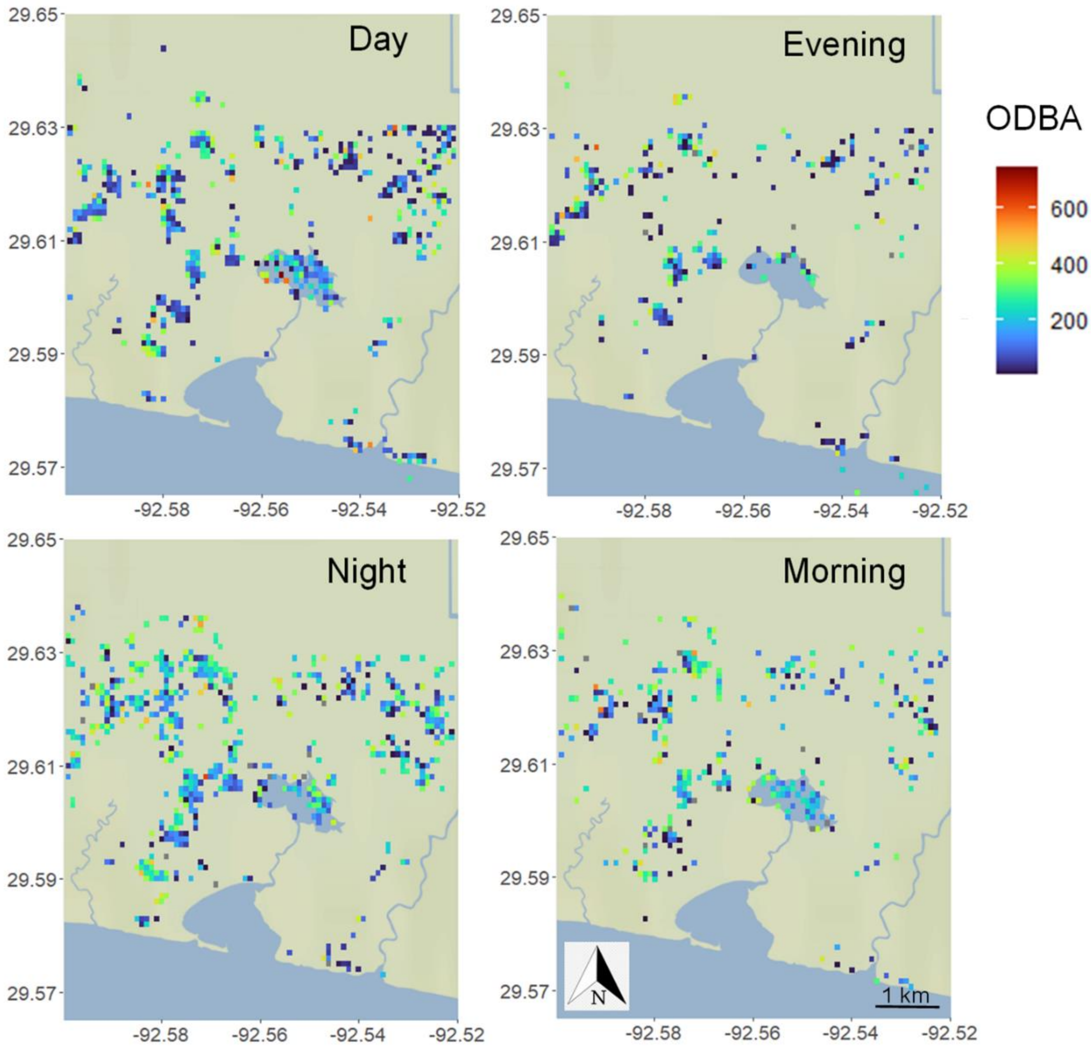

Figure 2.3. Map of one example subset of the study area in Vermillion Parish, Louisiana, in the unmanaged area of Rockefeller Wildlife Refuge. The 100-m grid cells show temporal variation in American avocet location and ODBA. Each panel represents one time of day and the color of grid cells represents mean ODBA of all points collected within the cell. Data came from 22 individuals using the area in 2020 and 2021.

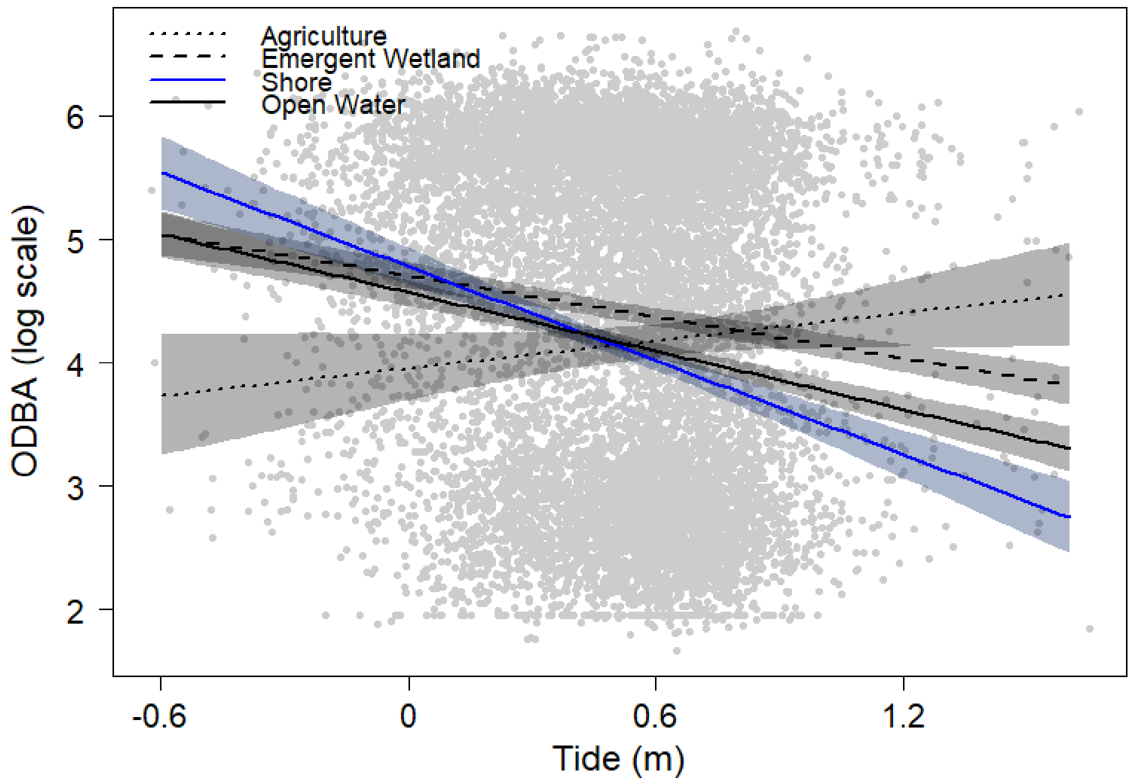

Figure 2.4. Predictions for ODBA on the log scale given an interaction between tide and landcover in Louisiana. Shaded ribbons represent the 95% credible intervals. Black lines indicate landcover types for which at least 80% of posterior samples were on the same side of 0 as the posterior mean, and blue indicates the reference condition, shore. Gray points represent the raw data points for ODBA in relation to tide.

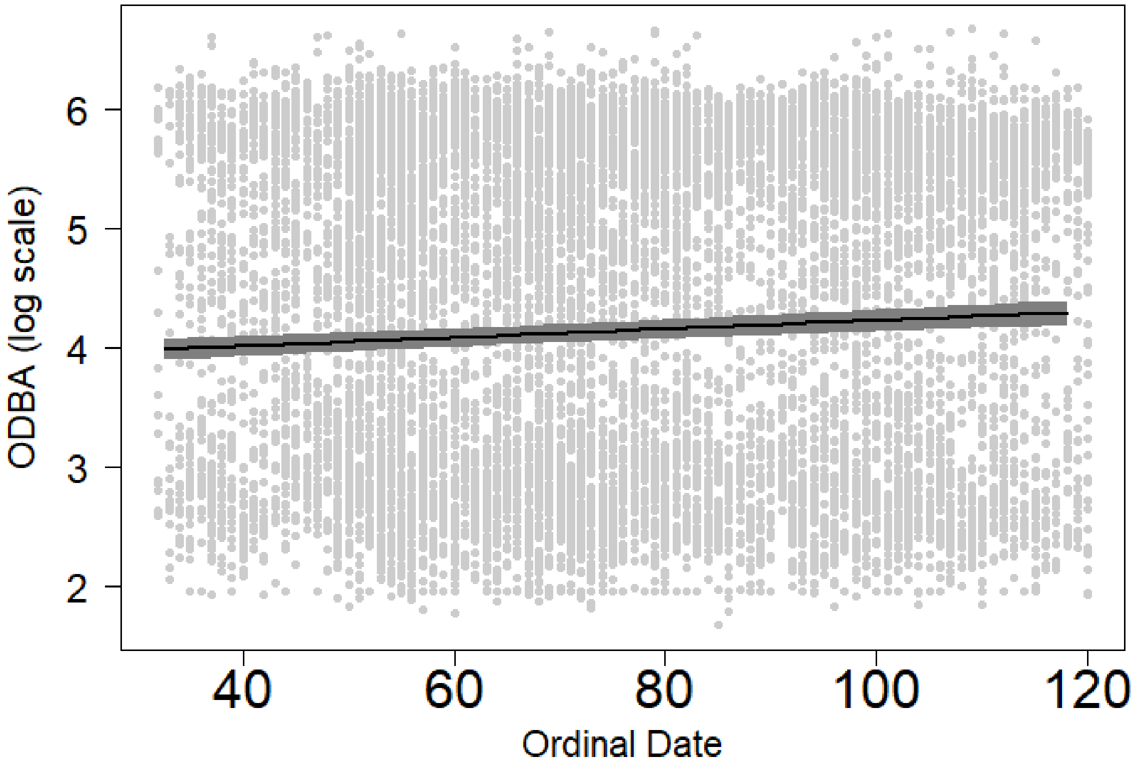

Figure 2.5. Prediction for the effect of ordinal date on ODBA on the log scale for the model run on data from American avocets in Louisiana in the months of February-April 2020-2021. The gray shaded ribbon represents the 95% credible interval and the gray points represent the raw data points for ODBA in relation to ordinal date.

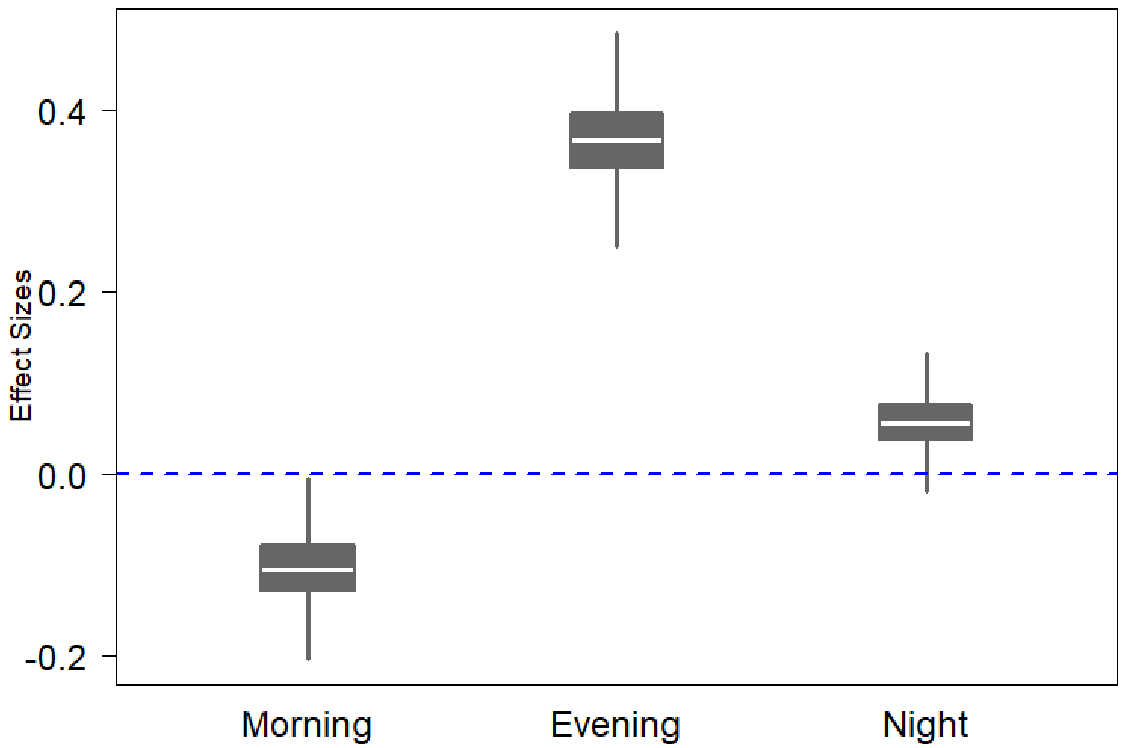

Figure 2.6. Posterior distributions of the effect of time of day on ODBA relative to the reference condition, day, indicated by the dotted blue line, from the model run on data for American avocets in Louisiana in the months of February-April 2020-2021. 95% (vertical bars) and 50% (boxes) credible intervals, in addition to medians (white horizontal bars) are shown for the effect of time of day on ODBA.

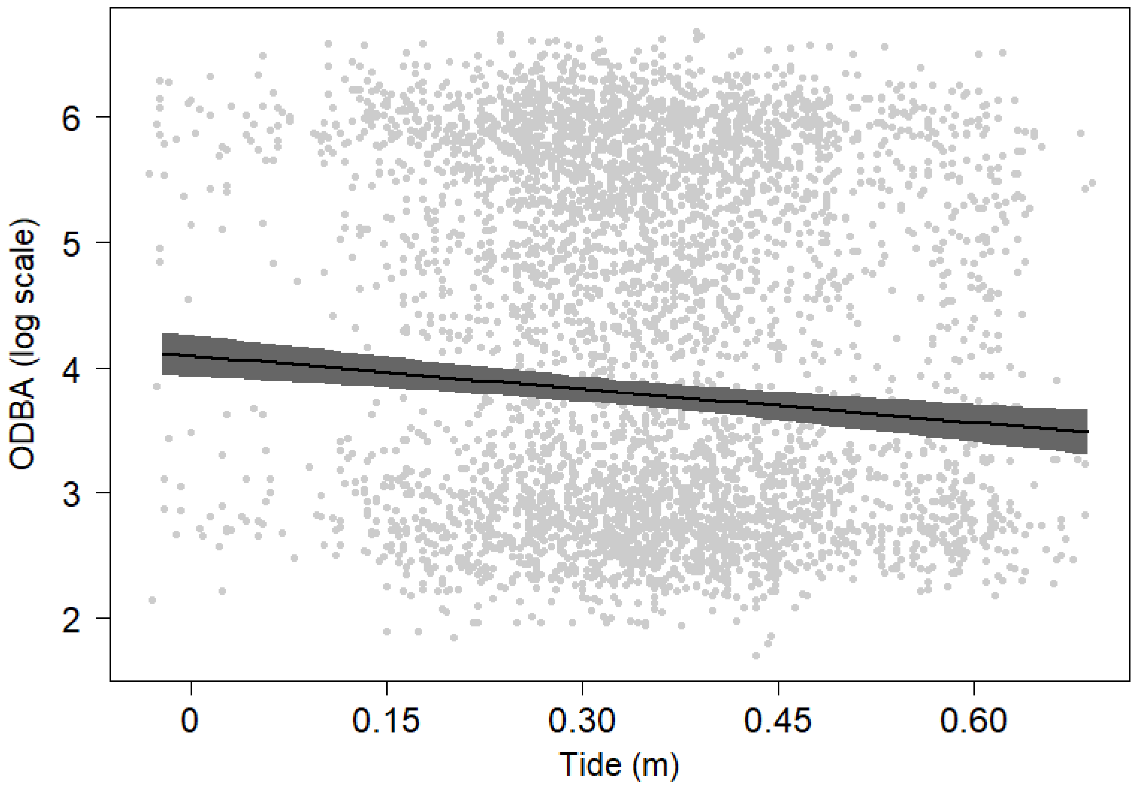

Figure 2.7. Prediction for the effect of tide on ODBA for the model run on American avocet data collected Texas in April 2021. The gray shaded area represents the 95% credible interval and the gray points represent the raw data points for ODBA in relation to tide.

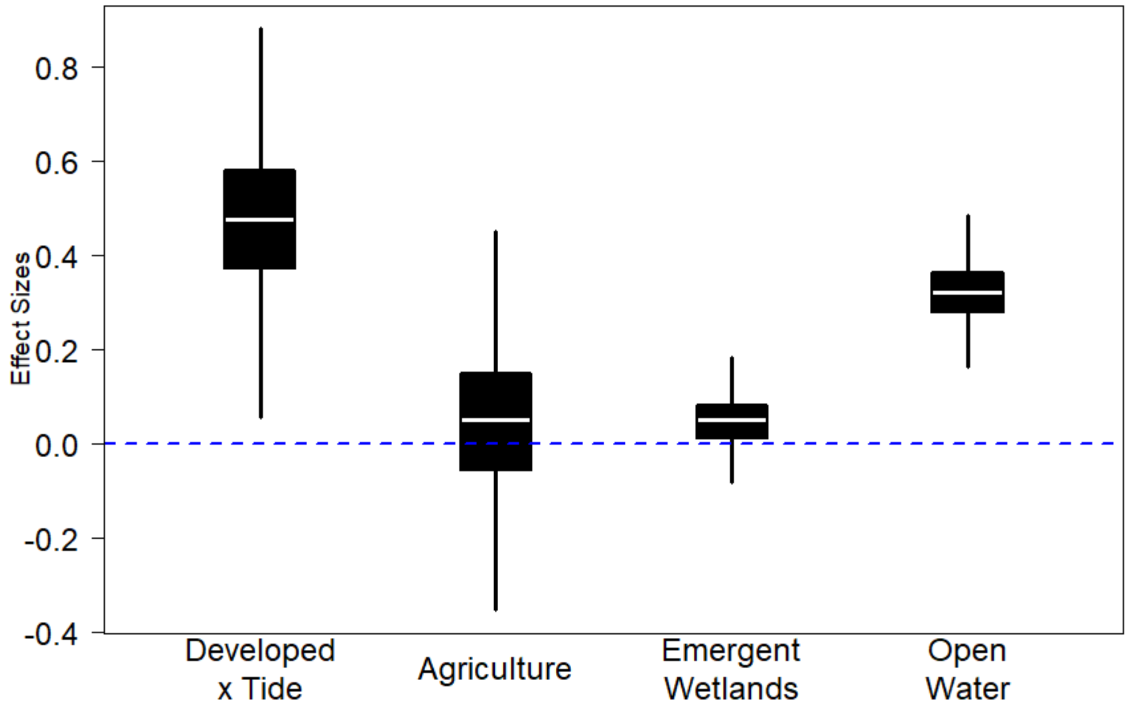

Figure 2.8. Posterior distributions of the effect of landcover on ODBA relative to the reference condition, shore, indicated by the dotted blue line from the model run on American avocet data collected in Texas in April 2021. 95% (vertical bars) and 50% (boxes) credible intervals, in addition medians (white horizontal bars) are shown for the effect sizes of each landcover type.

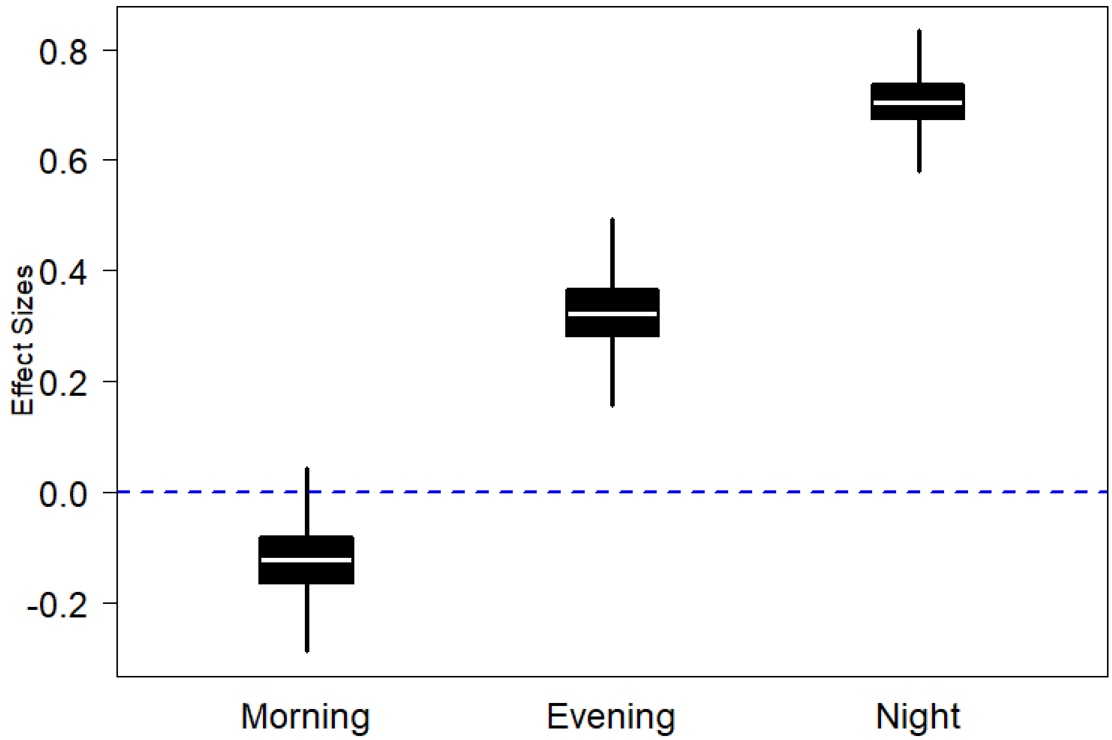

Figure 2.9. Posterior distributions for the effect of time of day on ODBA relative to the reference condition, day, indicated by the dotted blue line from the model run on American avocet data collected in Texas in April 2021. 95% (vertical bars) and 50% (boxes) credible intervals, in addition medians (white horizontal bars) are shown for the effect sizes of each landcover type.

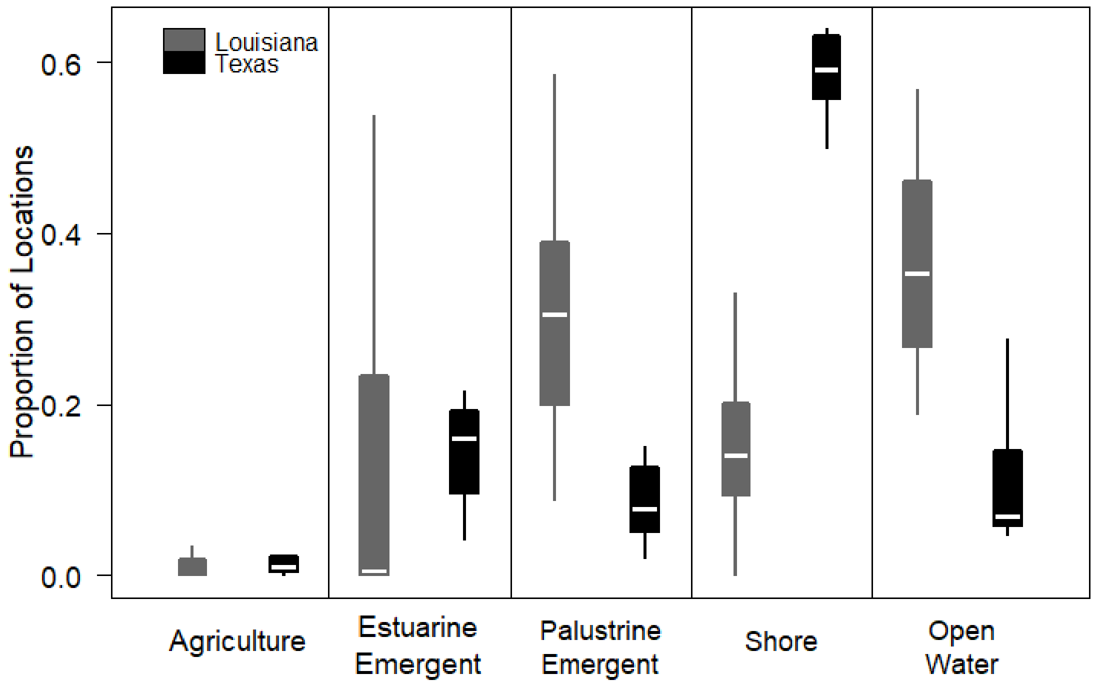

Figure 2.10. Boxplots of the proportion of all points collected in each landcover type for American avocets in Louisiana (gray) and Texas (black). Landcover types are separated by vertical black lines. 95% (vertical bars) and 50% (boxes) quantiles along with medians (white horizontal bars) are shown for each landcover type.

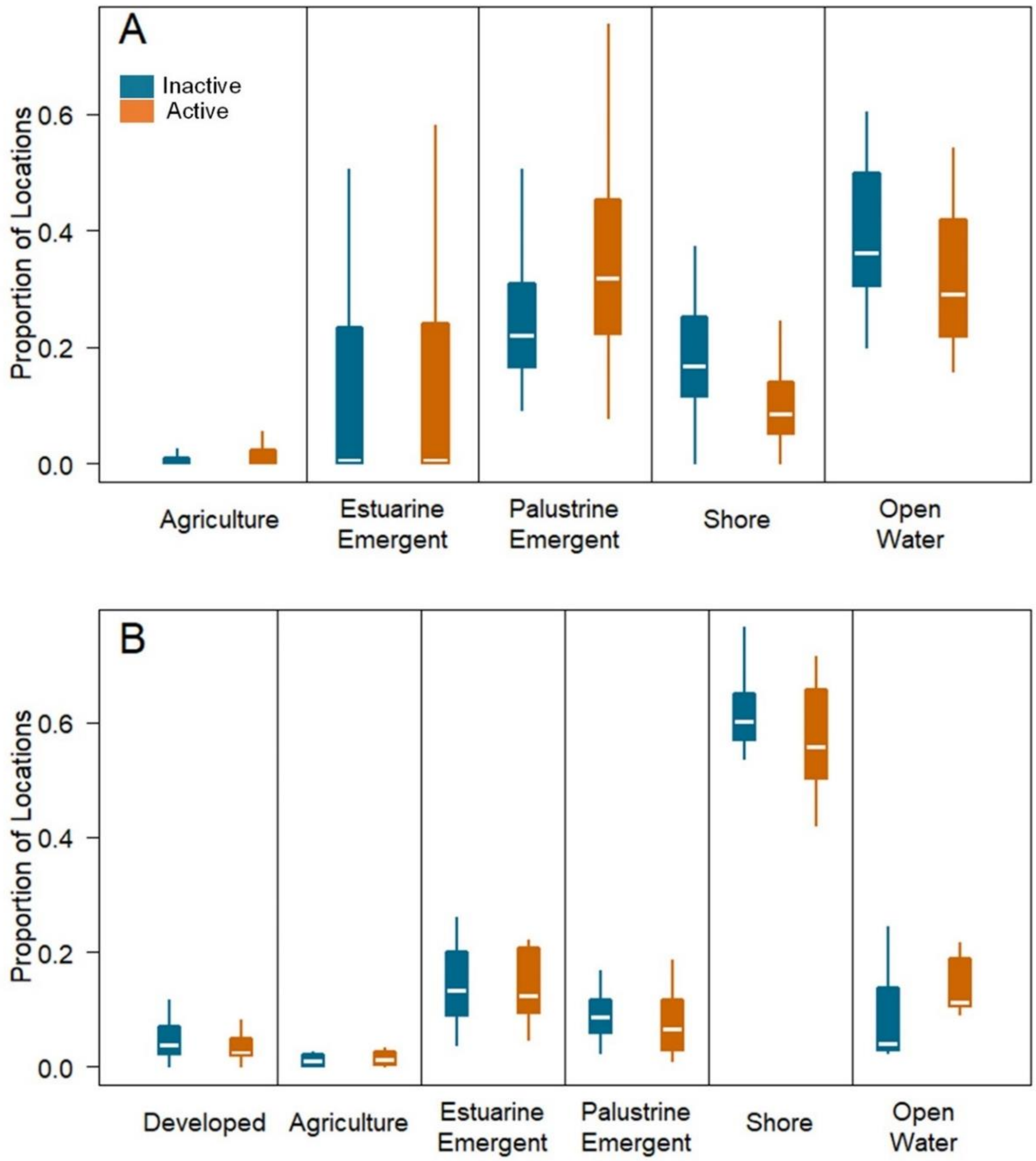

Figure 2.11. Boxplots showing the proportion of inactive (blue) and active (orange) points collected for American avocets in each landcover type for (A) Louisiana and (B) Texas. Landcover types are separated by vertical lines. 95% (vertical bars) and 50% (boxes) quantiles along with medians (white horizontal bars) are shown for each landcover type.

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CHAPTER 3

Comparing migration strategies among three shorebird species with short, medium, and long migration distances

Abstract

Shorebirds are one of the most threatened groups of birds worldwide, and they display an array of life-history characteristics. Migration strategy is a key behavioral characteristic guiding how migratory shorebirds time their annual cycles and use habitat. Understanding variation in migration metrics within and among migration strategies can be very useful for designing or modifying conservation plans that are meant to impact multiple species and life histories. We compared migration strategies among three species with short, medium, and long migration distances, respectively: American avocets (*Recurvirostra americana*), black-bellied plovers (*Pluvialis squatarola*), and Hudsonian godwits (*Limosa haemastica*). We found that avocets, with short migrations, showed the most within-species variation in migration duration, proportion of time in stopover, and stopover duration. Plovers and godwits showed less variation within-species in these metrics, but godwits showed the most variation in number of stopovers. There were significant differences between species in migration distance, number of stopovers, proportion of time in stopover, departure and arrival dates, and migration duration, but not mean stopover duration. We also tested the effects of removing data (simulating less frequent GPS collection) on migration metric calculations and found that even with substantially less GPS information, metrics related to phenology (departure and arrival dates, migration duration) could be estimated comparably to more frequent GPS information. However, inference of metrics related to stopovers was generally reduced. Our results characterized variation in migration strategies and set the stage for future

work conducting hypothesis tests of climate change and land use drivers, and incorporating other species to more broadly represent a gradient of life histories and facilitate further comparisons among species.

Introduction

Shorebirds are in decline globally and vulnerable to effects of anthropogenic development and climate change (Robinson et al. 2009, Galbraith et al. 2014, Wauchope et al. 2017). Their dependence on a broad range of habitat types makes them an important conservation focus and a group of species well-suited for examining resilience to change (Faaborg et al. 2010, Koleček et al. 2021, Piersma and Lindström 2004). Over half of all North American shorebirds are listed as species of conservation priority (Rosenberg et al. 2014), and their overall numbers are estimated to have declined by an average of 70% since 1973 (North American Bird Conservation Initiative 2016). Implementation of management plans for migratory birds can be limited by a lack of knowledge about how birds use habitats and move through landscapes (Faaborg et al. 2010). In North America, shorebirds migrating through the mid-continent are at particular risk of decline due to large-scale habitat change (Thomas et al. 2006).

A migration strategy refers to individual decisions in pathways and stopover sites, the timing of movements, and a balance of energy acquisition and expenditure; the collective migration strategies of individuals form our understanding about migration strategies of species (Colwell 2010). Migration strategies are shaped by spatial, temporal, and environmental pressures (Alerstam & Lindström 1990). Shorebirds display substantial variation in migration strategy within and among species. For example, red knots (*Calidris canutus*) have six subspecies worldwide, some of which winter in the southern hemisphere and others in the northern hemisphere, so although their diets are the same, subspecies vary in migration distance and stopover use (Piersma 2007). Anderson et al. (2019) observed that small, arctic-breeding shorebird species with longer-distance migrations followed a time-minimizing strategy (i.e., faster migration, fewer stopovers) while species with shorter migrations followed an energy-minimizing strategy (i.e., slower migration, more stops for refueling; Alerstam & Lindström 1990). Mid-continent shorebird species vary in the types of wetlands they are likely to use during spring migration, and migration strategy and resource availability are strongly linked (Skagen et al. 2005). A better understanding of migration strategy across species with different life-history characteristics can provide a foundation for disentangling drivers of shorebird declines and implementing conservation efforts in dynamic landscapes.

We conducted a multi-species analysis of migration strategy in shorebirds migrating through mid-continent North America. Migratory behavior and migration distance are often considered risk factors for species decline due to constraints associated with longer migration distances or less predictable habitat availability (Galbraith et al. 2014, Thomas et al. 2006, Both et al. 2010). Recent advances in tracking technology have enabled researchers to understand animal movement and behavior in increasing detail (Kays et al. 2015). Tracking technology can provide researchers with detailed information on bird movement, enabling characterization of migration strategies.

Tracking studies provide insight into individual movement, behavior, and decision-making but are often limited by focusing on a single species. We studied three species with different migration distances to capture variation in ecological characteristics and produce more generalizable conclusions: the American avocet

(*Recurvirostra Americana),* black-bellied plover (*Pluvialis squatarola*) and Hudsonian godwit (*Limosa haemastica*). American avocets (hereafter avocets) have a short migration distance. Avocets breed near ephemeral wetlands over a large part of the midwestern and western United States and southern Canada, from Texas to southern Alberta and Saskatchewan, and winter in Mexico and the southern United States (Ackerman et al. 2020). Individuals from different breeding populations migrate through coastal and inland North America, but specific routes are unknown (Ackerman et al. 2020). Avocets feed on invertebrates as well as occasional small fish and seeds, and usually feed in the water column (Ackerman et al. 2020, Boettcher et al. 1995, Dinsmore 1977). Black-bellied plovers (hereafter plovers) have a medium migration distance. The species is distributed worldwide, but in the western hemisphere, breeds across the Alaskan and Canadian arctic and winters on the coasts of southern North America, Central America, and northern South America (Poole et al. 2020). Plovers feed on aquatic and terrestrial invertebrates and are visual foragers (Poole et al. 2020). Hudsonian godwits (hereafter godwits) have a long migration distance. They forage on invertebrates by probing in mud and moist soil, and breed in boreal bogs and tundra sedge meadows in Alaska and the Canadian arctic, and winter in southern South America (Walker et al. 2020).

Our objective was to describe variation in migration strategy within and among three shorebird species with different migration distances and life histories. In general, we expected that (1) shorter migrations would be less constrained (more variation within species) than longer migrations, (2) shorter-distance migrations would follow an energy-minimizing strategy, while longer-distance migrations would follow a time-minimizing strategy, and (3) there would be significant differences among species in number of stopovers, migration duration, proportion of time in stopover, and departure and arrival dates because of the gradient in migration strategy from avocets to godwits. In addition, because we used devices with varying duty cycles, we aimed to test the effects of less frequent location information on resulting migration strategy summarizations, to contextualize variation among metrics and species.

Methods

Bird Movement Data

We captured all birds during the non-breeding season (Figure 3.1) using cannon nets and rocket nets, with the exception of avocets in Louisiana, which we captured at night by hand or with a dip net and spotlighting. We captured avocets at Rockefeller Wildlife Refuge in Louisiana in January and February 2020 and 2021 and the Laguna Madre area of Texas in April 2021. We captured plovers at Rockefeller Wildlife Refuge in January, February, and March 2019 and 2020 and at Laguna Madre in March, April, and May 2019, 2020 and 2021. We captured godwits on Isla Chiloé, Chile in January and March 2019, 2020 and 2021. Plovers were banded with a USGS metal band, avocets were banded with a USGS metal band and a green field-readable coded flag, and godwits were banded with a white plastic band and red field-readable coded flag. Bird captures in Louisiana and Texas were conducted under USGS permit (#21314), Texas Parks & Wildlife Scientific Research Permit (#SPR-812-965), and Louisiana Department of Wildlife and Fisheries Scientific Research and Collection Permit (#WDP-019-016) to B. Ballard, and work on Padre Island National Seashore in Texas was conducted under a

Research and Collection Permit (#PAIS-2021-SCI-0002) to D. Newstead. Louisiana and Texas captures were approved by University of Missouri (ACUC #9502) and Texas A&M University - Kingsville (ACUC #2018-10-30A). Captures in Chile took place under licenses (#7625/2018 and #296/2020) from the Government of Chile to J. Navedo and Bioethics Approval (#355/2019) from Universidad Austral de Chile.

We used four different models of GPS, GPS-acceleration (ACC) and Platform Terminal Transmitter (PTT) tracking devices from three different manufacturers: Lotek (Newmarket, Ontario, Canada), Ornitela (Vilnius, Lithuania), and Microwave (Columbia, MD, USA). The GPS and PTT devices transmitted data via the Argos satellite system, while the GPS-ACC devices transmitted through the Global System for Mobile Communication (GSM; i.e., cell phone) network. We used a different set of devices on each species depending on device and bird size (Table 3.1) to ensure that device mass would be approximately ≤3% of bird mass. In total, we deployed 136 tracking devices: 37 Pinpoint Argos Solar S and 8 Pinpoint Argos 75 devices on plovers; 37 Ornitrack-10 devices on avocets; and 29 Argos Solar PTTs and 25 Pinpoint Argos Solar S on godwits. For avocets, mean bird mass was 368.8 g ± SD 43.1. For plovers, mean bird mass was 213.4 g ± SD 19.4, and for godwits, mean bird mass was 327.3 g ± SD 53.0. In general, bird weight was lower earlier in the catching period and higher later in the catching period (i.e., birds were heaviest closer to spring migration). We attached tracking devices with a leg loop harness made of silicone, nylon, or elastic shock cord (Rappole & Tipton 1991, Sanzenbacher et al. 2000). We collected morphometric measurements from each bird, aged and sexed birds in the field according to morphology and plumage characteristics and later confirmed the sex of avocets and plovers using molecular methods (van der Velde et al. 2017).

Pinpoint Argos Solar S devices on plovers and godwits were programmed to collect a GPS fix every 2 hours (12 locations per day), while Pinpoint Argos 75 devices on plovers were programmed to begin collecting 1 location every 3 days from mid-April to mid-May, 1 point daily from mid-May to mid-July, and subsequently 1 point every 3 days. The Argos Solar PTTs on godwits transmitted Argos locations according to a duty cycle of 5 hours of transmitting opportunistically according to satellite configuration, followed by 24 hours of charging. All Ornitrack-10 devices on avocets in Louisiana in 2020, along with the 9 deployed in Texas in 2021, were initially deployed to collect one GPS fix per hour (24 per day) and one ACC fix every 6 minutes. For those in Louisiana in 2020, the GPS duty cycles were reduced to once every 4 hours (6 per day) during the winter season temporarily due to excessive battery drainage, and later increased to once every 2 hours (12 per day). ACC duty cycles were unchanged except if device battery fell below 25% capacity, then devices stopped collecting ACC data. In 2021, tracking devices in Louisiana were programmed to collect one GPS fix every 2 hours and one ACC fix every 20 minutes. The changes in duty cycle were due to differences in battery capacity given differences in specific device model (some were a newer version and had more memory capacity) and GSM coverage between sites.

Data from Lotek and Microwave devices were stored in Movebank (Kranstauber et al., 2011). We used Movebank to filter location quality based on Lotek Cyclic Redundancy Check status for Lotek device data and applied the Douglas Argos Filter (Douglas et al. 2012) to Microwave device data. Then, we used the SDLFilter package

(Shimada et al. 2012) in Program R to remove duplicate points and outliers based on a speed threshold of 150 km/hour. The SDLFilter package calculates speed based on GPS locations and timestamps and can also detect duplicate points in space and time. For the Ornitela devices, we filtered by removing GPS points with HDOP >10. Finally, we visually identified and removed several remaining outlier points, most of which showed erroneous future times or were located at 0 degrees latitude and longitude. We did not use ACC data in this analysis because not all devices could collect it.

Characterizing migration strategy

First, we subset data to include only tracks with at least one full spring migration with no multi-day gaps in data between wintering and breeding areas. We intended for devices to last through one spring migration, and they were programmed as such. Harness materials were not expected to last more than one year. Therefore, if a bird recorded more than one spring migration, we retained only the first spring following deployment due to increased data gaps within and among devices transmitting for more than one year. Then, for all Pinpoint Argos Solar S and Ornitrack-10 devices, we aligned duty cycles to retain one location every 2 hours using the move package (Kranstauber et al. 2020) in Program R (R Core Team 2021), which resulted in data for 14 avocets, 24 plovers, and 7 godwits. For the Pinpoint Argos 75 and Argos Solar PTT, we aligned duty cycles to retain one location every 24 hours using the move package, which resulted in data for 8 plovers and 4 godwits. In addition, 4 plovers, 14 godwits, and 6 avocets recorded partial migrations or did not migrate to breeding areas, and the remaining devices either recorded almost no data or only recorded pre-migration data. We used data from individuals with complete migrations (14 avocets, 24 plovers, and 7 godwits) to ascribe wintering and breeding areas, as well as stopovers, and calculated the total migration distance, number of stopovers, average stopover duration, proportion of time in a stopover, and winter departure and breeding area arrival dates.

Wintering and Breeding: We identified wintering areas using the first point of migration as the first of three consecutive movements >30 km that led to an eventual crossing to the breeding area (Soriano-Redondo et al. 2020). We ascribed all points before the first point of migration as wintering. This method produced consistent results regardless of duty cycle. To identify breeding areas for avocets, we ascribed any terminal location in migration that the bird arrived at after 15 May and remained until mid-June or when the device stopped transmitting as breeding. This was based on the arrival times for individuals with complete migration tracks and individuals with identifiable breeding locations. We did this because the broad breeding range of avocets did not allow for a latitudinal cutoff and we had incomplete data for the breeding season for many birds. For plovers, we used the 50% Kernel Density Estimate (KDE) of all points for each individual above 65 degrees N (following methods in Chapter 1) because all breeding plovers in our dataset bred above this latitude (Chapter 1). For godwits, we used the 50% KDE for points collected between 10 May and 5 June each year to correspond with their typical arrival times to breeding areas in Alaska (Senner 2012). The last point before entering the identified breeding area was ascribed as the last point of migration.

Stopovers: To identify stopovers, we first used the "distance" function in the move package (Kranstauber et al. 2020) in Program R (R Core Team 2021) to calculate distance between consecutive points for each bird. Then, we identified stopover sites based on a distance threshold from the previous point (Exo et al. 2019). A threshold of 30 km was chosen based on the distribution of step lengths between points and visual inspection of point clusters. After identifying whether or not each point was <30 km from the subsequent point, we used run length encoding to identify clusters. To identify stopover sites, we applied the following criteria for 2-hour duty cycles: (1) 3 or more consecutive points within 30 km of one another, or, at least 6 hours within the area, and (2) not within wintering or breeding areas. If there was only one point separating two stopovers or two stopovers overlapped in space, we ascribed them as the same stopover. We chose to classify short stopping periods as stopovers because birds may stop over for a variety of purposes that may influence their decision-making and fitness (Linscott & Senner 2021, Rakhimberdiev et al. 2016), and our high data resolution allowed us to identify stopover events that would not be detectable with less data. For our 24-hour duty cycles, we identified stopovers similarly, but did not apply a time threshold, so stopovers were identified based on a threshold of 30 km and allowed a stopover to be any instance of one or more points within 30 km of the next. Each stopover site was assigned a unique label. For both 2-hour and 24-hour duty cycles, if the first point of the stopover was >2 km from the second point, it was eliminated from the stopover, and if the first migration point following the last stopover point was <10 km from the last stopover point, it was included in the stopover. This was to avoid having points that were still flight or a stopover being classified incorrectly at the beginning or end of a stopover due to the rule set. The 2 and 10 km thresholds were based on visual inspection of all stopovers.

Migration Metrics: We calculated total migration distance by subsetting locations from 2-hour duty cycles to once per day, and for both 2-hour and 24-hour duty cycles, we used the sum of daily displacements (including stopover points) between the beginning and end of migration. Number of stopovers was the total number of stopovers identified for each bird. Migration duration was the time in days between the first and last point in migration. Proportion of time in stopover was the total time spent in stopover divided by the total time spent in migration. Departure and arrival dates were the ordinal dates on which birds departed wintering and arrived in breeding areas. Mean stopover duration for each bird was the mean of the time in hours spent at stopovers.

Comparing migration strategies

For the 2-hour duty cycles, we used a one-way ANOVA test to quantify differences among species in each migration metric and Bonferroni-adjusted pairwise t-tests to identify which species were significantly different from one another within each metric. All tests were run in Program R (R Core Team 2021). For the 24-hour duty cycles, we did not conduct an ANOVA test or pairwise t-tests due to the small sample size of godwits, but we summarized the results of migration metrics.

Testing the effects of reducing data

Because we had different duty cycles which made results between different groups of individuals less comparable, we used a modified version of the stopover protocol previously described and performed a data reduction test on our 2-hour duty cycle tags to examine variation among species and migration metrics when less frequent GPS location information was included. We used only data with complete migrations and no substantial gaps of time, as described above. We subset the same avocet, plover, and godwit data sets from a 2-hour duty cycle to a 4-hour, 8-hour and 24-hour duty cycle (i.e., 12, 6, 3, and 1 location per day, respectively) using the move package (Kranstauber et al. 2020).

Then, we ran a modified version of the stopover analysis on the same devices subset to three additional duty cycles. We used a 30 km distance threshold for all subset duty cycles. We did not set a minimum time threshold or combine stopovers based on location overlap or having only one point between them, which caused differences in migration metrics between the same individuals in the 12 point per day duty cycle for the comparison of migration strategies and this data reduction test. We simplified the rule set for this analysis because we aimed to compare how stopover metrics would change using a basic rule set that could apply across duty cycles rather than make the rule set as ecologically specific as possible as we did when making calculations to compare migration strategies. We calculated number of stopovers, migration duration, and proportion of time in stopover, as described above, for each subset data set.

Results

We used 62 partial and full migrations of avocets (*n*=20), plovers (*n*=28), and godwits (*n*=14) to map migration routes of the three species (Figure 3.2). Out of the birds which collected data through the spring and summer, two avocets remained in southern Texas and eight godwits did not migrate and instead spent the austral winter in Argentina. We used 45 full migrations with 2-hour duty cycles and complete data to characterize and compare migration strategies. We also present results for migration duration and departure and arrival dates from devices with 24-hour duty cycles and complete data, but due to small sample size (12; 8 plovers and 4 godwits) we did not use these to compare migration strategies.

Comparing migration strategies

Mean migration distance was significantly different among species (P=0.001 for one-way ANOVA, and P<0.001 for all pairwise t-test combinations; Table 3.2) 2234.65 km ± SD 450.37 for avocets, 5807.75 km ± SD 900.39 for plovers, and 13324.63 km ± SD 1219.25 for godwits (Figure 3.3a). Mean number of stopovers was lowest (4.92 ± SD 1.97) for avocets, intermediate (6.13 ± SD 1.73) for plovers and highest (8.42 ± SD 4.39) for godwits. A one-way ANOVA (P=0.01; Table 3.2) indicated that there were significant differences in number of stopovers across species. Godwits differed from avocets in number of stopovers (P<0.001 Figure 3.3b). Mean migration duration differed between species (19.57 days ± SD 15.16 for avocets, 22.79 days ± SD 4.12 for plovers, and 35.42 days ± SD 6.19 for godwits; P=0.002, Figure 3.3c, Table 3.2). Godwits had a significantly longer migration duration than avocets (P < 0.001) and plovers (P = 0.01). Mean proportion of time in stopover was 0.59 ± SD 0.25 for avocets, 0.68 ± SD 0.12 for plovers, and 0.46 ± SD 0.14 for godwits and there were significant differences (P=0.49, Fig 3.3e, Table 3.2) only in that plovers spend a significantly higher proportion of time in stopover than godwits (P=0.02). Differences in mean departure day from wintering areas were present according to a one-way ANOVA (P<0.001, Figure 3.4b, Table 3.2): 20 April for avocets (ordinal day 110.28 ± SD 14.93), 16 May for plovers (day 136.54 ± SD 3.95), and 10 April for godwits (day 100.85 ± SD 5.61). Departure day for avocets was significantly earlier for godwits than for both avocets (P<0.001) and plovers (P<0.001), as well as earlier for avocets than plovers (*P*<0.001). Mean arrival day on breeding areas also differed between species (*P*<0.001, Figure 3.4c, Table 3.2, with avocets arriving earliest (day 129.86 ± SD 11.50, approximately 9 May), followed by godwits (136.29 ± SD 7.61 approximately 16 May), and finally plovers (159.33 ± SD 4.24, approximately 8 June). Plovers had significantly later arrival dates than both avocets (*P*<0.001) and godwits (*P*<0.001), but avocets and godwits were not different (*P*=0.23). Mean stopover duration was 52.03 hours ± SD 46.3 for avocets, 66.01 hours ± SD 28.05 for plovers, and 56.75 hours ± SD 33.31 for godwits. However, mean stopover duration was not significantly different among any of the three species (*P*=0.49; Figure 3.3e, Table 3.2).

In general, we saw the most variation in migration metrics within avocets, indicating that their short migration allows individuals the greatest plasticity in migration strategy. Plovers and godwits, with medium and long migrations, showed less variation within metrics, indicating less plasticity.

Testing the effects of reducing data

With the modified stopover rule set using the same data (expected to yield different values for metrics using 2-hour duty cycles than the analysis above), the number of stopovers remained consistent for avocets for the 2 (7.75 ± SD 3.5), 4 (7.08 ± SD 3.03), and 8 (6.9 ± SD 3.90) -hour duty cycles, and was lower with the 24-hour duty cycle (2.91 SD 2.71). However, the number of stopovers for plovers and godwits steadily declined as fewer points were collected per day (Figure 3.5). For plovers a mean of 10.7 ± SD 3.07 stopovers were ascribed using a 2-hour duty cycle, but only 2.4 ± SD 0.78 with the 24-hour duty cycle. For godwits a mean of 13.7 ± SD 7.04 stopovers were ascribed using a

2-hour duty cycle but only 4.7 ± SD 1.50 with the 24-hour duty cycle (Figure 3.5). Migration duration changed very little with reduced data (Figure 3.6). Proportion of time in a stopover was reduced with less than 6 points per day for avocets, but was fairly consistent for plovers and godwits (Figure 3.7).

Migration duration for birds with 24-hour duty cycles

Based on findings from testing the effects of reduced data, we chose to present only migration duration and departure/arrival information from our devices with 24-hour duty cycles. The sample sizes for these devices were 8 plovers and 4 godwits. Mean migration duration was 23.13 ± SD 7.95 for plovers and 30.5 ± SD 7.55 for godwits. Mean departure day from wintering areas was 133.38 ± SD 5.58 (approximately 13 May) for plovers and 110.5 ± SD 20.94 (approximately 20 April) for godwits; and mean arrival day to breeding areas was 156.50 ± SD 7.03 (approximately 5 June) for plovers and 141.00 ± SD 14.09 (approximately 21 May) for godwits (Figure 3.8).

Discussion

We compared migration strategies among American avocets, black-bellied plovers, and Hudsonian godwits, which were chosen for their short, medium, and long migration distances. On the spectrum of time-minimizing to energy minimizing, avocets were generally energy minimizing with many short stopovers (or occasionally, very short migrations), plovers were time-minimizing, and godwits departing wintering areas with a time minimizing strategy for the oceanic part of their migration but switched to a more energy-minimizing strategy with more stops after they reached North America. We found a substantial difference between at least one pair of species in every migration metric we tested except mean stopover duration. We found that the effect of data reduction on estimates of migration metrics varied among species and metrics. Migration duration and proportion of time in stopovers can be consistently estimated with very little data (e.g., one GPS position per day), but the number of stopovers was strongly influenced by frequency of location information.

Migration Strategies and Patterns

Our results augment previous knowledge of migration routes for our three focal species. Our study was the first to track avocets captured on the Gulf Coast, and the first to track black-bellied plovers captured in Louisiana. For avocets, little has been known about their specific routes, but our data showed that they stopover and pass through areas farther east of their breeding range than commonly thought (Ackerman et al. 2020). Our results also add to knowledge of migration routes for black-bellied plovers in mid-continent North America and contribute to previous studies of Hudsonian godwit migration (e.g., Senner et al. 2014, Linscott et al. 2022). As expected, some godwits did not migrate and spent the austral winter in Argentina instead of migrating to the Northern Hemisphere to breed (Navedo & Ruiz 2020). Avocets are known to breed in the Texas coastal bend (Rappole & Blacklock 1985), and some of our birds remained there though the breeding season, suggesting that avocets exhibit a partial migration strategy in this area (Chapman et al. 2011).

We expected that godwits would have the most constrained migration strategy (i.e., least variation in migration metric values among individuals), plovers would be intermediately constrained, and avocets would be the least constrained based on migration distance (Zhao et al. 2017). However, inconsistent with our predictions, we did not find this pattern across all 3 species. For avocets, with a broad latitudinal breeding range and relatively short migration, it appears that many migration strategies are used. Longer migrations, although strategies may be more constrained, allow more space and time for variation in migration metrics to be introduced by factors such as poor weather conditions (e.g., Briedis et al. 2017) or sub-optimal stopover conditions (e.g., Herbert et al. 2022). This could explain why in many metrics, godwits showed more within-species variation than plovers even though we expected the long migrations of godwits to make them the most constrained. Because godwits are migrating over more space and time, there may be more opportunity for climate and land use effects on migration metrics to accumulate and cause variability among individuals.

Although there were not significant differences in stopover duration among the three species, plovers had the highest mean stopover duration and individuals tended to consistently make an extended stop in southern Saskatchewan (Figure 3.2). Semipalmated sandpipers (*Calidris pusilla*), which are also known to follow a time-minimizing migration strategy, have a longer stopover duration at high-quality stopover sites than lower-quality sites (Herbert et al. 2022), so the stopover sites in southern Saskatchewan could be indicative of high-quality areas for plovers. However, for comparing and applying our results to other species, it is important to note that larger-bodied shorebirds are more likely to have time-minimizing strategies in spring and fall (Zhao et al. 2017), and our focal species are all relatively large shorebird species. Smaller species with similar migration distances and morphology may have to stop more often or have otherwise different strategies.

Continuing climate and land use change may further constrain migration strategies for all three species we studied. Plovers and godwits travel through and stop over in the Prairie Pothole Region (PPR), and avocets stop over and breed there. Wetlands in the PPR are dynamic and expected to become more unpredictable and less productive as climate change advances (Rashford et al. 2016), so habitat may be reduced in quality, quantity, or both, and these effects will be variable across the PPR (Johnson et al. 2005). Additionally, drier conditions are expected to shift shorebird stopover distributions northward and toward more permanent wetlands, while wetter conditions are expected to bring a more southern distribution in temporary wetlands within the PPR (Steen et al. 2018). Fluctuations in temperature and precipitation are expected to increase with climate change so their effects could be variable (Niemuth et al. 2010). Reduced habitat quality could increase the length of time required to refuel, and therefore increase migration duration. In addition, the breeding range for avocets has contracted substantially over time due to loss of habitat in the eastern United States and overhunting (Ackerman et al. 2020), so wetland loss in the PPR could further contract their range. Although the PPR is only a small part of the path from Chile to Alaska, many of their stopovers occur there, in addition to most stopovers by plovers (Figure 3.2). In the future, changes in wetland availability and productivity in the PPR could alter their migration strategies and negatively influence their survival and reproductive success (Johnson et al. 2005, Steen et al. 2018).

Given that plovers and godwits seem the most constrained in migration strategy (i.e., metrics were most consistent across individuals in their migration strategy) they could be at risk if key stopover areas are degraded or destroyed (Studds et al. 2017) or if change occurs at different rates at different parts of the annual cycle (Both & Visser 2001). Although avocets appear to have the most flexible migration strategy, plovers and godwits have more flexible feeding strategies (Poole et al. 2020, Walker et al. 2020), so studies focused on an array of life-history characteristics such as foraging strategy, habitat associations, and social behavior would provide a more holistic picture of the likely effects of global change on species with different migration strategies.

Considerations for Data Quality

We are confident that our 24-hour duty cycle devices captured migration duration and proportion of time in stopover precisely for all species, given we found no substantial change in those estimates when reducing location information from 2-hr intervals to 24-hr intervals.. However, reduced location information did lead to missing short stopovers which could be ecologically important for functions such as rest and information exchange (Linscott & Senner 2021, Schmaljohann et al. 2022). For avocets, number of estimated stopovers did not increase from using 1 location per day to using 3 or more locations per day. This may be because many avocet stopovers were long enough to be detected with few locations. However, for plovers and godwits, the number of stopovers detected steadily increased with the number of points per day, showing that their stopovers are of various lengths and more data allows detection of more stopovers. Their long migrations also allow more space and time over which birds can choose to stopover, and short stopovers may be missed with less frequent data. We suggest that if research objectives require an understanding of stopover location or behavior, practitioners should program devices to a frequent duty cycle (e.g., 3+ locations per day), but can use less frequent duty cycles (e.g., 1 location per day) if understanding migratory routes or phenology are of greater interest.

Device effects on birds can be a significant issue in avian movement ecology (Bodey et al. 2018, Brlík et al. 2020, Whidden et al. 2007), so we encourage consideration of deployment outcomes when planning studies. We deployed 136 devices in the winter and spring with the intention of collecting data through the summer. Out of our 136 deployments, 67 (49%) resulted in complete data through the summer with no substantial time gaps, including avocets and godwits that did not migrate. Deployment success differed by species and device type. For avocets, 43% of deployments yielded complete data. We encountered device failure for most devices in the first year of the study due to memory and battery problems. We know that there were at least 2 cases of mortality or dropped devices, in one case it appears the bird was depredated based on location and ACC data, but that nearly all avocet deployments were successful for at least 3 months. Unfortunately, the fate of many devices is unknown because data can only be acquired if the device has stayed on the bird and maintained sufficient battery and memory capacity to upload when the bird returns to GSM coverage. For plovers, the success rate was 70%. We observed four cases in which the bird died or dropped the device during migration. The remaining device failures occurred in the solar devices before the start of migration. Our banded plovers were resighted on several occasions without tracking devices in Texas (J. Loghry, personal observation) and Louisiana (S.

Clements, personal observation) and these may have been individuals that dropped their devices early or after summer. All deployments of fixed-battery (Pinpoint Argos 75) devices yielded both spring and fall migration data. For godwits, success rate of deployments was 31%. At least 35% of devices fell off or failed within days or before birds left wintering areas, and the rest of the failures occurred during the migration or breeding seasons. Many of these birds were also later resighted and individually identified by field-readable flags (J. Linscott, unpublished data). Although we did not expect to acquire quality data from every device deployment, as a 48% failure rate has been reported across animal ecology (Hofman et al. 2019), more detailed evaluation of the causes of device failure and effects of devices on birds across species and device types is important and should be undertaken in future studies.

Conclusions

Shorebirds with different migration distances and life-history strategies will be vulnerable to climate and land use change in different ways in the years ahead, so it is important to characterize bird movement and behavior across species. Our results show that avocets, with a short migration distance, have high plasticity in migration strategy. Plovers and godwits had less variation within species, which we interpret means that their longer migrations follow a more constrained pattern. We assume that constrained migratory birds could be more susceptible to climate and land use change. Variability in strategy among birds with different migration distances highlights the need for community-level research and conservation efforts.

Tables

Table 3.1. Information about tracking devices used in this study. Pinpoint Argos 75 devices were deployed on black-bellied plovers (BBPL), Pinpoint Argos Solar S on BBPL and Hudsonian godwits (HUGO), Argos Solar PTT on HUGO, and Ornitrack-10 on American avocets (AMAV).

Device Name	Manufacturer	Mass (g)	Location Data	Data Upload	% Bird Body Mass		
					AMAV	BBPL	HUGO
Pinpoint Argos 75	Lotek	3.7	GPS	Argos	NA	1.70%	NA
Pinpoint Argos Solar S	Lotek	6.6	GPS	Argos	NA	3.00%	2.02%
Argos Solar PTT	Microwave	5.0	Argos Doppler Shift	Argos	NA	NA	1.53%
Ornitrack-10	Ornitela	10.0	GPS	GSM	2.70%	NA	NA

Table 3.2. Results of one-way ANOVA to identify differences in 7 migration metrics among three species, American avocets, Black-bellied plovers, and Hudsonian godwits.

	one-way ANOVA Results		
Migration Metric	P-Value	F-Value	DF
Migration Distance	<0.001	399.19	2
Number of Stopovers	0.012	4.96	2
Migration Duration	0.002	7.12	2
Proportion Time in Stopover	0.018	4.48	2
Mean Stopover Duration	0.496	0.71	2
Departure Time	<0.001	61.524	2
Arrival Time	<0.001	72.474	2

Figures

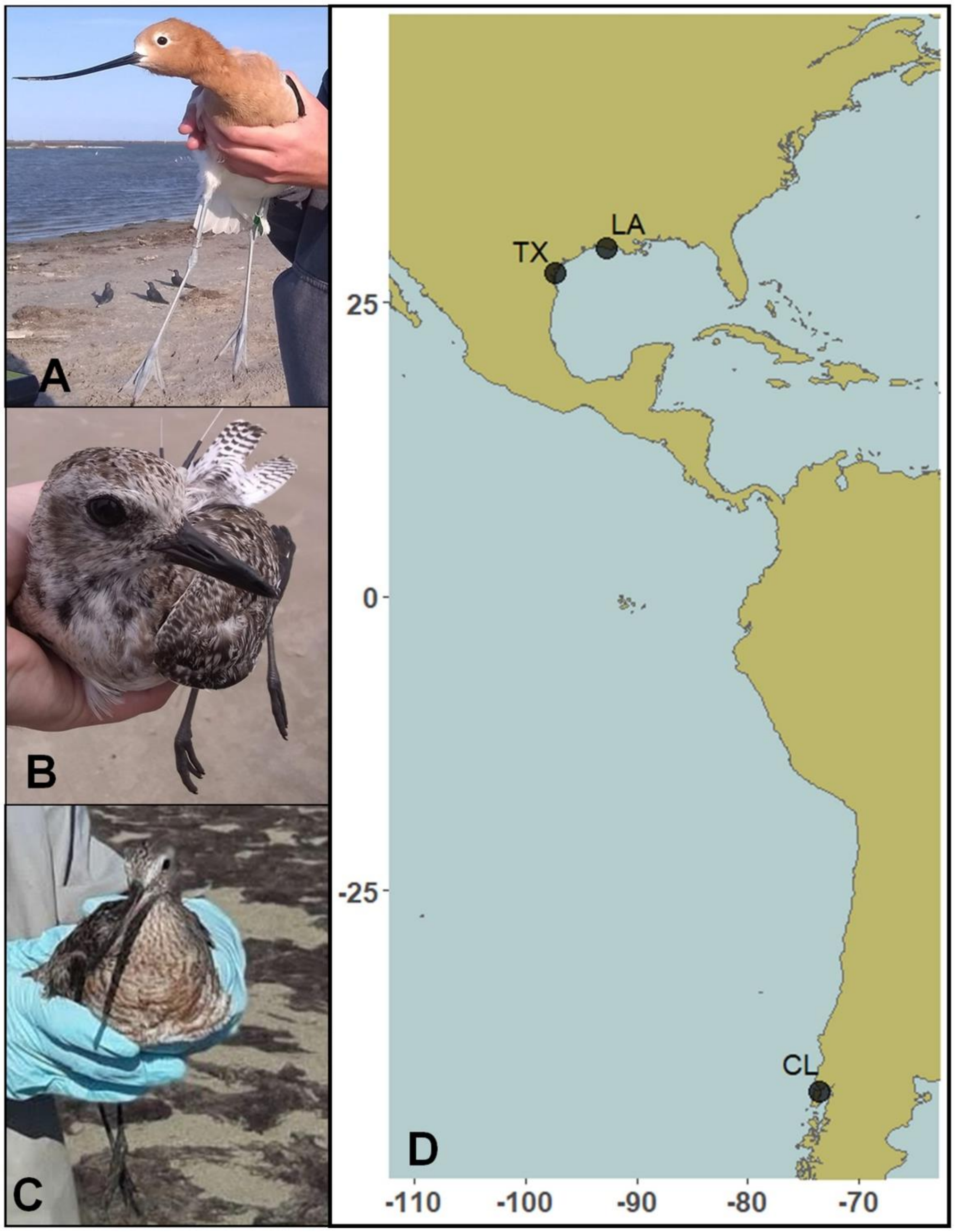

Figure 3.1. Pictures of an American avocet (A), black-bellied plover (B) and Hudsonian godwit (C), as well as a map of capture sites (D). Avocets and plovers were captured in Texas, USA (TX) and Louisiana, USA (LA), while godwits were captured in Chiloé, Chile (CL).

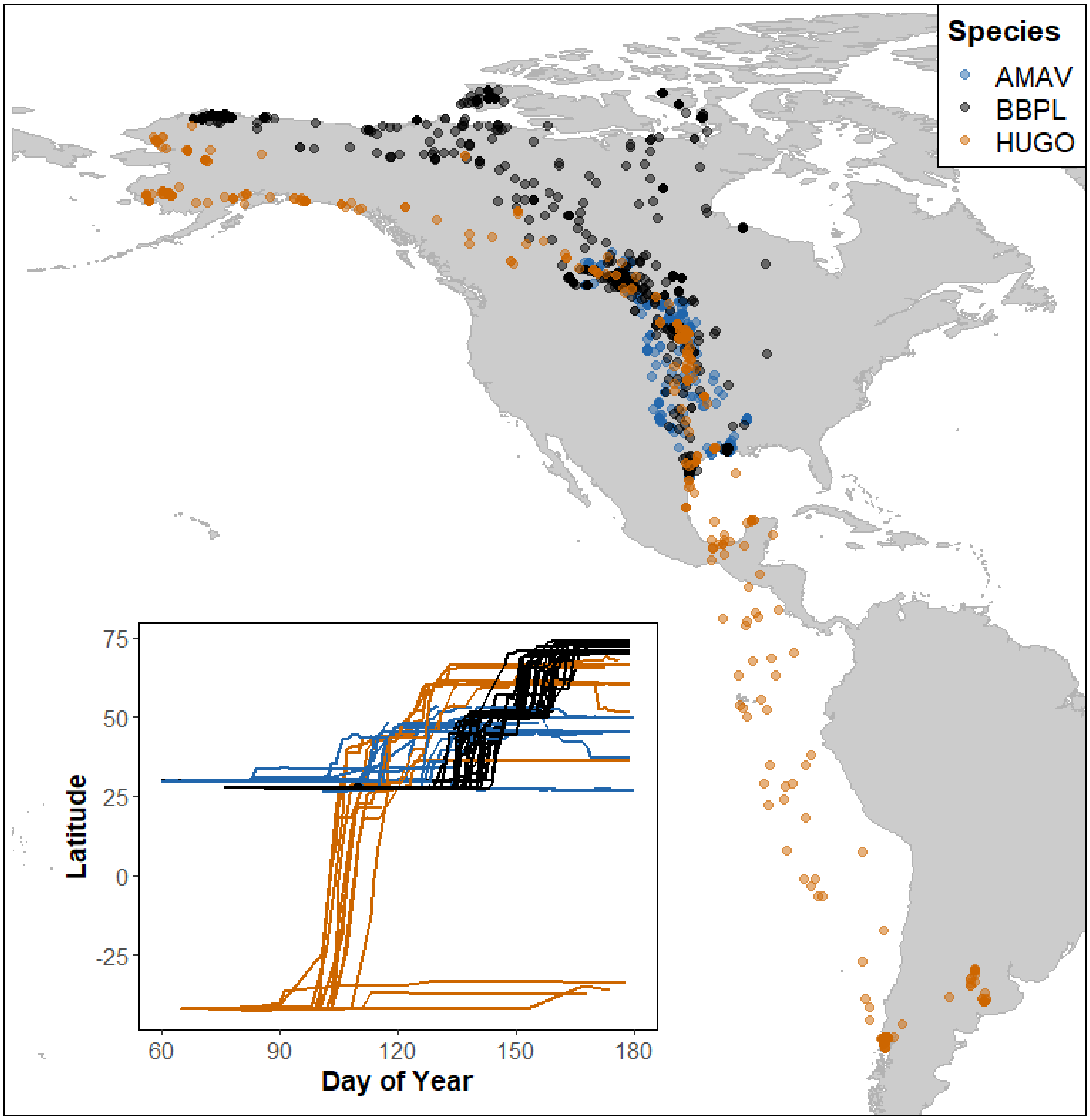

Figure 3.2. Map of daily locations between March and July 2019-2021 and inset plot of latitude by date for 62 American avocets (AMAV), black-bellied plovers (BBPL), and Hudsonian godwits (HUGO). In the map, each point represents the daily location of a bird, and in the inset plot, each line represents an individual bird.

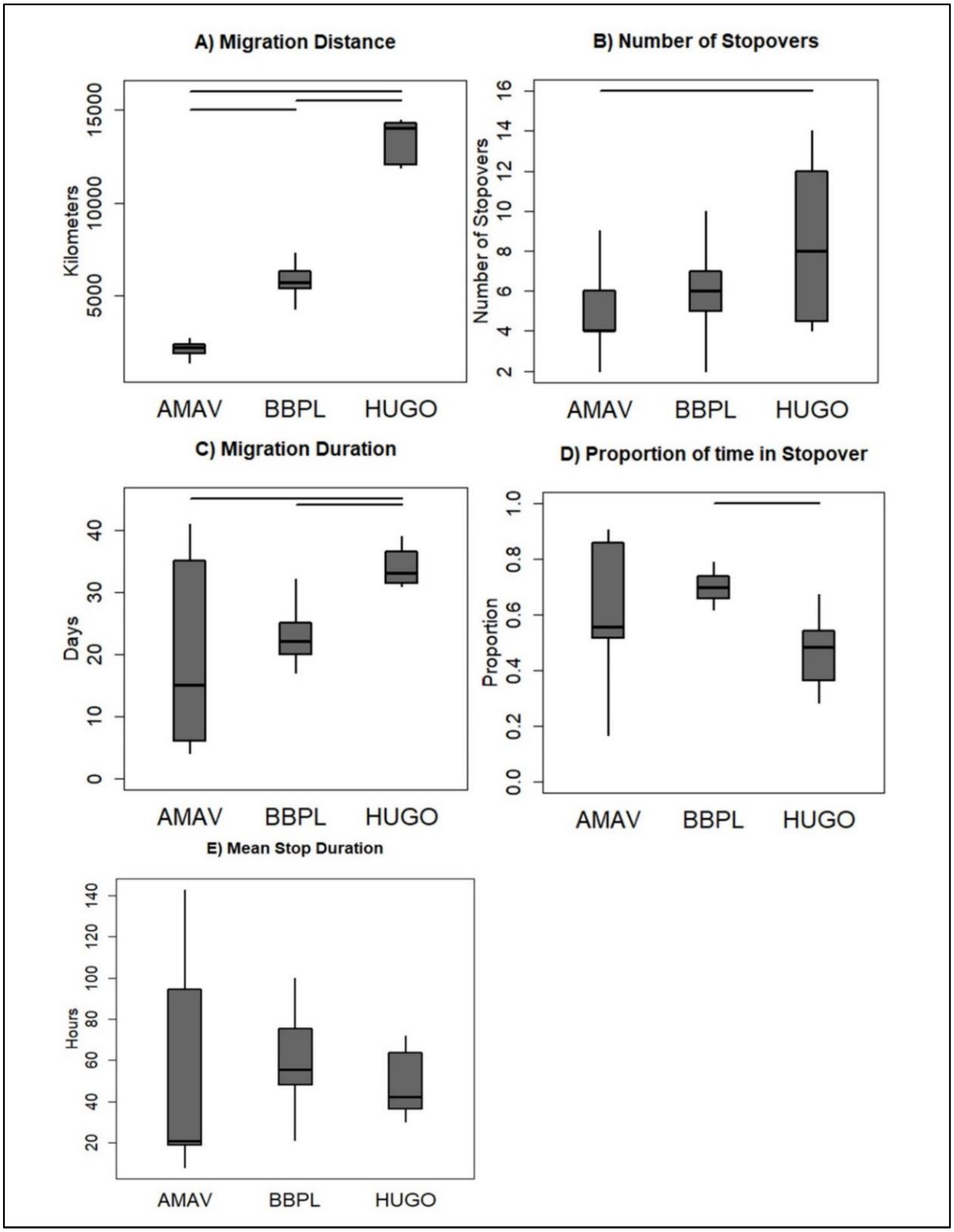

Figure 3.3. Boxplots of migration metrics summarized across all individuals of each species, American avocet (AMAV), black-bellied plover (BBPL), and Hudsonian godwit (HUGO). Bars between boxes indicate a significant difference between the species based on the results of pairwise t-tests.

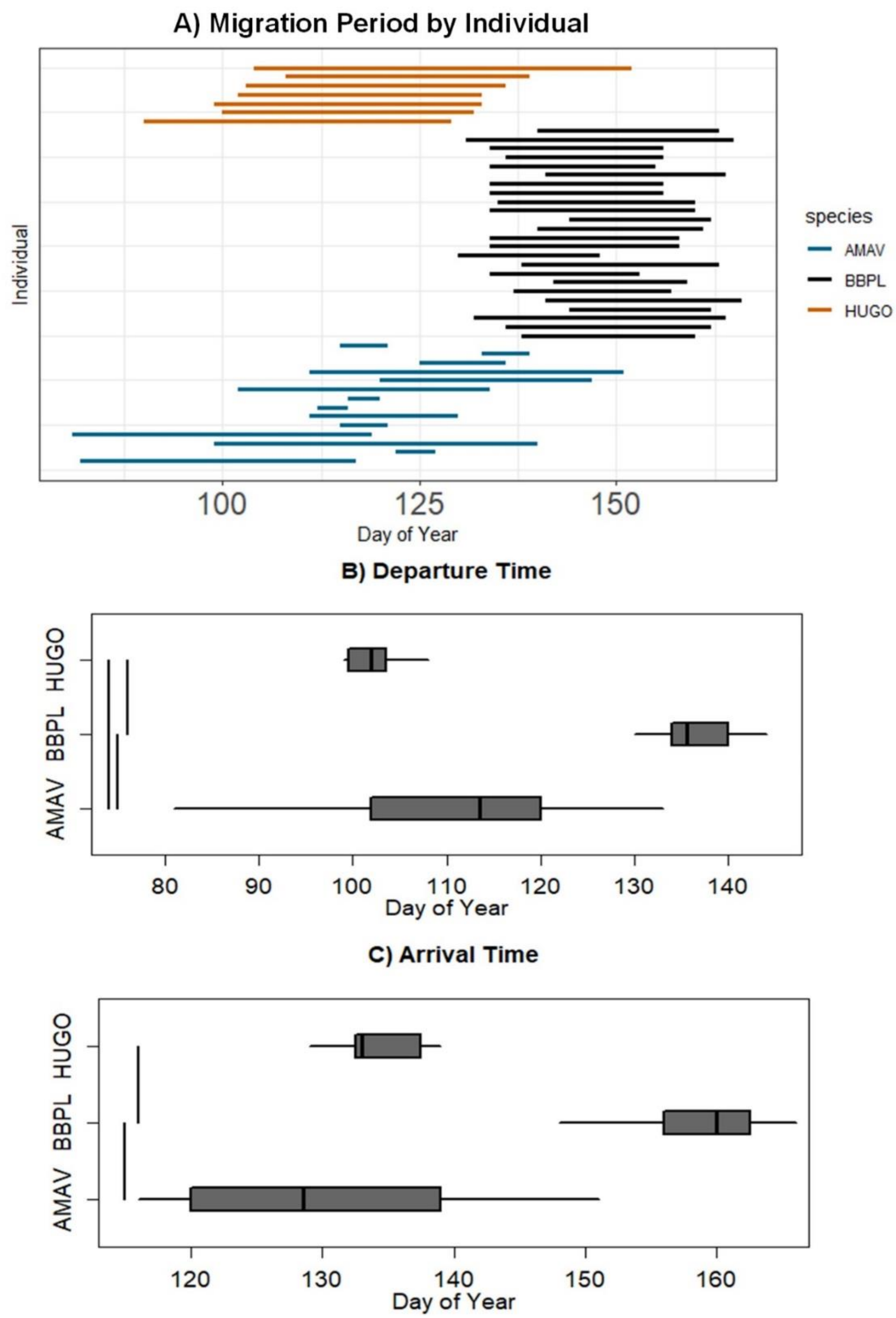

Figure 3.4. Migration period across day of year for each of 45 individuals with 2-hour duty cycles and complete migrations (A), in addition to boxplots summarizing departure and arrival dates across individuals within each species. Bars between boxplots indicate a significant difference between species based on the results of pairwise t-tests.

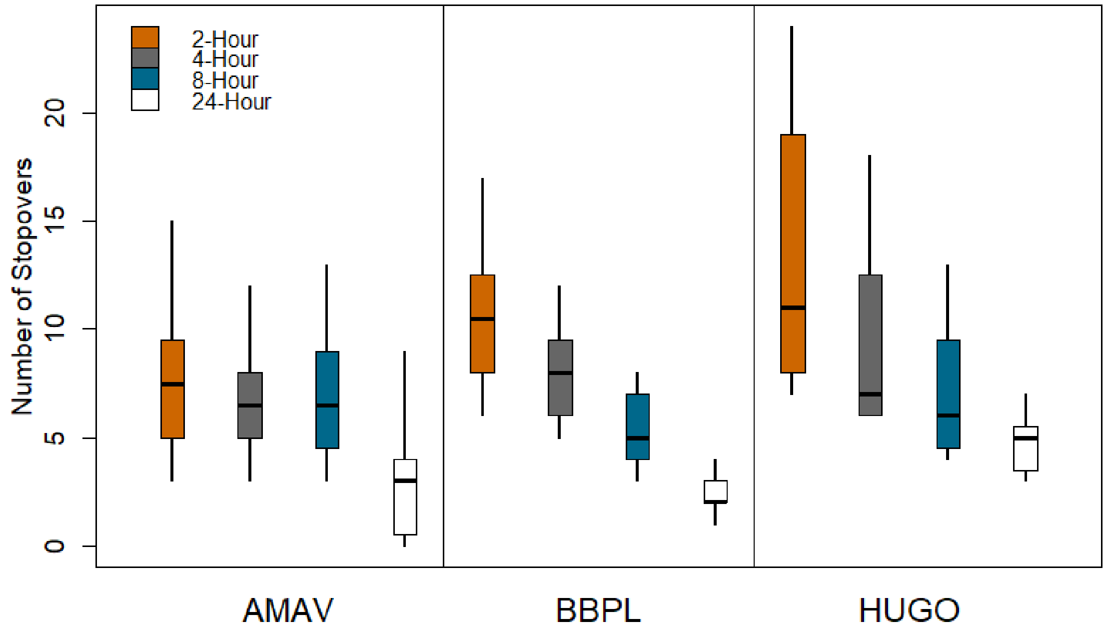

Figure 3.5. Number of stopovers identified using 2-, 4-, 8-, and 24-hour duty cycles subset from 2-hour duty cycle data. American avocets (AMAV), black-bellied plovers (BBPL), and Hudsonian godwits (HUGO) are separated by the vertical black lines.

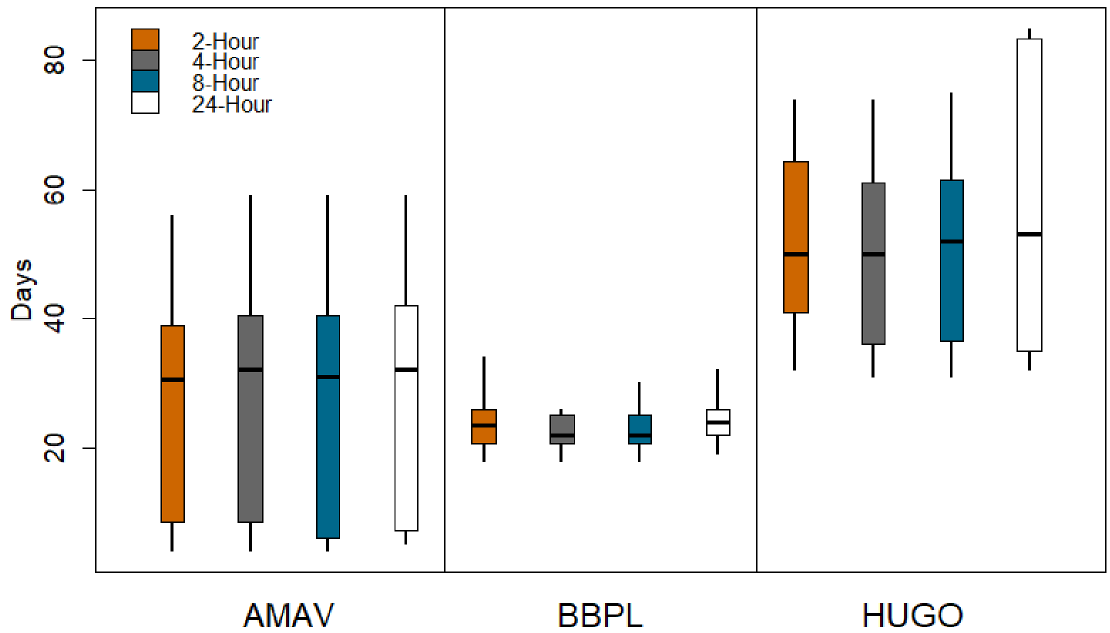

Figure 3.6. Migration duration calculated using 2-, 4-, 8-, and 24-hour duty cycles subset from 2-hour duty cycle data. American avocets (AMAV), black-bellied plovers (BBPL), and Hudsonian godwits (HUGO) are separated by the vertical black lines.

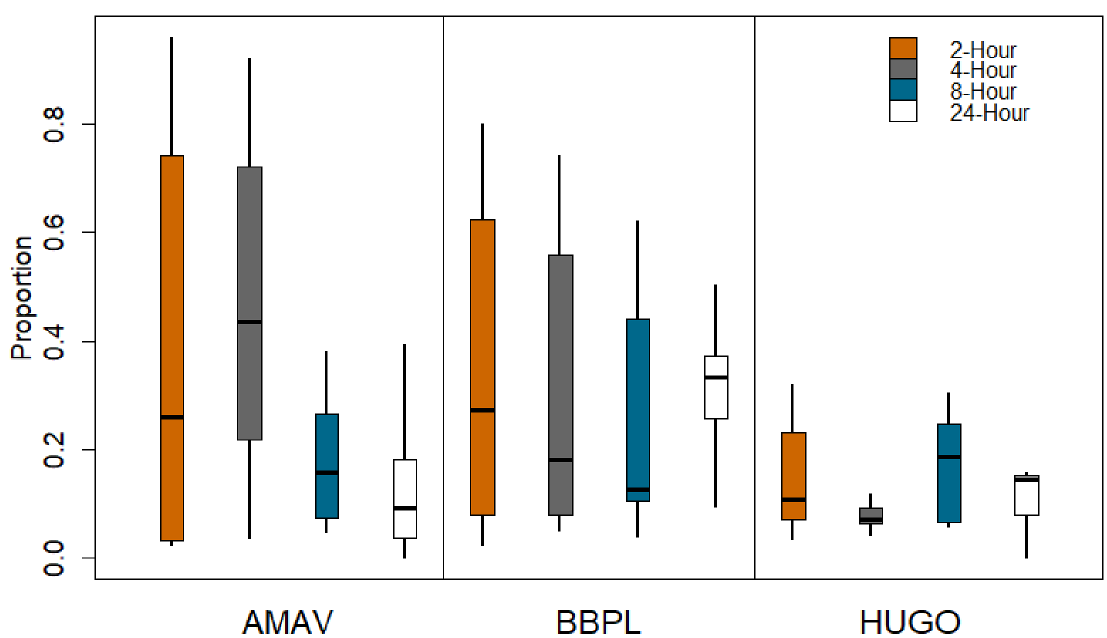

Figure 3.7. Proportion of time in stopover calculated using 2-, 4-, 8-, and 24-hour duty cycles subset from 2-hour duty cycle data. American avocets (AMAV), black-bellied plovers (BBPL), and Hudsonian godwits (HUGO) are separated by the vertical black lines.

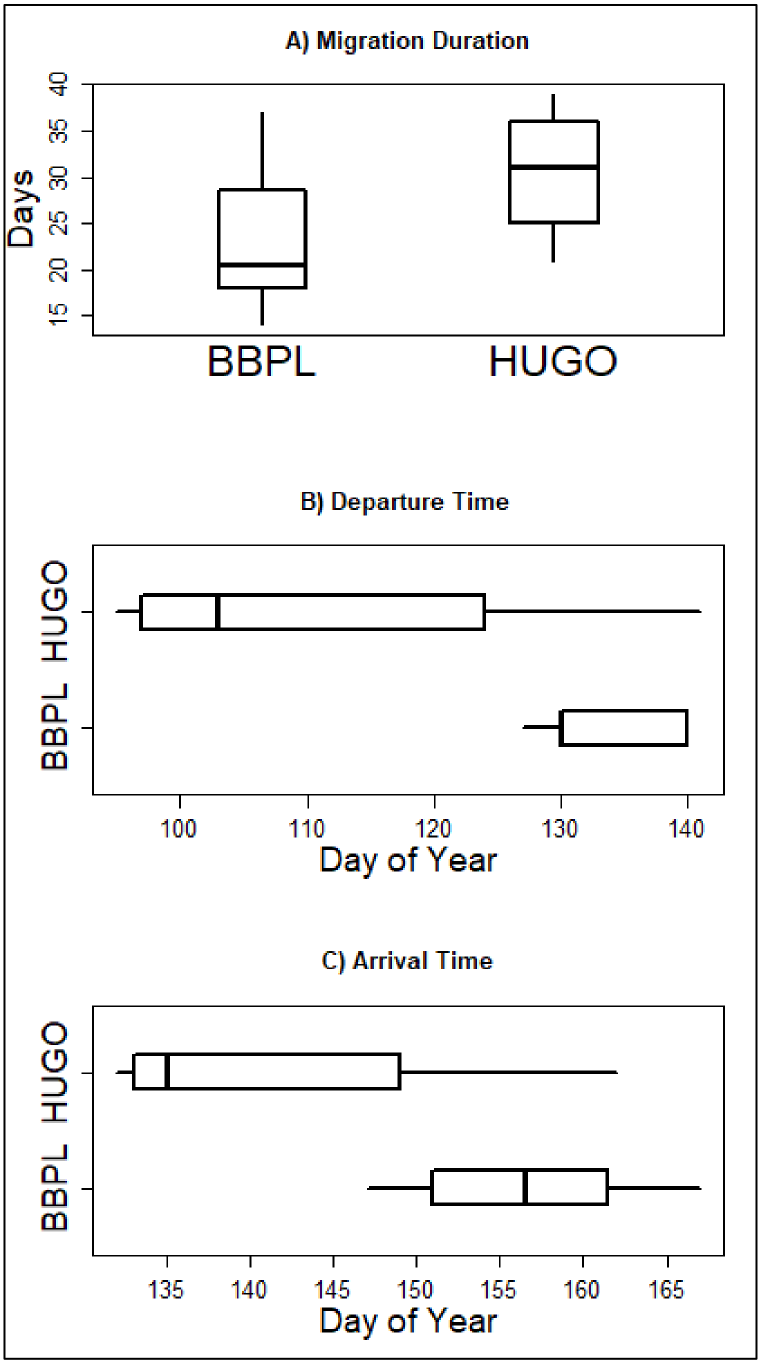

Figure 3.8. Results for migration metrics from devices with 24-hour duty cycles and complete migration data for black-bellied plovers (BBPL) and Hudsonian godwits (HUGO).

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CHAPTER 4

Trade-offs in performance of six lightweight automated tracking devices for birds

Abstract

Researchers should consider the costs and benefits of using tracking devices and choose devices that will optimize information gained with minimal effects on study organisms. With numerous technological advancements and devices marketed for avian research, selecting an optimal device and data collection interval (i.e., duty cycle) can be difficult. We evaluated six tracking device types from two manufacturers (Pinpoint 10 [1-g; Lotek], Pinpoint Argos 75 [4-g; Lotek], Pinpoint Argos Solar S [6-g; Lotek], Ornitrack-10 [10-g; Ornitela], Ornitrack-15 [15-g; Ornitela], Ornitrack-N35 [35-g; Ornitela]) and varied duty cycles to quantify (1) fix success rate for all units, (2) precision of location information for all units, and (3) battery voltage given the effects of duty cycle and reduced light for solar rechargeable units (Ornitrack-10, Ornitrack-15, Ornitrack-N35). Fix success rates for Pinpoint 10, Pinpoint Argos 75, Ornitrack-10, Ornitrack-15 and Ornitrack-N35 units were overall >0.95. However, the Pinpoint Argos Solar S units had a lower fix success rate that varied with duty cycle intensity. The Pinpoint Argos 75, Pinpoint Argos Solar S, and Ornitrack-10 units were more precise (≥99% points were collected within 20 m of one another) than the Pinpoint 10, Ornitrack-15, and Ornitrack-N35 units (>80% of points collected within 20 m of one another). For all devices, batteries maintained a high charge (i.e., battery lost during the dark hours was recovered or mostly recovered during the day) under high and intermediate light levels, and low and intermediate duty cycles. Light explained more variation in battery voltage than duty

cycle. We encourage investigators to evaluate devices prior to deployment on wild birds to maximize data quality relative to their research questions.

Introduction

Tracking technologies have many applications and provide opportunities to answer questions in basic and applied ecology (Wilmers et al. 2015, Williams et al. 2021). Detailed tracking of animal movements has allowed researchers to quantify habitat selection (Broman et al. 2014, Anderson et al. 2019), migration (Hays et al. 2014), foraging behavior (Dreelin et al. 2018, Campbell et al. 2019) and demographic rates (Benson et al. 2018). Because many research objectives require tracking wildlife, and researchers strive to minimize negative effects of devices on animals, there is strong incentive to develop smaller devices with greater capacity to collect data, particularly for birds (Kays et al. 2015; López-López 2016). Recent advancements in smaller and lighter tracking devices have provided more opportunities for use by bird researchers (e.g., Shipley et al. 2018). The frequency of published studies using tracking devices on birds has increased substantially, by an average of 16.7% per year between 1990 and 2015 (López-López 2016). With rapid developments in bird tracking, understanding the capabilities of available devices and factors affecting their performance is critical.

Investigators designing studies should consider the capacity to obtain quality data relative to the potential negative impact associated with using markers or tracking devices on animals (Murray and Fuller 2000). Although some studies have revealed negligible effects of tracking devices on birds (Naef-Daenzer et al. 2001, Therrien et al. 2012), tracking devices are likely to affect behavior in some way with potential downstream effects on fitness. Numerous studies have shown that tracking devices have small, but significant, negative effects on birds in terms of reproductive success, survival, or behavior (Barron et al. 2010, Costantini and Møller 2013, Bodey et al. 2018, Brlík et al. 2020). For example, Severson et al. (2019) compared survival between Greater Sage Grouse (*Centrocerus urophasianus*) with lighter, neck collar design tracking devices and heavier, rump-mounted solar tracking devices. Their results showed that the heavier rump-mounted solar GPS tracking devices reduced survival compared to the lighter VHF neck-collar devices, suggesting that device weight and attachment position in addition to the presence of solar panels influenced survival. Whidden et al. (2007) observed that deployment of tracking devices on adult Tufted Puffins (*Fratercula cirrhata*) significantly affected chick growth rate and fledging success and ultimately decreased productivity. High rates of device failure and low recapture rates along with the cost of tracking devices often lead to small sample sizes (Hebblewhite and Haydon 2010). Given the likely negative consequences of tracking devices, and that units often do not perform as well or for as long as expected (Matthews et al. 2013, Hofman et al. 2019), understanding the quality of data that can be acquired from tracking devices is critical for evaluating the costs and benefits of their use in the context of animal wellbeing.

An important step to optimizing study designs is evaluating the performance of tracking devices and the capacity of devices to collect the information necessary to meet research and conservation objectives. For automated tracking devices in particular (e.g., those that upload data via the satellite or Global System for Mobile communication [GSM] network), technology is developing rapidly, and independent tests of device performance are needed beyond those conducted by manufacturers. Understanding the attributes of devices such as fix success (whether the device successfully collects a GPS data point), precision, and battery capacity is important. Most evaluations of tracking devices have been restricted to those used for large mammals (e.g., Johnson et al. 2002, Di Orio et al. 2003, Graves and Waller 2006). More recently, smaller automated tracking devices for different animals have been tested, often to assess the environmental effects on device performance in the field, and have revealed effects of satellite availability and habitat conditions on device performance. For example, McMahon et al. (2017) tested the performance of two different Global Positioning System (GPS) device types designed for rabbits, first in a stationary position in the field and second on animals, and their results suggested that habitat features, such as burrows, and poor satellite geometry both negatively influenced the quality of data acquired from the devices. Byrne et al. (2017) tested the performance of GPS/GSM devices placed in a variety of stationary positions to emulate different bird behaviors and exposed devices to different conditions of cloud and forest cover. They also deployed units on Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*) and found environmental and behavioral effects on tracking device performance. However, testing the effects of species and habitat characteristics on device performance may not fully explore variation in the performance of the devices themselves. Surprisingly, there are few examples of tests comparing the performance of lightweight automated tracking devices designed for birds (e.g., Byrne et al. 2017). Testing lightweight bird-tracking devices with several different specifications in a standardized way will be useful for avian ecologists and biologists considering tracking-device options for optimal performance to answer specific research questions.

We evaluated the performance of six different lightweight satellite and GSM tracking devices with GPS or GPS-acceleration (ACC) capabilities designed for use on birds of various sizes, from songbirds to large waterfowl. Our objectives were to (1) measure fix success of different device types with different duty cycles (intervals of data collection), (2) evaluate spatial precision of locations collected among different device types, and (3) evaluate the effects of duty cycle (i.e., interval of data collection) and light level on battery voltage (for solar-rechargeable devices which record battery voltage). We predicted that across manufacturers, larger devices would have greater fix success and precision due to larger solar panels and batteries increasing the capacity for energy acquisition and storage over longer periods of time, and, therefore, data acquisition. In addition, we predicted that the effects of both light and duty cycle would explain significant variation in battery voltage, and effects would be greatest for smallest devices because of a reduced capacity to capture light and store energy given their smaller solar panels and batteries. We aimed to test tracking device performance under standardized conditions, absent of variation introduced by field conditions to explore the best-case scenarios for data collection by these tags under different duty cycles and shade conditions.

Methods

We tested six different tracking devices of different sizes and manufacturers, and with varying data transfer methods, all intended to be used on birds (Table 4.1). The Pinpoint 10 (n=9), Pinpoint Argos 75 (n=10), and Pinpoint Argos Solar S (n=4) devices were manufactured by Lotek (Newmarket, Ontario, Canada; lotek.com; note that although some of these devices upload data via the Argos satellite system, we used GPS, not Argos Doppler Shift, data for this study), and the Ornitrack-10 (n=9), Ornitrack-15 (n=9), and Ornitrack-N35 (n=6) devices were manufactured by Ornitela (Vilnius, Lithuania; ornitela.com). We were not able to acquire devices representative of all manufacturers, so only a subset of tracking devices available on the market were included in the study, however, the two manufacturers of devices we used allowed us to include variation in device mass, fixed or solar-rechargeable batteries, and data upload systems (Table 4.1). We were not able to acquire an equal number of devices of each type, so there was some variability in sample sizes among different device types (Table 4.1).

The Pinpoint 10 stored data to be manually downloaded, Pinpoint Argos 75 and Pinpoint Argos Solar S devices uploaded data via satellite connection for the initial test and we downloaded data manually for the other tests due to their frequent duty cycles and to avoid unnecessary data management fees. Ornitrack-10, Ornitrack-15, and Ornitrack-N35 devices uploaded data via the GSM network. The Pinpoint 10 and Pinpoint Argos 75 devices were fixed battery, whereas all other device types tested were solar-rechargeable. The Pinpoint 10 devices we tested were used for a study of Tree Swallows (*Tachycineta bicolor*; Elgin 2019), the Pinpoint Argos 75 and Pinpoint Argos Solar S devices were purchased for use on medium-sized and large shorebirds, and the Ornitrack-10, Ornitrack-15, and Ornitrack-N35 devices were purchased for use on large shorebirds, dabbling ducks, and geese, respectively.

We chose an experimental approach rather than analyzing data from wild birds to standardize the testing conditions and ensure that we were testing performance of the devices and not environmental or species characteristics. We attached devices to wooden stakes or boards to hold them in a fixed position parallel to the ground and kept them >5 m apart to prevent the devices from interfering with each another, as recommended by manufacturers. Devices were positioned the same distance from the ground and a variety of orientations. We used this study design to conduct all tests. All testing for precision, fix success, and battery response to light and duty cycle for all device types took place in an open field near Ricardo, Texas, in a flat area with GSM coverage that allowed daily data upload for GSM devices. Using this study area and design controlled for species, landscape, or environmental factors that could reduce device performance in a real-world study.

Before proceeding with tests of fix success rate, precision, and battery response to duty cycle and light, we first tested whether devices would function prior to using them in subsequent tests. As recommended by device manufacturers, for initial testing, we programmed devices to collect one GPS location (point) every two hours over the course of a 10-hour period, and allowed at least three opportunities for satellite or GSM upload for devices that required it. With the exception of the Pinpoint 10 devices, which had been deployed one to five times per device on Tree Swallows over a period of two days for each deployment, and re-charged after each deployment (Elgin 2019), devices had not been used prior to our initial trials. Deployments of the Pinpoint 10 devices were brief, and initial testing did not lead us to suspect that previous deployments affected device performance for this study.

Fix success rate. We assigned one to four devices of each type to one of three duty cycles of varying intensities relative to the size of the device (Table 4.2). The Pinpoint 10, Pinpoint Argos 75, and Pinpoint Argos Solar S devices collected GPS data only, and the Ornitrack-10, Ornitrack-15, and Ornitrack-N35 devices collected one ACC burst every 6 min for 3 sec at 10 Hz, in addition to the GPS points described in Table 4.2. Although we often set ACC sensor intervals specific to device size when deployed on wild birds, we did not vary ACC collection among devices or device types in an effort to focus tests of precision on GPS data, and duty cycle and light level on battery recharge. For Lotek devices, we used the manufacturer's estimate of battery life duration under different duty cycles for fixed-battery devices, and their estimates of the number of points that could be reasonably collected per day for solar-rechargeable devices (Tables A3.4 & A3.5). For Ornitela devices, we based the duty cycles on our ongoing research with these units on migratory birds. We designed three duty cycles for tests: (1) a conservative (low) duty cycle similar to what would be expected for use by practitioners, (2) an intermediate (medium) duty cycle to test device performance under a more intense, but also realistic duty cycle, and (3) an intense (high) duty cycle intended to push the devices to the anticipated limit. We chose duty cycles that overlapped among some device types for direct comparison (e.g., we tested the same duty cycles for both the Pinpoint Argos Solar S and Ornitrack-10 devices, with partial overlap for the Ornitrack-15 and Ornitrack-N35 devices; Table 4.2), but also wanted to test the devices at what we anticipated should be near their maximum capacity during the study period based on size and specification. We chose intense duty cycles to emulate how devices would perform when they had been deployed for an extended period of time and their capacity for performance may be reduced, as the time a device can collect quality data is a critical consideration in study design. For all duty cycles, we collected data for 18 consecutive days beginning in October 2019, manually downloaded data from the Lotek devices and accessed data for the Ornitela devices uploaded via GSM using the manufacturer's online user interface. We manually downloaded Lotek data to ensure we would obtain all data collected by the devices, as some of our duty cycles were expected to potentially outpace the rate of transmission though Argos satellites (see Table A3.4). We assessed fix success for all functional devices by calculating the number of points collected in proportion to the number expected given the duty cycle and duration of test. We summarized results by calculating the mean and 95% confidence interval (CI) of fix success rate across individual devices of each device model.

Precision. We estimated location precision by calculating the great circle distance between pairs of points using the fields package (Nychka et al. 2017) in Program R (R Core Team 2020). We chose to compare 18 randomly selected points collected by each device (or 36 for the Pinpoint Argos Solar S devices to increase sample size) during the duty cycle test. Eighteen was the minimum number of GPS points collected by our combinations of device type and duty cycle. All devices were tested for precision in the same location and time period. We determined the mean and 95% CI for the difference between each pairwise distance and the median pairwise distance for each device type (pooled across individual devices of each type) to quantify precision and calculated the proportion of pairs of points within 5, 10, 20, and 100 m of one another to show precision in scales that may be considered in questions related to bird habitat use and movement.

Effect of duty cycle and light on battery voltage. To evaluate device performance given variation in duty cycle and the amount of light reaching device solar panels, we programmed devices to different duty cycles, manually varied light conditions, and observed battery level. We ran this test only on the Ornitela devices (Ornitrack-10, Ornitrack-15, and Ornitrack-N35) because they were solar rechargeable and recorded battery voltage with each GPS fix. We excluded the Pinpoint Argos Solar S units because, although solar rechargeable, they did not provide information about battery voltage for us to evaluate their performance. We assessed battery performance using the same duty cycles as the previous test (with the exception of the Ornitrack-N35 devices where we only used the “Low” and “Medium” duty cycles to have more than one device in each duty cycle because we only had six Ornitrack-N35 devices). We applied three treatments: natural light (0% light reduction), 54% of available light (46% light reduction), and 18% of available light (82% light reduction). We applied the treatments by stretching and attaching one (46% light reduction) or two (82% light reduction) layers of shade cloth to a wooden frame about 7 cm above devices. We measured the amount of light in foot-candles (fc; lumens per square foot) the devices were exposed to every 30 min between 06:30 and 18:00 from 7 to 13 December 2019 using an Extech model 401025 light meter (Extech Instruments, Waltham, MA) to determine the percent of light available under each treatment. We calculated the amount of light available to each device at each 30-min interval based on the percent of available light and assumed 0 fc of light at times before sunrise and after sunset. This gave us a light measurement every half hour for each device over the study period and we were able to estimate light measurements under the shade treatments by multiplying the measured amount of natural light available by the percent light reduction from the shade cloth treatments. In our study area, the 7-day average of natural light intensity at 17:00 UTC (12:00 local time) was 774 fc. Light intensity varied by day, time of day, and shade treatment so, by adding treatments, we exposed devices to a wide range of light conditions that would be similar to different latitudes and weather conditions beyond our study area (Figure 4.1).

To evaluate the importance of light and duty cycle to battery level, we developed a regression that used the location obtained closest to sunset (23:00 UTC) by each device on each full day data were collected and the amount of light (fc) summed across all times data were collected (i.e., every 30 min between 11:30 and 23:00 UTC; 06:30 and 18:00 local time) along with duty cycle and time as a predictors of battery voltage. The cumulative light data were used to quantify how well devices were able to sustain their battery levels on days with different conditions of light and duty cycle, with light as a continuous variable. Our regression can be mathematically represented as $B_{ik} = \alpha + \beta_1 T_i + \beta_2 L_i + \beta_k D_i$, where we estimated battery level (B) on a logit scale as a function of time (T), summed light (L), and duty cycle (D; with levels k of duty cycle) with α as the intercept. We modeled Ornitrack-10, Ornitrack-15, and Ornitrack-N35 device types separately. Due to the small number of days over which the study took place, we also ran a second regression for each device type that included all data points collected as part of the study (as opposed to summarizing daily). In this case, we represented light as a categorical variable, but the increased number of observations allowed us to include interactions between light and time and duty cycle and time, and random effects for individual device. However, we found that results were similar (Tables A3.1-A3.3; Figure A3.1) so chose to present the simpler, more interpretable cumulative light models.

We ran models in JAGS (Plummer 2003), through Program R (R Core Team 2020) with the jagsUI package (Kellner 2015). For all models, we used vague priors and ran 3 chains for 5000 iterations, with a burn-in of 2000 iterations and thin of 5. Thus, our parameter estimates were each based on 1800 posterior samples. We monitored convergence based on R-hat <1.05 and visually inspected chains to ensure they were well-mixed for all three tracking device sizes (Brooks and Gelman 1998). To summarize results, we plotted posterior samples for the effect of light level on battery level as well as the effects of the medium and high duty cycles relative to the effect of the low duty cycle for each device type on battery level. We identified which predictors were significant based on whether 0 was within the 95% CI.

Results

Fix success rate. The mean fix success rates for Pinpoint 10 (mean [μ] = 1.00, 95% CI 0.99, 1.00), Pinpoint Argos 75 (μ = 0.96, 95% CI 0.99, 1.00), Ornitrack-10 (μ = 1.00, 95% CI 1.00, 1.00), Ornitrack-15 (μ = 1.01, 95% CI 0.99, 1.03) and Ornitrack-N35 (μ = 1.00, 95% CI 1.00, 1.00) were >0.95 (Table 4.3). Although most devices had consistent fix success rates across the three duty cycles, the fix success rate decreased as the intensity of the duty cycle increased for the Pinpoint Argos Solar S units (μ = 0.53, 95% CI 0.30, 0.76; Table 4.3).

Precision. We found variability in precision among device types, measured as the difference between each pairwise distance (m) and the median pairwise distance (Table 4.4). The Pinpoint Argos 75 (mean distance from median [μ] = 0.94, 95% CI 0.89, 0.98) and Pinpoint Argos Solar S (μ = 1.26, 95% CI 1.21, 1.31) units were the most precise devices, and 100% of pairs of points were <20 m from one another. For the Ornitrack-10 (μ = 2.65, 95% CI 4.17, 4.84) units, 98% of pairs were <20 m. The Ornitrack-N35 (μ = 6.01, 95% CI 5.49, 6.53) units had 89% of pairs <20 m. The Pinpoint 10 (μ = 7.83, 95%

CI 7.37, 8.29) and Ornitrack-15 (μ = 7.81, 95% CI 7.20, 8.43) units were the least precise, with 84% and 82% of pairs <20 m, respectively. All points across device types had 99-100% of pairs <100 m.

Effect of duty cycle and light on battery voltage. For all devices, batteries sustained a high level of charge (i.e. battery lost during the dark hours was recovered or mostly recovered during the day, resulting in no or negligible net loss of battery voltage from the beginning to end of the study and voltage at the highest point of each day remaining over 80%), except under the lowest light levels and most frequent duty cycle (Figure A3.2). For the cumulative light models, the 95% credible interval (CRI) for light did not overlap 0 for any tracking device size (Ornitrack-10 posterior mean [β] = 1.04, 95% CRI 0.72, 1.36; Ornitrack-15 β = 0.78, 95% CRI 0.51, 1.07; Ornitrack-N35 β = 0.69, 95% CRI 0.19, 1.08; Figure 4.2). For the Ornitrack-10 devices, both the medium and high duty cycles (med β = -0.62, 95% CRI -1.43, 0.19; high β = -0.48, 95% CRI -1.22, 0.20) had 95% CRIs overlapping 0, but there was still evidence of a duty cycle effect as 93% and 91% of posterior samples were <0 for the medium and high duty cycles, respectively. For the Ornitrack-15 devices, the medium duty cycle did not differ significantly from the low duty cycle, but the high duty cycle did differ (med β = -0.23, 95% CRI -0.99, 0.50, 73% of posteriors <0; high β = -0.78, 95% CRI -1.36, -0.12). For the Ornitrack-N35 devices, we found no evidence for a difference in effect between the low and medium duty cycles (med β = 0.23, 95% CRI -0.52, 1.01; 74% of posteriors >0). We ascribe an effect as significant when the 95% CRI of the posteriors does not overlap 0 (i.e., no effect). We see that for all three device types light had significant positive effects on battery, while the effects of duty cycle were not significant (Figure 4.2). Predictions of battery levels based on cumulative light, duty cycle, and time show that battery voltage expected across time and cumulative light level differed among duty cycles, but was expected to remain high through the duration of the study (Figure 4.3).

Discussion

Our results show that there are trade-offs among device models in their capacity to successfully obtain fixes given different duty cycles, collect precise data, and maintain battery charge under different duty cycles and light conditions when operating in a standardized environment. The larger devices were not more reliable, have higher fix rates, or produce better location precision. Instead, most devices, with the exception of the Pinpoint Argos Solar S units, had high fix success even when collecting frequent data so we would anticipate good performance from the device types included in our study, if outside factors such as satellite configuration, topography, or GSM coverage are ideal. Nearly all points collected by each device were within 20 m of each another, demonstrating that all device types showed good precision for most research objectives. The Pinpoint Argos 75, Pinpoint Argos Solar S, and Ornitrack-10 devices were the most precise, and studies where these tracking devices are used for larger species of birds may experience trade-offs, i.e., selecting a smaller device with greater precision vs. selecting a device with a large solar panel, battery, and memory capacity, but lower precision. As predicted, light had greater effects on battery voltage for the Ornitrack-10 devices than the Ornitrack-15 or Ornitrack-N35 devices in our study. Testing battery levels under different conditions of light and duty cycle revealed that devices were able to recover battery each day except under the lowest amounts of light (18% available light) and most intense duty cycles, and that light had a more significant effect on battery voltage than duty cycle. Based on studying the function of the devices in a controlled area in the absence of environmental, landscape, or species variation, we anticipate good performance in terms of fix success, precision, and battery voltage under a variety of duty cycle and light availability conditions. However, many factors independent of the device itself can be expected to affect device performance.

Our results should be used cautiously because we expect that units deployed on birds will not perform as well as they will under experimental conditions. We did not aim to replicate field conditions across a broad geographic range, but rather explore the performance of the devices themselves, controlling for external factors. We anticipate substantial variation in topography, tag orientation, light availability (i.e., foliage, day length), GSM coverage, and satellite geometry to be introduced by deploying devices on wild animals, which could affect data acquisition (Recio et al. 2011, Byrne et al. 2017). The strong fix success of most devices even at the most frequent duty cycle in our study was unexpected because we anticipated that they would not perform well with high-intensity duty cycles based on study designs for wild birds (e.g., Elgin 2019, Cunningham 2019) and manufacturer recommendations (Tables A3.4 & A3.5). However, more frequent duty cycles can be slightly more efficient, which may have been a factor in our study. Additionally, for all devices except the Pinpoint Argos Solar S, overall fix success was higher than the 78% overall fix success rate found in a meta-analysis of 167 studies including 16 different types of devices of various sizes (Hofman et al. 2019) and the 65.8% overall success rate from a meta-analysis of studies using collars of different types and sizes on mammals (Matthews et al. 2013). Higher fix success is expected in a controlled environment without animal mortality or imperfect device recovery. Our study area had no objects obstructing satellites for GPS data acquisition or restrictions on GSM data transfer, whereas, in studies of free-ranging animals, both of these restrictions may be present. The Pinpoint Argos Solar S devices did not collect all expected data at any duty cycle, but fix success at the lowest duty cycle (i.e., 12 points per day) was similar to that of many field studies (Hofman et al. 2019).

Here, we can speculate that differences in these devices may be partially due to device characteristics, but statistically testing the effects of device components on performance was outside the scope of this study so we cannot predict the attributes of devices driving variation in performance. Our results suggest that location estimates from some devices are generally less precise than location estimates from others. The Pinpoint 10 devices were the smallest we tested, and size of the components of the device may explain their lower precision (Hofman et al. 2019). The Ornitrack-15 and Ornitrack-N35 devices were less precise than the Ornitrack-10 devices, and this may be because the type of GPS module used to make the Ornitrack-10 devices was different than that used for the Ornitrack-15 and Ornitrack-N35 devices and was able to record more precise GPS locations (R. Zydelis [Ornitela], pers. comm.). For the Ornitela units, difference in precision appear to be a result of parts used for manufacturing, and this may explain variation across device types with different parts. All devices included in the precision test used GPS satellites to obtain locations, and were tested in the same location at the same time, so it is not likely that precision differences were the result of different satellite configurations. However, for most ecological questions, differences in precision among these devices should not be enough to substantially affect inference from the data.

Our categorical light model showed a significant positive effect of light on battery performance at all duty cycles and that, although duty cycle was not a significant predictor of battery level at the end of each day over the course of the study, our results suggest that battery performance will decline more with greater duty cycles with the same amount of light (Figs. 4.2 & 4.3). This may mean that some devices will not be able to fully recover battery voltage during the day that is lost during the night due to an intense duty cycle. Unlike the cumulative light model that showed significant effects of light, but not duty cycle, on battery performance, the categorical light model presented in the supplementary material showed that both light reduction and duty cycle often have a significant negative effect on battery voltage (Tables A3.1-A3.3, Figure A3.1). Most devices, regardless of device type and duty cycle, were able to recover their battery voltage even with a 46% reduction in light (Figure A3.2). As a result, even if shaded by vegetation, feathers, or a short daylength, the Ornitrack-10, Ornitrack-15, and Ornitrack-N35 devices that we tested should be able to collect at least 24 GPS points per day while maintaining a full battery level. However, if these devices will be exposed to low light conditions, we recommend that investigators reduce the duty cycle (some devices allow duty cycle to be reduced remotely, such as the Ornitela devices tested here) because device performance is likely to be reduced in practice compared with experimental conditions. Importantly, this test was conducted in an area with predictable GSM coverage and no obstructions to GPS signals such as buildings, mountains, or dense vegetation, so our study design did not test for battery depletion due to multiple failed GSM upload attempts or poor GPS signal strength. We recommend programing devices to a more conservative duty cycle than our results suggest if the extent of GSM coverage is unknown. Our results should also be interpreted cautiously due to the short time period and small sample size with which we ran the cumulative light models. Nonetheless, results from this test allow greater understanding about the capacity of these solar-rechargeable devices and our test demonstrates a framework for testing that could be used similarly on additional devices from other manufacturers.

Conclusion. We suggest that investigators select units based on project objectives, accepting a potential trade-off in duty cycle intensity and battery type (fixed or solar-rechargeable) and precision, given bird size and study location. Our results show that, in the case of the six device types we tested, there are trade-offs between device and types in their capacity to collect points frequently and/or precisely, and these should be considered in relation to bird size because the largest device that could be reasonably deployed on a bird may not always be the best choice. Understanding these trade-offs may be useful when evaluating which type of tracking device to use. For example, the Ornitrack-15 and Ornitrack-N35 devices performed well in the fix success and light reduction tests and thus, the Ornitrack-15 units could be used instead of the Ornitrack-N35 units. The Pinpoint Argos 75 and Pinpoint Argos Solar S devices were the most precise so could be selected if precision is important for a study or if the duration of the device lifespan is not a concern because larger devices and batteries can be expected to degrade more slowly. Our results also show that reduced light levels should not substantially affect the capacity of these devices to collect data under conditions with flat topography and good GSM coverage and moderate to conservative duty cycles. Although conclusions from this study are limited to two manufacturers and six device types, we recommend that more devices from different manufacturers also be tested in a similar framework. When investigators are interested in looking beyond the performance of the devices to determine how they are likely to function in specific study systems, we also recommend testing devices under conditions similar to those in which they will be used because light, landscape, and satellite conditions can cause differences in performance beyond what is due to the tracking device itself. Device manufacturers could make the results of similar tests available to purchasers, and a consistent series of tests among tracking device types for birds and other taxa would improve practitioner decision-making.

Tables

Table 4.1. Specifications of tracking devices: manufacturer, attachment type, mass, whether they are solar-rechargeable or fixed-battery, data transfer method (manual, in which the data must be downloaded directly from the device's memory storage; satellite, in which data are uploaded via satellite network to be downloaded by the user; GSM, in which data are uploaded via cell phone network to be downloaded by the user), data collected (GPS or GPS and ACC), sample size for fix success and precision tests (NFP), and sample sizes for tests of battery voltage (NB). For the two devices with satellites as a data transfer method, we downloaded data manually, but units deployed on wild birds would upload data via the satellite network.

Device	Manufacturer	Attachment	Weight (g)	Battery	Data transfer	Data	NFP	NB
Pinpoint 10	Lotek	Backpack	1	Fixed	Manual	GPS	9	NA
Pinpoint Argos 75	Lotek	Backpack	3.7	Fixed	Satellite	GPS	10	NA
Pinpoint Argos Solar S	Lotek	Backpack	6	Solar-rechargeable	Satellite	GPS	4	NA
Ornitrack-10	Ornitela	Backpack	10	Solar-rechargeable	GSM	GPS-ACC	9	9
Ornitrack-15	Ornitela	Backpack	15	Solar-rechargeable	GSM	GPS-ACC	9	9
Ornitrack-N35	Ornitela	Collar	35	Solar-rechargeable	GSM	GPS-ACC	6	6

Table 4.2. Number of locations collected per day (evenly spaced throughout the entire 24-hour period of each day) under different duty cycles used for the six device types in this test. Duty cycles were all used for 18 days for evaluating fix success rate and seven days for evaluating effects of light level and duty cycle on battery charge. For devices that collect ACC data (Ornitrack-10, Ornitrack-15, and Ornitrack-N35), duty cycles also included a 3-sec burst of ACC every 6 min at 10 Hz.

Device	Locations per day		
	"Low" Duty Cycle	"Medium" Duty Cycle	"High" Duty Cycle
Pinpoint 10	1	2	3
Pinpoint Argos 75	1	2	3
Pinpoint Argos Solar S	12	48	72
Ornitrack-10	12	48	72
Ornitrack-15	24	48	72
Ornitrack-N35	48	72	144

Table 4.3. Proportion of fixes successfully acquired out of fixes expected, averaged across all units within each duty cycle and device type.

	Fix Success			
Device	Overall	"Low" Duty Cycle	"Medium" Duty Cycle	"High" Duty Cycle
Pinpoint 10	1.00	1.00	1.00	0.99
Pinpoint Argos 75	0.96	1.00	1.00	0.91
Pinpoint Argos Solar S	0.53	0.87	0.46	0.39
Ornitrack-10	1.00	1.00	1.00	1.00
Ornitrack-15	1.00	1.00	1.00	1.00
Ornitrack-N35	1.00	1.00	1.00	1.00

Table 4.4. Frequency of distances between pairs 18 randomly selected points collected by each tracking device (see sample sizes in Table 4.1), pooled across all devices of each type.

	Proportion of pairs within:			
Device	5 m	10 m	20 m	100 m
Pinpoint 10	0.32	0.56	0.84	1.00
Pinpoint Argos 75	0.96	1.00	1.00	1.00
Pinpoint Argos Solar S	0.91	0.99	1.00	1.00
Ornitrack-10	0.69	0.92	0.98	1.00
Ornitrack-15	0.33	0.60	0.82	0.99
Ornitrack-N35	0.45	0.71	0.89	1.00

Figures

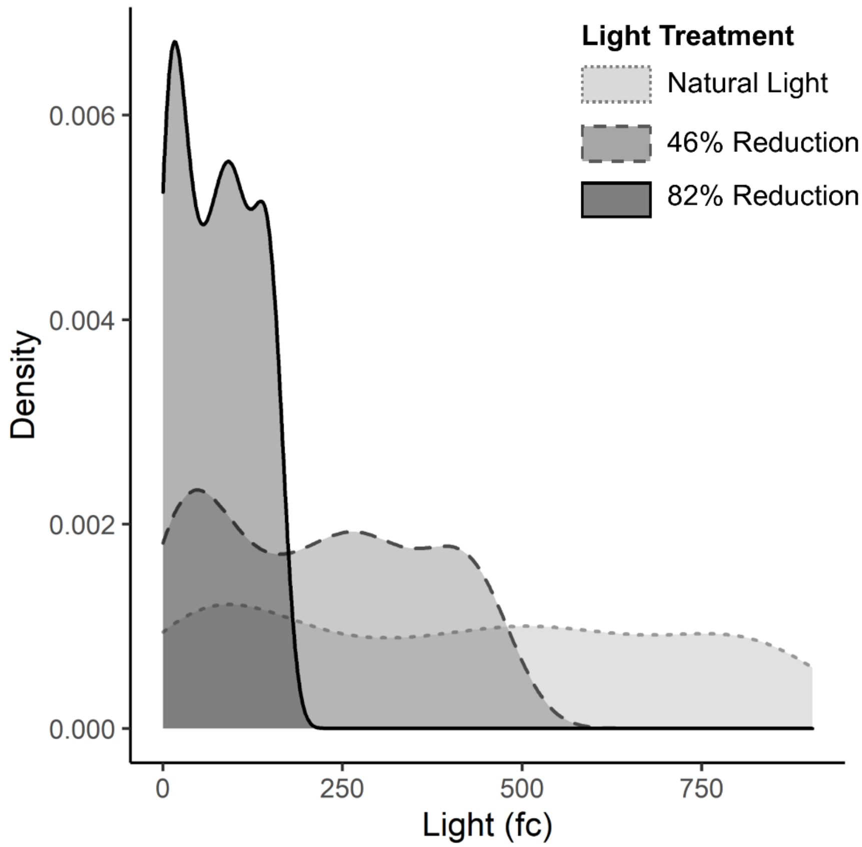

Figure 4.1. Density plots of light measurements in foot-candles (fc) between 06:30 and 18:00 CST for the three light treatments applied to devices during the experiment (in southern Texas, USA, from 7 to 13 December 2019): Natural light (0% Reduction), 46% Reduction, and 82% Reduction. Note that for all light treatments, light measurements during the night were assumed 0.

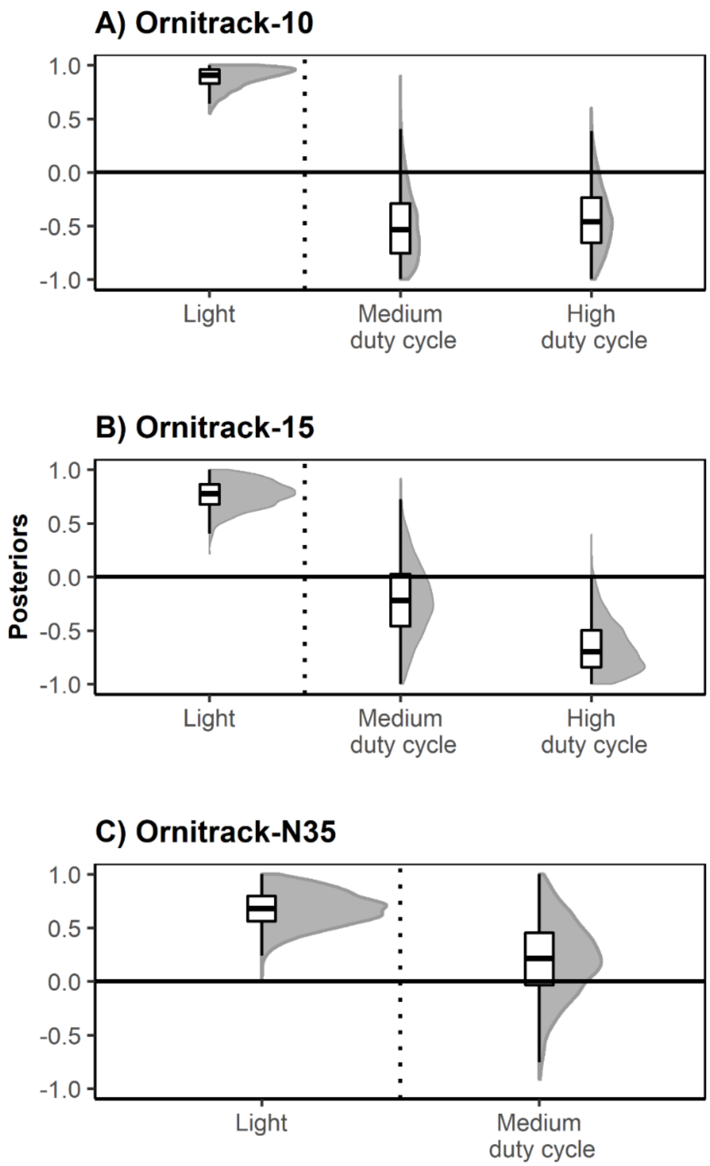

Figure 4.2. Posterior distributions of estimated effect sizes for light level and duty cycle effects on battery life in the cumulative light model. The dotted vertical line separates light from duty cycle within each device type. Effects of medium duty cycles (48, 48, and 72 points per day) and high duty cycles (72, 72, and 144 points per day) pictured are relative to the lowest duty cycle level (12, 24, and 48 points per day) for each of the device types (Ornitrack-10, Ornitrack-15, and Ornitrack-N35 devices, respectively). The box plot represents the median, 50% CRI, and 95% CRI for each light level and duty

cycle effect, while the shaded area represents the posterior distribution. When the 95% CRI of the posteriors does not overlap 0, we assume a credible effect. Here, we see that for all three device types light had positive effects on battery, while there were no credible effects of duty cycle.

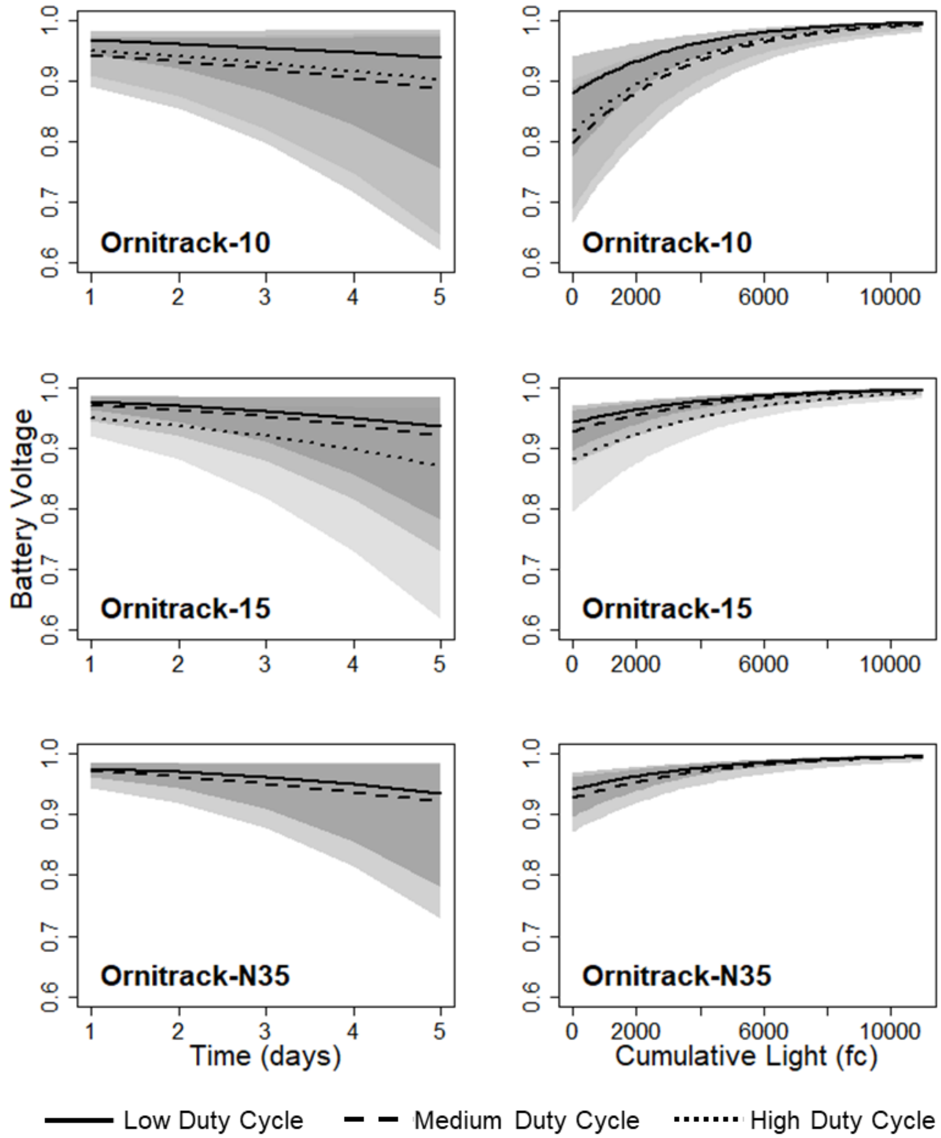

Figure 4.3. Percent battery voltage predictions for each duty cycle for each device type over time (left) and cumulative light level (right), respectively for Ornitrack-10, Ornitrack-15, and Ornitrack-N35 devices. Low, medium, and high duty cycles are 12, 48, and 72 locations per day, respectively, for Ornitrack-10 devices, 24, 48, and 72 locations per day for Ornitrack-15 devices, and 48, 72, and 144 locations per day for Ornitrack-N35 devices. Cumulative light measurements are foot-candles (fc) at 30-min intervals

added over a 24-hour period. The 95% CRIs are represented by gray shading and follow the low, medium, and high duty cycles in order.

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CHAPTER 5

Modelling associations between animal social structure and demography

Abstract

Successfully navigating a complex social environment can influence fitness (i.e., survival and reproductive success), which can cascade to outcomes in demography and population dynamics. Extensive research has focused on the mechanisms and drivers of fitness variation that result from differences in social structure and interactions, and separately, the effects of demography on population change. However, there have been few attempts to address the effects of social structure on population dynamics through demography. Here, we first review the effects of social structure and individual social position on fitness. We then address knowledge gaps, including the relationship between social structure and population dynamics, the carry-over effects of social conditions, and the differential effects of social variables on specific demographic rates. We also review statistical tools and data requirements for the analysis of social networks and demography. We then propose that knowledge gaps could be filled by using joint modelling approaches. We used a simulation study to highlight the potential use of social networks to inform survival, a key demographic parameter. We developed a model that combines social network and survival (Cormack-Jolly-Seber) analyses and evaluated its performance to place inferences under different group structures and sampling scenarios using simulated data. Our results show that valid inferences on social and survival parameters and their connections can be achieved with realistic sample sizes, but precision is improved with more complete information (i.e., fewer missing individuals).

Based on our review and simulation study, we suggest that further development of integrative modelling approaches can yield greater understanding and improved power to make predictions about the effects of social environments on populations and the feedback of population dynamics on social structure.

Introduction

Population dynamics are driven by the combined survival and reproductive success of the members of the population, that is, patterns of individual fitness (Metcalf & Pavard 2007). Therefore, factors that influence individual fitness drive changes in abundance and composition of populations over time (Begon et al. 1986; Figure 5.1). For example, selection by individual sedge warblers (*Acrocephalus schoenobaenus*) for habitat with taller vegetation increased individual reproductive success, and sites with greater reproductive success experienced population expansion (Zając et al. 2008). Because animals often form groups with complex and dynamic social structures, social characteristics of individuals should also influence fitness (e.g., Riehl & Strong 2018, Lambin & Krebs 1993) and thus population dynamics. Social structure emerges from the content and quality of interactions among individuals together with how interactions are patterned in space and time (Hinde 1976; Whitehead 2008). Although social relationships have been widely demonstrated to have direct and indirect effects on fitness (Lehmann et al. 2015; Wey et al. 2013), links between social structure and demographic outcomes have been less studied.

Here we aim to discuss concepts and highlight knowledge gaps related to relationships between social structure and demography, and use a simulation study to demonstrate a joint analysis of social and demographic data. We first discuss literature related to social structure and fitness, and links to demography. Then, we describe analytical tools used in social network and demographic analyses. We then provide an approach for linking social structure with demography by jointly modelling social networks and survival models, and evaluate model performance under different scenarios of sampling design and group structure which may affect data quality. Based on results from our simulation study, we suggest additional applications for using these approaches to address knowledge gaps between social structure and population dynamics.

The relationship between social structure and fitness

Social structure can benefit survival in animals through a diversity of mechanisms. Examples include decreased predation (Griesser et al. 2006) or improved access to food and foraging efficiency (Sridhar et al. 2009, Lihoreu et al. 2017) of individuals within genetically related and unrelated groups. Social associations can also influence reproductive success, for example through benefits of synchronous reproduction and resource use (Riehl & Strong 2018), cooperative breeding in family groups (Langen 2000) and through reduced stress resulting from grouping (Cameron et al. 2009). Related individuals often form close social associations resulting in increased fitness. For example, female fitness is positively correlated with brood-rearing-group relatedness in common eiders (*Somateria mollissima*; Jaatinen et al. 2012); and female Townsend's voles (*Microtus towndsendii*) improve survival rates when living in association with first degree relatives in an experimental study (Lambin & Krebs 1993). Additionally, at younger ages, the extent of sociality among relatives influences survival probability for female rhesus macaques (*Macaca mulatta;* Brent et al. 2017). Nonetheless, there are important costs of sociality as grouped individuals can facilitate spread of disease (Evans et al. 2020) or induce intraspecific competition (Carrete et al. 2006), whereby social associations may decrease survival or reproductive success. Social conditions are expected to influence demographic rates, which are a collective consequence of fitness (Metcalf & Pavard 2007). However, the effects of social structure on populations through demographic rates remain little understood.

Population dynamics will also influence social structure through the addition or removal of individuals from populations through births, deaths, immigration, or emigration (reviewed by Shizuka & Johnson 2020). Further, population structure characteristics, such as the distribution of individuals over space and time (Spiegel & Pinter-Wollman 2020), or social responses of individuals to changing habitat conditions (Genovart et al. 2020) may also affect patterns of social associations, meaning that demography and population dynamics also feedback on social structure. Given the prevalence of sociality in animal populations, it is important to understand the causes and consequences of social structure and population dynamics.

Knowledge gaps associated with social structure and demography

Technological and methodological developments have enabled the collection of increasingly detailed data on animal social interactions (Krause et al. 2013), demography, and population dynamics (e.g., Schaub & Abadi 2011). There are three key knowledge gaps that we suggest could be addressed by jointly analyzing social and demographic information.

First, we should better understand the connections between social structure and population dynamics. Second, while there is a growing body of literature on the effects of social characteristics on fitness (see above), few studies have linked social structure in one season or life stage to survival or reproductive success in future seasons or life stages. Studies which have done this include Stanton & Mann (2012), who found that calf social structure in male bottlenose dolphins (*Tursiops* spp.) influenced their survival as juveniles, and Culina et al. (2015), who found that winter social structure in male great tits (*Parus major*) affected mating decisions during the breeding season. Conditions affecting an individual at one stage of the year or life history can have substantial effects on fitness in subsequent stages (Harrison et al. 2011; van de Pol et al. 2006), but few studies explicitly focus on the carry-over effects of social conditions. Social structure is known to affect subsequent social status of individuals and structure of groups, for example, in songbirds and hyenas (Firth & Sheldon 2016; Ilany et al. 2015), so it is likely that social structure also has carry-over effects on fitness (McDonald 2007). Third, different components of social structure (e.g., individual, local, and network-level measures of social structure) likely affect different demographic rates, but such relationships have been difficult to explore with demographic data alone. Social network and survival analyses combined may yield more holistic information compared with findings from separate analyses.

Quantitative approaches

The capacity to answer complex questions related to social structure and demography could be improved by developing joint modelling approaches that use individual-level social structure data to inform demographic rates. Previous studies (e.g., Ellis et al. 2017; Brent et al. 2017) have evaluated correlations between social covariates and mortality risk in animals, and this concept could be expanded on by extending analysis to using social information to inform population dynamics through demography. We propose an analysis that probabilistically links social networks and survival models to provide a more detailed view of interactions between social structure and population dynamics. Jointly modelling social structure and survival leverages data collected at the individual level to explore effects of individual social decisions and environments on survival probability within a survival model. Additionally, questions related to differences in survival among groups within the social network could be explored. Understanding carry-over and cross-seasonal effects of social structure can be improved by using social information as part of a survival analysis. Finally, modelling connections between social structure and survival provides a baseline for future work fully integrating multiple data streams for greater capacity to investigate the feedback of social and demographic variables on one another.

Social network analysis

Social network analysis is an analytical framework for quantifying social structure and dynamics that is valuable to link individual-level behavior with population-level processes (Krause et al. 2007). Social network analysis exploits graph theory to represent individuals as nodes and the associations, interactions, or relationships between them as edges, which may or may not be weighted or directional (Whitehead 2008). Collecting network data is feasible when researchers can uniquely identify individuals and record interactions or associations between them (e.g., Aplin et al. 2012). Data collection can also be facilitated by using bio-logging technology to record interactions or associations remotely (Krause et al. 2013; Williams et al. 2020). Social network measures can be calculated to quantify the properties of the network as a whole or to describe the position of individuals within the network (Silk et al. 2017; Wey et al. 2008). Two examples of network-level measures are density (also “edge density”) and average path length. Density is the proportion of completed edges in the network (i.e., the proportion of interactions to potential interactions). Average path length is calculated from the path lengths (the shortest number of edges connecting two individuals), and is lower when individuals are more interconnected with one another (Silk et al. 2017; Wey et al. 2008).

A different set of characteristics can be captured using individual-level (i.e., node-level; those with one value for each individual in the network) social network measures, including degree and clustering coefficient. Degree is the number of other nodes that a focal node is connected with, and is a measure of social centrality (Newman 2003; Whitehead 2008). Centrality quantifies an individual’s importance or influence within a network, and there are numerous ways to compute this measure (Wey et al. 2008). Centrality can be associated with individual characteristics influencing survival or reproductive success (e.g., Ryder et al. 2009). Clustering coefficient is an individual-level measure that quantifies local transitivity in the network structure surrounding a node (i.e., whether an individual’s connections are themselves inter-connected; Whitehead 2008). It ranges from 0 (none of an individual’s associates are connected themselves) to 1 (an individual’s direct connections are all interconnected with each other). The clustering coefficient measures associations among the associates of a given individual within the network, which can be related to behavior (Mann et al. 2012). Of note, the social centrality and clustering coefficient of an individual are not necessarily closely related; individuals with the same centrality may exhibit very different clustering coefficients (Brent 2015).

Incorporating multiple social and demographic variables could improve understanding of relationships between social structure and fitness. Network measures can be used as response or explanatory variables in statistical models fitted to test individual- and population-level hypotheses related to social structure (Croft et al. 2011). For example, McDonald (2007) showed that centrality in early life predicted changes in the social status of male long-tailed manakins (*Chiroxipia linearis*) in later life. Similarly, Ellis et al. (2017) evaluated social network data in relation to mortality risk and found that closeness and degree influenced probability of mortality for male killer whales (*Orcinus orca*). While these and other studies have correlated multiple network measures with behavioral or demographic outcomes, the implications of such relationships for population dynamics have received minimal attention. An important next step is to expand these ideas by using social network measures in demographic models to quantify the population-level implications of individual-level social characteristics. Because survival and social networks can often be derived from similar information, it is intuitive to examine the possibility of incorporating social information in survival models.

Survival models

Survival is a key component of population dynamics. A variety of intrinsic and extrinsic features, such as body condition (Hall et al. 2001), sex, age (Garratt et al. 2015), habitat and environmental factors (Gibson et al. 2017) can influence survival. Our simulation study and discussion will focus on linking social and survival information, but social and reproductive success data can also be linked in statistical analyses based on regression approaches.

There are many survival models available to practitioners, with varying data requirements, assumptions and inferences (Kéry & Schaub, 2012). Most survival models use data from individually identified animals (e.g., via capture-recapture or telemetry), and may assume either a closed population in which no individuals move in or out, or an open population in which there can be emigration and/or immigration. If individuals can be followed with great certainty (i.e., their alive/dead status is known at every encounter occasion), as is common in studies using telemetry or tracking devices, then known-fate models can be used. If there is uncertainty about whether the individual is alive or dead and recapture or resighting data are collected (i.e., the true fate of the individual is not known at every occasion), then imperfect detection can be modeled explicitly in open population models such as Cormack-Jolly-Seber (CJS) models (apparent survival is estimated and true survival is a latent parameter; Cormack, 1964; Jolly, 1965; Seber, 1965).

Capture-recapture and tracking data are commonly collected for monitoring survival (Kéry & Schaub 2012; Wilmers et al. 2015). These data can also be used to infer social networks (Gimenez et al. 2019) if we assume that: 1) individuals that are co-captured or observed in the same location are associating with one another (gambit of the group assumption; Franks et al. 2010), and 2) we can infer social relationships among individuals by monitoring their associations over time. For example, Perkins et al. (2009)

defined social contact as when individuals were observed in the same spatial location within the same time period and constructed a network with a node for each individual and an edge for each time two individuals co-occurred. They tested both capture-recapture and tracking methods to obtain co-occurrence data, and found that network structure differed between the two data collection methods. This example highlights the importance of considering the implications of study system and sampling design characteristics for interpretation of results.

Sampling design and modelling considerations

It is important to consider the consequences of variation in study designs and population characteristics. Capture-recapture studies are often more cost-effective than tracking studies, so are likely to have larger sample sizes. However, imperfect detection is a feature of capture-recapture data. Tracking technology can yield detailed information about individuals, and also be used to detect animal associations (Barkley et al. 2020; Krause et al. 2013). Although there are some cases in which capture-recapture or tracking data can be applied to nearly entire populations (Firth & Sheldon, 2016; Strandburg-Peshkin et al. 2015), cost, time or other concerns usually limit sample size and frequency of data collection, so it is important to evaluate the strength of the conclusions that can be made with varying amounts and quality of data (Silk 2017). Due to the effects of missing data, there are uncertainties associated with precision and bias from characteristics of populations and study designs when modelling social structure and demographic rates such as survival.

Both known-fate and open capture-recapture models are flexible for inclusion of group or individual covariates, which may change or remain constant through time (Kéry & Schaub, 2012). We can quantify the influence of hypothesized predictors of survival through regression-based estimates, which can serve as a framework to test competing hypotheses. In addition, because the structure of populations and sampling effort can affect data quality, and missing information can substantially affect inference from social networks (Silk 2017; Silk et al. 2015; Davis et al. 2018; Smith & Moody 2013), precision and bias associated with different sampling effort and social structure scenarios should be evaluated when using these approaches. Bayesian statistics are particularly well suited for propagating and describing precision and accuracy in ecology (Ogle 2009).

Here, we used social network measures as individual covariates in Bayesian CJS models to explicitly link social structure and demography. The goals of this simulation were to demonstrate an approach for jointly modelling social structure and survival under a variety of group structures and scenarios likely to be encountered in real-world populations and evaluate model performance in terms of precision and bias under each scenario. More specifically, we aimed to learn (1) whether the model would perform well enough to make unbiased inferences about social structure and survival and (2) what the implications of different sampling scenarios are for the precision and bias of parameter estimates.

Methods

Model structure for combining social network analysis and Cormack-Jolly-Seber survival models

Individual information

We considered a population with *N* individuals that live in *K* social groups, sampled over a time period of *T* years. To create a social network for the population, we first assumed that each individual can be distinguished with individual-level covariates *X1* and *X2*. We assumed that *X1* followed a normal distribution with mean 0 and unit standard deviation and *X2* followed a Bernoulli distribution with a probability of 0.5. In ecological studies, these covariates could represent continuous attributes such as size or categorical attributes such as sex. In this framework, variation in number of groups introduced variation in social network metrics (Figures 5.2, A4.1). We also assumed that individuals were evenly distributed among the *K* groups.

Social Network

We assumed that the probability of a social relationship (edge) between each pair of individuals (i.e., edge) is determined by the influence of covariates on the mean values of *X1* and *X2* of these two individuals while also considering whether they belong to the same group or not. More specifically, we calculated the probability of an edge between individuals *i* and *j* in the same group (internal edge) as

$$logit(\pi_{i,j}) = logit(\omega^{[Int]}) + \beta_1^{[Int]} \times \frac{X_{i,1} + X_{j,1}}{2} + \beta_2^{[Int]} \times \frac{X_{i,2} + X_{j,2}}{2},$$

where $\pi_{i,j}$is the probability of an edge between individuals *i* and *j*, $\omega^{[int]}$ is the mean probability of an internal edge, and $\beta_1^{[Int]}$ and $\beta_2^{[Int]}$ are the effects of covariates *X1* and *X2* on the probability of an internal edge, respectively.

Similarly, for individuals belonging to different groups, we calculated the probability of an edge between them (external edge) as:

$$logit(\pi_{i,j}) = logit(\omega^{[Ext]}) + \beta_1^{[Ext]} \times \frac{X_{i,1} + X_{j,1}}{2} + \beta_2^{[Ext]} \times \frac{X_{i,2} + X_{j,2}}{2},$$

where $\omega^{[Ext]}$is the mean probability of an external edge, and $\beta_1^{[Ext]}$ and $\beta_2^{[Ext]}$ are the effects of covariates *X1* and *X2* on external edge, respectively.

We used these two regressions to make an $N \times N$ symmetric matrix of edge probabilities. Note that individuals cannot be connected with themselves (diagonal set to 0). Then, we assumed that connection between individuals *i* and *j* (connection 1, otherwise 0) followed a Bernoulli distribution such that:

$E_{i,j} \sim \text{Bernoulli}(\pi_{i,j})$.

Each binary (unweighted) edge between individuals in this network could be seen to indicate the presence of a social relationship between them which could be inferred from observing (or bio-logging) patterns of interactions or associations. From the resulting matrix, we calculated degree (*DEG*) and clustering coefficient (*CLU*) for each individual. We chose degree and clustering coefficient as representative social network measures because they measure different aspects of an individual's social network position and are frequently uncorrelated (Brent 2015), respond in different ways to sampling effects (Silk et al. 2015), and have been found to influence fitness, including survival. Nuñez et al. (2015) found degree to be an important predictor of survival in juvenile feral horses (*Equus caballus*) and Lehmann et al. (2016) found clustering coefficient to be an important predictor of survival for Barbary macaques (*Macaca sylvanus*). While we chose only these two metrics in our example, our modelling approach can be easily extended to include more network metrics if they are biologically relevant to specific hypotheses.

We calculated degree by summing the number of connections that each individual *i* had such that:

$$DEG_i = \sum_{j=1}^{N} E_{i,j}.$$

Clustering coefficient is calculated as the proportion of completed connections between the associates of an individual relative to the number of possible connections between associates of an individual. To calculate clustering coefficient, we first created a sub-network of individuals from 1 to M_i for any individuals that were connected with individual *i*, then used the following equation to calculate clustering coefficient if the degree of individual *i* was >1 (clustering coefficient was 0 of degree ≤ 1):

$$CLU_i = \sum_{j=1}^{M_i} \sum_{k=1}^{M_i} E_{j,k} / [DEG_i \times (DEG_i - 1)].$$

Survival

We assumed that survival was influenced by the social environment by letting survival probability be a function of degree and clustering coefficient such that:

$$logit(\varphi_i) = \alpha + \beta^{[Deg]} \times DEG_i^{[st]} + \beta^{[Clu]} \times CLU_i^{[st]},$$

in which φ_i was the survival probability of individual *i*, $DEG_i^{[st]}$ was its degree standardized to have mean 0 and unit standard deviation, $CLU_i^{[st]}$ was its standardized clustering coefficient, and $\beta^{[Deg]}$ and $\beta^{[Clu]}$ represented the effect of degree and clustering coefficient on survival, respectively.

We assumed that all individuals were alive in the first year (i.e., $t = 1$). From the second year (i.e., $t \geq 2$), we used the survival probability calculated above to predict survival of individual i, $S_{i,t}$, given that it was alive in the previous year using a Bernoulli distribution such that

$$S_{i,t} \sim Bernoulli(S_{i,t-1} \times \varphi_i).$$

Thus, we generated an $N \times T$ survival history matrix in which $S_{i,t} = 1$ represented that individual *i* was alive in year *t* and $S_{i,t} = 0$ otherwise. Note that we assumed that the social network did not change over time by assuming that individuals that were removed from the population due to mortality were always replaced by a new individual with similar social characteristics (and therefore social network position). In this way, we considered a static social network in this study. We considered that such an assumption is adequate to evaluate precision and bias associated with varying population and data collection characteristics. Our approach could be extended to using social network measures from dynamic networks. However, a computationally-efficient modelling approach that more fully incorporates dynamic social networks and their effects on demography would be beneficial to develop (Farine 2017).

Encounter History Matrix

Field studies often collect incomplete information about social networks and survival. To simulate realistic data, we generated an $N^* \times T$ encounter history matrix such that

$C_{i,t} \sim Bernoulli(S_{i,t} \times p)$,

in which $C_{i,t} = 1$ represented that individual *i* was captured in year *t* and $C_{i,t} = 0$ otherwise, and *p* was the capture probability. Note that rows with all 0's (i.e., individuals that were not captured during the study period) were removed from the data. Not all individuals were captured during the study (i.e., $N^* < N$), so an individual's information (i.e., $X1$, $X2$, and its group) was known only when it was captured at least once and edge information was known only if both associating individuals were captured.

Simulation study evaluating scenarios of group structure and sampling

For each run of the simulation, we generated a data set using the model described and then analyzed the simulated data using the data-generating model to obtain posterior samples for each parameter. We then compared the posterior samples with the true values to evaluate bias and precision associated with the model. We considered four combinations of two recapture probability values (*p* = 0.3 and 0.7) and two numbers of groups which resulted in different network structures (*K* = 10 and 2; Figure 5.2). We used *p* = 0.3 to represent a lower recapture probability and *p* = 0.7 to represent a higher recapture probability (Schaub et al. 2004). We used 10 groups to represent a population with a lower degree and clustering coefficient; mean degree was 6.25 and mean clustering coefficient was 0.35 across all individuals in 50 simulations (Figure A4.1). We used 2 groups to represent a population with a higher degree and clustering coefficient; mean degree was 21.4 and mean clustering coefficient was 0.74 across all individuals in 50 simulations (Figure A4.1). Thus, these four combinations represented different sampling conditions and group structures that may be encountered in studies across animal ecology (Sah et al. 2019). We considered a time period of 10 years (T) for sampling and a population size of 50. We simulated 50 data sets for each combination, resulting in a total of 200 simulations. We also attempted simulations for a population size of 100 with 10 groups. However, for this sample size the model took ~24 days to converge, due to the exponentially increased size of the network. Therefore, we excluded all N = 100 simulations from this analysis and anticipate that if reasonable inference can be achieved with a small sample size, similar (or improved) inference can be gleaned with a larger sample size.

We also analyzed the simulated data in a CJS model without network information. In this naïve CJS model, only constant survival and recapture probabilities were estimated and compared to the mean survival and recapture estimates from the data-generating model.

We ran the model in Jags (Plummer 2003) through Program R version 4.0.0 (R Core Team 2020) using the JagsUI package (Kellner 2018). We used vague priors. We ran 3 chains with an adaptive phase of 2000, and then 4000 iterations including 2000 burn-in without thinning, yielding 6000 posterior samples for each parameter. We monitored convergence by visual inspection of traceplots and R-hat <1.05 (Brooks & Gelman 1998). We evaluated our model results by calculating precision as the root mean square error (RMSE) $\sqrt{\sum \frac{(\beta_{posterior} - \beta_{True})^2}{nmcmc}}$) using *nmcmc* posterior samples $\beta_{posterior}$ and the true values β_{True} . We calculated bias as the difference between posterior samples and the true value. We then compared precision and bias between different situations mentioned above.

Results

Precision: For most parameters, the simulations with p = 0.7 had higher precision (lower RMSE) than those with p = 0.3 within each group size (Figure 5.3, Table 5.1). This was expected considering that with a fixed population size, a higher recapture probability will result in fewer missing individuals and therefore more information about the social network and survival. An exception is that we found very little difference in the precision of recapture probability when p = 0.7 or 0.3. Some parameters were estimated more precisely with a 10-group population, while others were estimated more precisely with the 2-group population. For example, the probability of external edges was more precise for 10-group populations, while the probability of internal edges was more precise for the 2-group populations. This also is expected because the 10-group populations will have more external edges than the 2-group, and the 2-group populations will have more internal edges than the 10-group, and with less information the model would be expected to be less precise. However, the 95% credible intervals (CRI) overlap within each parameter for all scenarios so we would not expect these differences in precision to substantially affect inference from the model.

Bias: We did not find evidence of bias in most cases (<0.20; Figure 5.4). The only exception is that the model slightly underestimated the effect of clustering coefficient on survival when there were 10 groups and p = 0.3 (Table 5.1). With the higher number of groups, the low recapture probability did not provide enough information to estimate the effect of clustering coefficient on survival in a non-biased way.

We also compared results of the CJS model with the social network incorporated to results of a naïve CJS model run (i.e., without social information), using the same data. These results showed that with N = 50 and p = 0.7, precision of inference about survival and recapture probability was the same as with the naïve CJS, while with N = 50 and p = 0.3. Precision based on the 95% CI was also similar, but there were more outliers in the social network CJS model (Figure A4.2).

Discussion

We reviewed links between social structure and population dynamics and demonstrated joint modelling of social networks and survival. Based on our simulation study, we found that a model evaluating social network metrics on survival performed well under all combinations of 10-group and 2-group social structures and 0.3 and 0.7 recapture probabilities. Precision varied across scenarios but the 95% CI of RMSE overlapped for all parameters, including the effects of network metrics on survival, with minimal bias (<0.20). These results suggest that (1) inferences about relationships between degree and clustering coefficient and survival are reasonable at a range of detection probabilities, and (2) differences in sampling scenarios did not influence bias but small sample sizes and recapture probabilities led to reduced precision for most parameters. While we linked two specific social network measures to survival, similar questions could be explored for other demographic rates or social network metrics. For example, a regression could be used to examine reproductive success as a response variable, or betweenness, which counts the number of shortest paths between individuals that pass through an individual (Farine & Whitehead 2015), as an explanatory variable to examine whether a more global measure of social centrality influences survival.

With an ability to glean inference on the relationships between social structure and demographic rates, several knowledge gaps can be formally addressed. First, we can more deeply examine separately-reported social structure and demography by applying survival models to connect social structure and population change. This is advantageous because integrating behavioral information into demographic models can improve inference about population patterns (Genton et al. 2015; Gerber 2006). Second, quantifying social structure allows linkage of individuals and populations to study carry-over effects by exploring downstream consequences of social relationships for fitness (Cantor et al. 2020; Firth & Sheldon 2016). Demographic models similar to those used to study survival and carry-over effects (e.g., Blomberg et al. 2014; Duriez et al. 2012) could be adapted to incorporate information on social relationships to quantify carry-over effects of social structure. In this way, researchers can quantify links between social structure and demographic rates, and examine social environment along with other environmental variables such as weather or landscape characteristics. Third, we can use the same approach to explore how changes in social structure might differentially affect demographic rates using IPMs.

Considerations associated with imperfect detection of individuals

As expected, our model provides parameter estimates with greater precision when more individuals in the population are captured. Our simulation results were consistent with past findings that sparse data could lead to incorrect inferences. Our comparison of the network CJS model to a naïve CJS model suggested that incomplete network information in model runs with low recapture probability could lead to biased estimates of survival and generate outliers. Therefore, in similar contexts to those simulated here, and if social information is not of interest there is no benefit to using a social network to try to improve survival estimates in this framework. However, the 95% and 50% CIs of beta values of the same survival and recapture probabilities overlapped substantially when network and naïve CJS models were compared (Figure A4.2), so we would not expect the network component to affect the model's inference of survival with a low recapture probability. To avoid problems associated with outliers, we recommend running the model multiple times to examine the variability in results if recapture probability is low. We verified that adding social information to the model may not substantially influence model fit, but combining social and survival data does allow for estimates of how social structure and survival are linked.

We also saw variation in precision of parameter estimates among the scenarios where we ran the network CJS model that were consistent with previous studies that examined differences in effects of incomplete information on different network measures (e.g., Silk et al. 2015, Smith & Moody 2013). Given that network data are relational, and some network metrics, including clustering coefficient, are more susceptible than others, such as degree (Gilbertson et al. 2021; Silk et al. 2015), incomplete data may lead to imprecise inferences in some cases. For example, in 10-group populations, mean RMSE for the effect of degree on survival for simulations with 0.3 recapture probability (RMSE = 0.73) was about twice that of simulations with 0.7 recapture probability (RMSE = 0.37), while mean RMSE for the effect of clustering coefficient on survival for 0.3 recapture probability (RMSE = 1.01) was over 2.5 times greater than for 0.7 recapture probability (RMSE = 0.39). In their effects on survival, the improvement in RMSE for clustering coefficient seen with the 0.7 recapture probability compared with the 0.3 recapture probability was substantially larger relative to that for degree. This suggests that clustering coefficient was more sensitive to missing data and the imprecise estimates of clustering coefficient carried forward to influence survival estimates. We recommend that if applying this or a similar approach, researchers interested in interactions between clustering coefficient and demographic rates should design sampling so that at least 50% of individuals are marked. Silk et al. (2015) found most network metrics to be precisely and accurately estimated with at least 50% of individuals detectable, and our results comparing 0.3 and 0.7 recapture probabilities were consistent with this. The differences between our results for degree and clustering coefficient as explanatory variables of interest support previous findings that measures taking into account indirect connections are more susceptible to sampling effects (e.g., Silk et al. 2015). Sampling effects for other network metrics (e.g., global measures of centrality such as betweenness or closeness) may vary with network size and structure in a different way to clustering coefficient and degree (Smith & Moody 2013). Examining implications of sampling effects on the use of different network metrics within demographic modelling frameworks would be a valuable topic for further research. In the meantime, we suggest exploring characteristics of the network when choosing network metrics to ensure they will be ecologically informative and allow for accurate inference given potential limitations in the data being used (such as sampling effects).

The amount of missing individuals is also an important consideration when studying social structure and demography with tracking data. Small capture probabilities often associated with animal tracking projects may make it difficult to combine social and survival information due to the difficulty of reconstructing network information from small subsets of individuals. Tracking data may be particularly limiting for inference in some cases; infrequent detections of a small number of individuals can cause inference to be influenced more by the metrics used or the configuration of the population (Gilbertson et al. 2021). We attempted a known-fate model with simulated known-fate tracking data on a small population (n = 50) with a capture probability of 0.3, and parameters for the model associated with the social network did not converge. Therefore, we would suggest that where feasible, combining tracking and capture-recapture data would be optimal for studies testing social effects on demographic processes. Combining these two sources of data will better inform social structure and interactions, and provide more accurate information about survival of some individuals.

Interestingly, our simulations also suggested that the network structure of the social system being investigated can influence precision and bias in parameter estimates. In our model, the proportion of external (i.e., between-group) edges is higher when the number of groups is higher. We found greater precision in parameter estimates related to external edges when there were 10 groups, while the opposite was true when there were only 2 groups. Thus, practitioners should anticipate a reduction in precision when data are sparse. The probability of edges was driving the structure of the social network and network metrics, and there were always more internal edges in the 2-group scenarios and always more external edges in the 10-group scenarios. In a real-world situation we would know far less about mechanisms determining network structure, but it is important to consider how characteristics of a social system beyond population size could affect the sensitivity of the analysis to missing data.

Although there were differences in precision among different social structures and sampling scenarios, it is important to note that there was minimal bias. Therefore, our results suggest that this approach can be used with the metrics we demonstrated even with a substantial amount of missing data as long as the decrease in precision with less data is considered when interpreting results (at least in frequently encountered social structures and in the absence of sampling biases). However, before using social network data in a survival model, researchers should be aware of the quality of social network data and the precision and accuracy with which they can estimate network measures, as uncertainty in the network will propagate to uncertainty in survival estimates.

An extension using IPMs

Integrated population models (IPMs) use demographic and population survey data in a holistic framework (Schaub & Abadi 2011). In IPMs, survival can be estimated with capture-recapture, band-recovery or telemetry data (Kéry & Schaub 2012). Reproductive success can be estimated via counts of young or age ratios (Arnold et al. 2018). Survival and reproductive success data can be used to estimate additional parameters such as immigration to explain population dynamics. Many spatial and environmental drivers of demographic rates have been examined using IPMs (e.g., Rushing et al. 2017; Zhao et al. 2019), and individual variation in characteristics such as age, size or cohort effects can be incorporated (Plard et al. 2019). Social information, such as degree or clustering coefficient, could similarly be included. We have demonstrated how social information could be incorporated into a survival model, which is often a component or sub-model of IPMs. In this way, IPMs could be used to examine how components of social structure could be affecting demographic rates. Due to the joint likelihoods within IPMs, they are promising for studying the feedback of demography on social structure. It is also possible to include a social network as part of the IPM, which could allow survival, productivity, immigration, and emigration to be examined together through incorporating many data sources into one model. The IPM approach may be useful to answer questions about how social structure and demography are linked, but there are challenges associated with joint analysis of multiple data streams. As with any model, sparse data can challenge parameter estimation, but IPMs are structured for multiple data sources to estimate demographic parameters (Kéry & Schaub 2012). Additionally, combining different sources of data requires complex models that require a long computing time and large computing power to run, resulting in computational limitations. For example, the CJS approach we demonstrated becomes much slower when recapture probability is reduced or population size increased. The time required could be limiting to studies with large populations and/or low recapture probabilities. Developing efficient likelihoods when integrating social network analyses and IPMs will be essential to improve their practical value.

Applications in ecology

Our ability to make inference on survival based on the study of social structure could increase the utility of social data in population ecology. Because selection depends on fitness which cascades to population processes, linking social structure with demographic rates could be useful for studying how different social systems evolve. Additionally, there is likely feedback between demography and social structure, therefore, linking social structure and demography could provide a more complete understanding of how social structure changes as populations change (Shizuka & Johnson 2020). These links could be useful for applied ecology and enhancing conservation research and its applicability. For example, incorporating social data can tighten estimates of population trends in some cases (Gerber 2006), and conservation actions could be better informed by these estimates. Habitat use is a key component of ecology and conservation of species, could be related to group navigation or social cues, so integrating social behavior into movement or habitat selection analyses may allow for inferences to be placed about critical habitat for populations (Greggor et al. 2016). In addition, social integration and status influence survival (Snyder-Mackler et al. 2020), for example by buffering against disease or environmental stressors (Young et al. 2014), and facilitating disease transmission (Evans et al. 2020). Thus, indirect effects of disease and environmental stressors on population dynamics and the adaptive value of social strategies could also be better understood by examining social structure and demography together.

Quantifying relationships between social structure and demographic rates may further provide a better understanding of how life history characteristics that may affect resilience of populations to environmental change. Overall, we see great potential in developing statistical models that integrate social structure and demography, however to do so, limitations in data quality and computing power must be considered. Our review provides a framework for quantifying relationships between social structure and demography to leverage behavioral information for addressing basic and applied questions in ecology.

Tables

Table 5.1. Means and 95% CRIs for RMSE and difference for each model parameter across all 50 runs of each simulation.

Simulation		**Parameter**	**RMSE**		**Bias**	
Recapture Probability	Number of Groups		Mean	95% CRI	Mean	95%CRI
0.3	**10**	*Effect of Degree on Survival*	**0.73**	(0.29, 1.91)	**-0.06**	(-1.50, 1.81)
		Effect of Clustering Coefficient on Survival	**1.07**	(0.37, 3.37)	**-0.43**	(-2.62, 2.43)
		Probability of External Edge (PEE)	**0.01**	(0.00, 0.02)	**0.00**	(-0.01, 0.02)
		Probability of Internal Edge (PEI)	**0.16**	(0.08, 0.25)	**0.03**	(-0.36,0.28)
		Effect of x1 on PEI	**1.07**	(0.44, 3.50)	**0.19**	(-2.42, 3.30)
		Effect of x1 on PEE	**0.33**	(0.15, 0.67)	**-0.04**	(-0.83,0.64)
		Effect of x2 on PEI	**2.56**	(0.81, 12.1)	**0.99**	(-3.19, 12.56)
		Effect of x2 on PEE	**0.64**	(0.35, 1.21)	**0.05**	(-1.23, 1.53)
		Survival Probability	**0.07**	(0.03, 0.35)	**-0.02**	(-0.29, 0.09)
		Recapture Probability	**0.05**	(0.03, 0.09)	**0.01**	(-0.09, 0.12)
0.7	**10**	*Effect of Degree on Survival*	**0.37**	(0.20, 0.84)	**0.07**	(-0.65, 0.94)
		Effect of Clustering Coefficient on Survival	**0.39**	(0.23, 0.76)	**-0.12**	(-0.91, 0.69)
		Probability of External Edge (PEE)	**0.01**	(0.00, 0.01)	**0.00**	(-0.01, 0.02)
		Probability of Internal Edge (PEI)	**0.12**	(0.06, 0.24)	**-0.01**	(-0.29, 0.21)
		Effect of x1 on PEI	**0.61**	(0.30, 1.45)	**0.08**	(-1.38, 1.49)
		Effect of x1 on PEE	**0.25**	(0.12, 0.44)	**-0.01**	(-0.50, 0.57)
		Effect of x2 on PEI	**1.26**	(0.63, 2.77)	**0.47**	(-2.02, 3.26)
		Effect of x2 on PEE	**0.48**	(0.29, 0.87)	**-0.03**	(-1.03, 0.96)
		Survival Probability	**0.04**	(0.02, 0.06)	**0.00**	(-0.08, 0.07)
		Recapture Probability	**0.05**	(0.03, 0.07)	**-0.01**	(-1.06, 0.08)
0.3	**2**	*Effect of Degree on Survival*	**1.10**	(0.27, 3.91)	**0.55**	(-1.01, 4.49)

		Effect of Clustering Coefficient on Survival	**1.17**	(0.29, 5.75)	**0.27**	(-1.58, 4.48)
		Probability of External Edge (PEE)	**0.02**	(0.00, 0.05)	**0.00**	(-0.02, 0.06)
		Probability of Internal Edge (PEI)	**0.06**	(0.03, 0.09)	**0.00**	(-0.12, 0.12)
		Effect of x1 on PEI	**0.33**	(0.15, 0.99)	**0.03**	(-0.80, 0.87)
		Effect of x1 on PEE	**0.48**	(0.23, 1.03)	**0.06**	(-0.98, 1.24)
		Effect of x2 on PEI	**0.57**	(0.34, 0.97)	**-0.05**	(-1.12, 1.17)
		Effect of x2 on PEE	**1.03**	(0.49, 2.39)	**-0.17**	(-2.70, 1.97)
		Survival Probability	**0.07**	(0.03, 0.19)	**-0.02**	(-0.21, 0.11)
		Recapture Probability	**0.05**	(0.03, 0.09)	**-0.01**	(-0.10, 0.10)
0.7	**2**	*Effect of Degree on Survival*	**0.39**	(0.23, 0.64)	**0.13**	(-0.59, 0.95)
		Effect of Clustering Coefficient on Survival	**0.40**	(0.23, 0.73)	**-0.05**	(-0.88, 0.78)
		Probability of External Edge (PEE)	**0.01**	(0.00, 0.02)	**0.00**	(-0.01, 0.03)
		Probability of Internal Edge (PEI)	**0.04**	(0.02, 0.11)	**0.01**	(-0.08, 0.11)
		Effect of x1 on PEI	**0.22**	(0.12, 0.39)	**0.03**	(-0.42, 0.46)
		Effect of x1 on PEE	**0.33**	(0.15, 0.81)	**0.05**	(-0.56, 0.90)
		Effect of x2 on PEI	**0.43**	(0.25, 0.90)	**0.00**	(-0.95, 0.89)
		Effect of x2 on PEE	**0.70**	(0.38, 1.35)	**0.01**	(-1.39, 1.64)
		Survival Probability	**0.04**	(0.02, 0.07)	**-0.01**	(-0.09, 0.06)
		Recapture Probability	**0.05**	(0.03, 0.07)	**-0.01**	(-0.11, 0.08)

Figures

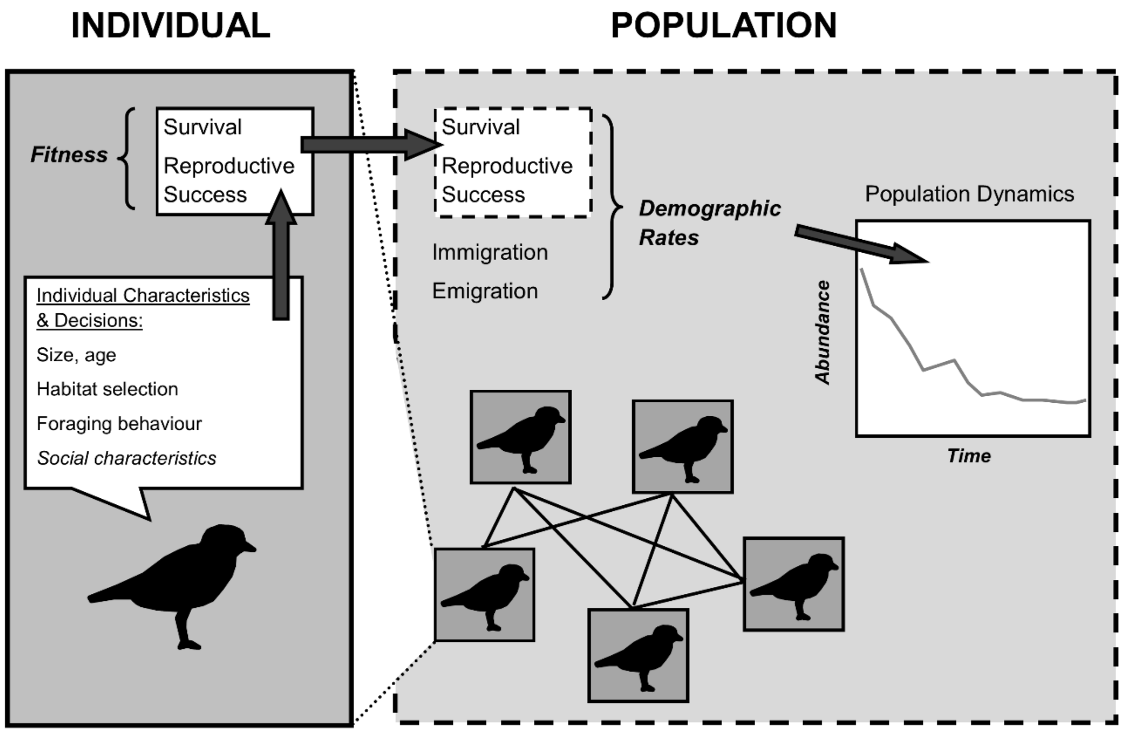

Figure 5.1. Conceptual diagram illustrating how individual characteristics and decisions influence population dynamics through demography. At the individual level (solid line boxes), individual characteristics, including social characteristics, affect survival and reproductive success (fitness). The survival and reproductive success of many individuals in combination make up the survival and reproductive success at the population level (demography; dashed box), where demographic rates (survival, reproductive success, immigration, and emigration) drive population abundance over time.

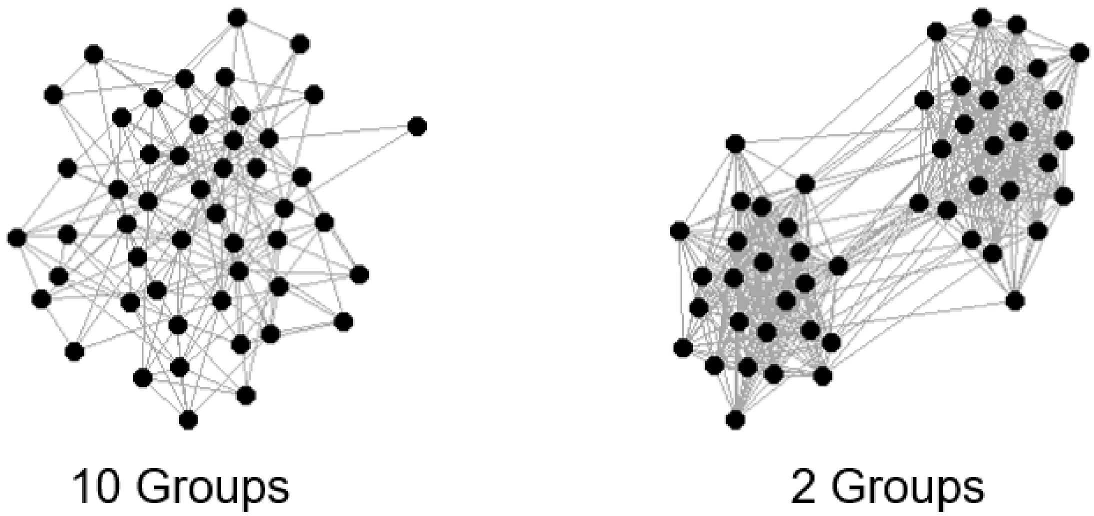

Figure 5.2. Examples of a 10-group and 2-group social network for a population of 50 individuals generated from our social network simulation code.

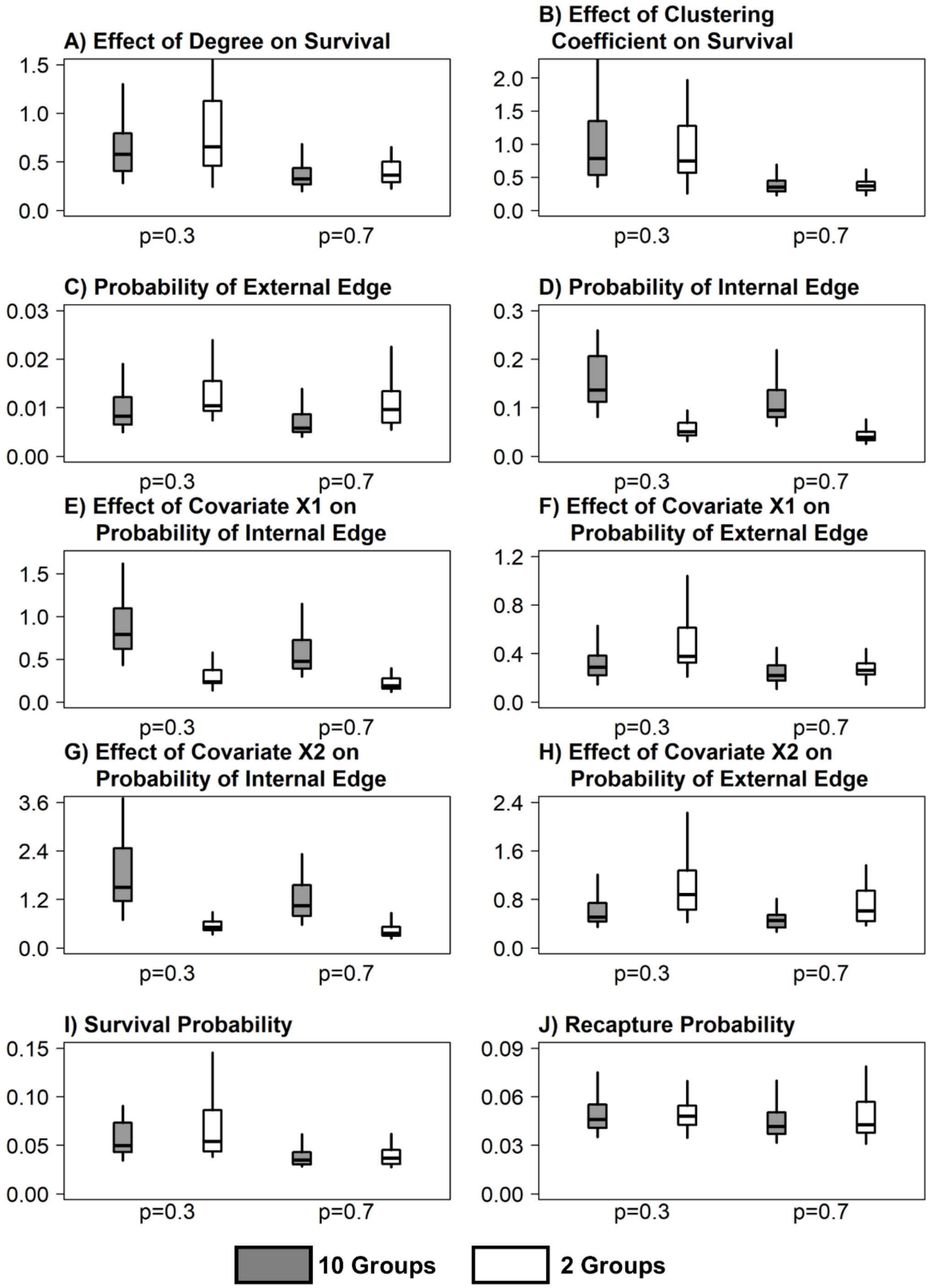

Figure 5.3. RMSE, representing precision, for all model parameters across 50 runs of each simulation (excluding outliers). The 10-group and 2-group simulations for both recapture probabilities are shown in a panel for each parameter.

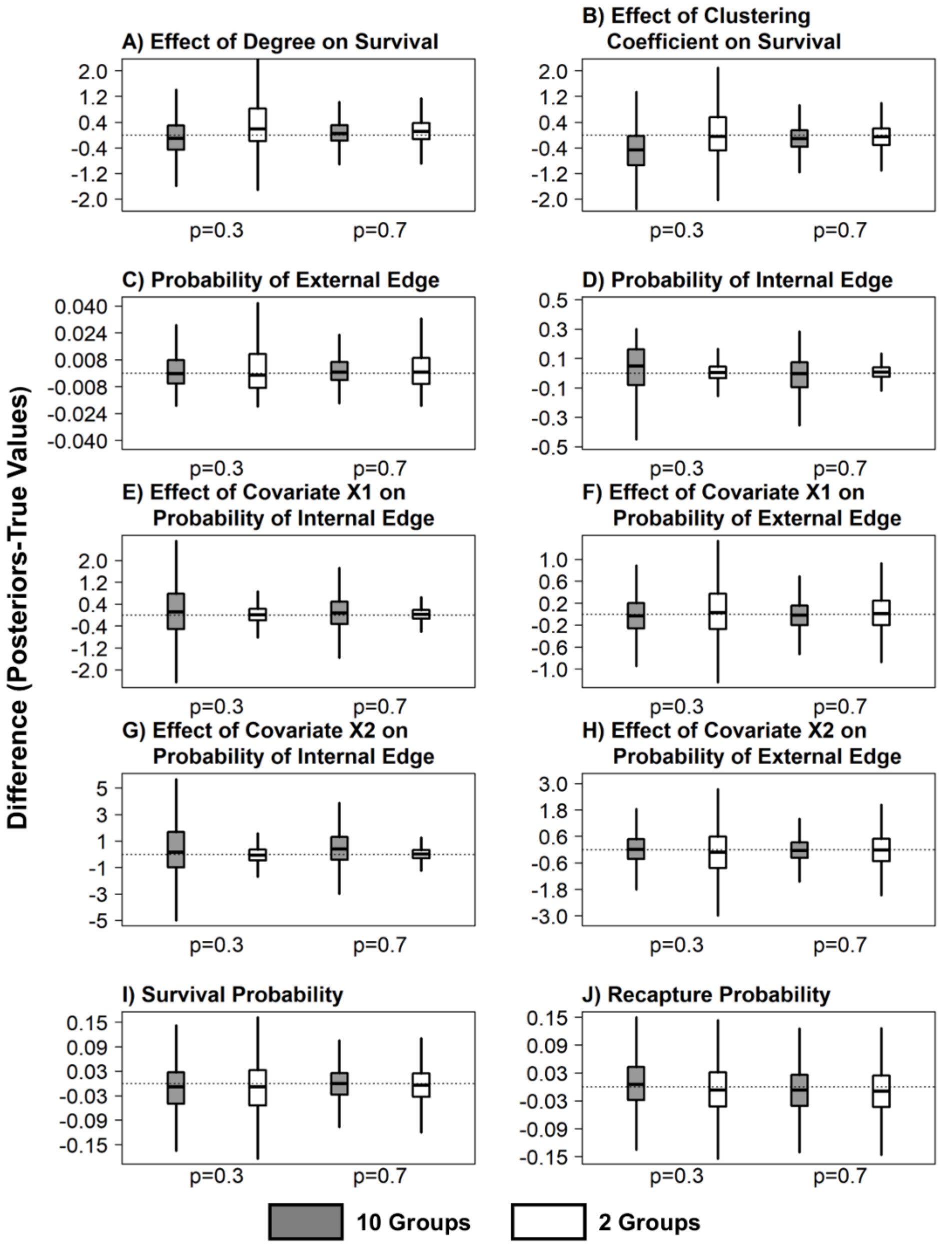

Figure 5.4. Bias (i.e., difference between posterior samples and true values) for all parameters across 50 runs of each simulation (excluding outliers). The 10-group and 2-group simulations for both recapture probabilities are shown in a panel for each parameter. The dotted line indicates 0. We consider a lack of evidence for bias when 0 is within the 50% credible interval (box).

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APPENDIX I

Supplementary Information for Chapter 1

Table A1.1 – Pairwise correlation coefficients (*r*) between weather covariates in the hierarchical model. (in order: tailwind, NDVI, breeding storms, migration storms, migration temperature, breeding temperature, winter temperature, breeding cumulative precipitation, migration cumulative precipitation, winter cumulative precipitation, and spring precipitation rate. Values over the threshold of 0.40 are highlighted in gray.

	TWDm	NDVI	STb	STm	TPm	TPb	TPw	PRCb	PRCm	PRCw	PRRm
TWDm	1.0	0.19	-0.28	0.15	-0.02	0.00	0.00	0.07	0.13	-0.03	0.21
NDVI		1.00	0.08	-0.28	0.05	0.40	0.26	0.27	0.19	0.13	0.26
STb			1.00	-0.17	0.26	0.46	-0.18	0.20	0.35	0.28	0.00
STm				1.00	-0.41	-0.06	-0.43	-0.14	-0.35	-0.02	0.09
TPm					1.00	-0.08	0.24	0.23	0.27	-0.06	-0.10
TPb						1.00	-0.19	0.23	0.15	0.47	-0.03
TPw							1.00	0.39	0.45	0.13	-0.28
PRCb								1.00	0.53	0.28	-0.10
PRCm									1.00	0.47	0.04
PRCw										1.00	-0.05
PRRm											1.00

Table A1.2. Summary of weather covariate data calculated across each season of interest, migration tailwind (TWDm), migration NDVI (NDVI), migration storms (STm), breeding storms (STb), migration temperature (TPm), breeding temperature (TPb), winter temperature (TPw), winter cumulative precipitation (PRCw), migration cumulative precipitation (PRCm), and migration precipitation rate (PRRm).

Covariate	Mean	Min	Max	SD
TWDm (m/s)	1.95	0.21	3.58	0.87
NDVI	0.36	0.27	0.48	0.06
STm	1.75	0.00	4.00	1.11
STb	0.83	0.00	4.00	0.92
TPm (K)	289.83	286.22	293.18	1.98
TPb (K)	277.92	275.00	284.42	2.19
TPw (K)	287.29	286.00	290.43	1.62
PRCw (cm)	415.13	184.17	655.00	140.97
PRCm (cm)	84.48	36.14	216.54	44.07
PRRm (g/m^2/s)	0.003	0.001	0.007	0.002

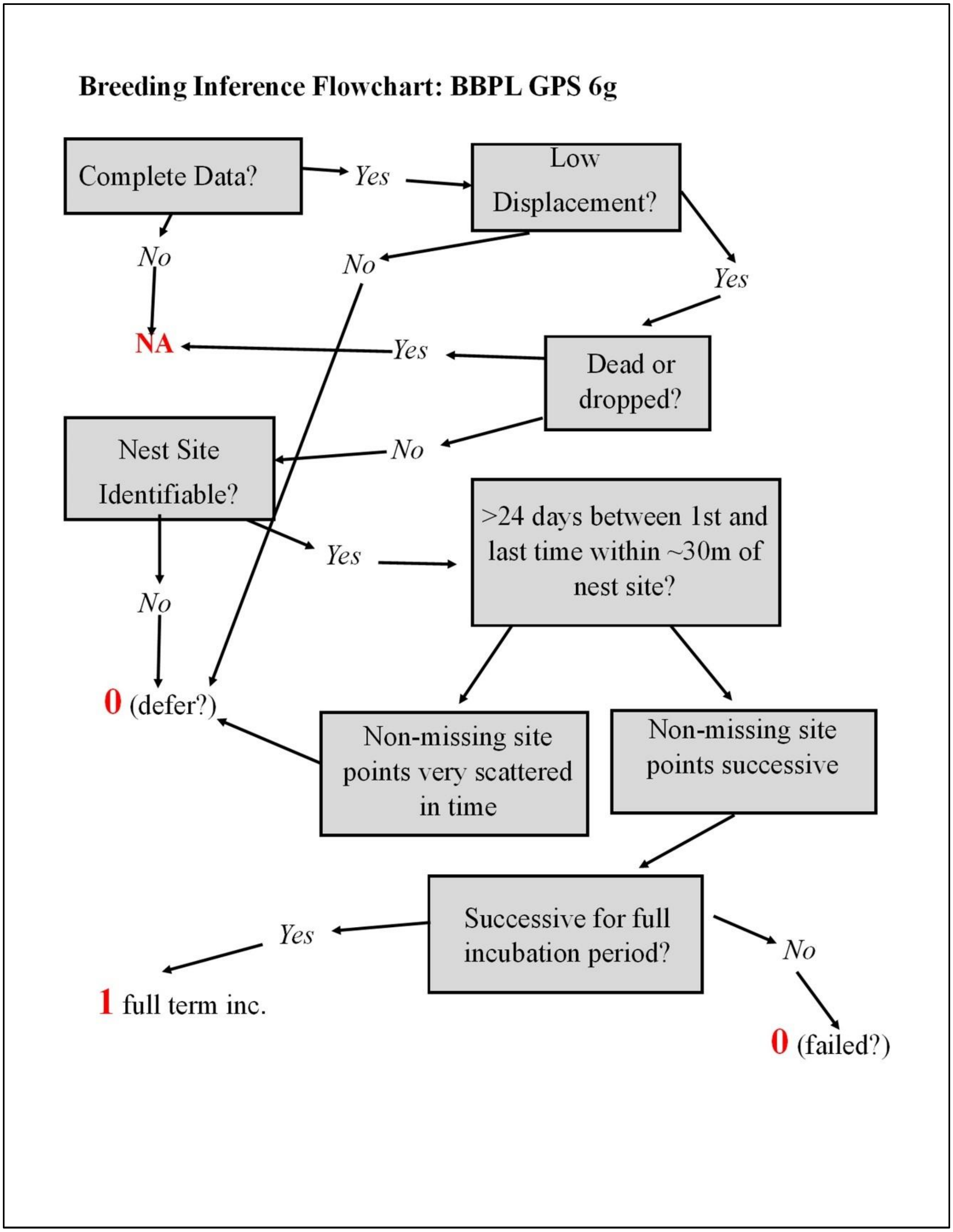

Figure A1.1. Flowchart for identifying breeding status. For analysis, we ascribed successful reproduction (1) as full-term incubation, and reproductive failures and deferrals (0) were combined due to uncertainty in distinguishing between a deferral and a very short breeding attempt.

Model Code for Chapter 1

```
# iterations, thin, burn in, chains

ni <- 10000

nt <- 5

nb <- 4000

nc <- 3


# m10 - herirarchical model with breed, number of stopovers, and mig duration


sink("m10.jags")

cat("

   # likelihood

   model{

   for (i in 1:N){

     nstop[i] ~ dnorm(mu2[i], tau2)

       mu2[i] <-  stm*storm_mig[i]  +nd2*ndvi[i]+ tpw2*temp_w[i] + tpm2*temp_mig[i]
+pcmc*precip_mig_c[i]+ pcmr*precip_mig_r[i]+ alpha2

     migdur[i] ~ dnorm(mu1[i], tau1)

       mu1[i] <- tw*mtwd[i] + tpw*temp_w[i] + nd*ndvi[i] + tpm*temp_mig[i]
+pcw*precip_w[i]+ alpha1

     breed[i] ~ dbern(p[i])

       logit(p[i]) <- ns*nstop[i] + md*migdur[i]  +tb*temp_br[i] +stb*storm_br[i]
+pcb*precip_br[i]  + alpha

   }


   # priors

   alpha ~ dnorm(0, 0.001)

   alpha1 ~ dnorm(0, 0.001)

   alpha2 ~ dnorm(0, 0.001)
```

```
    ns ~ dnorm(0,0.001)
    ps ~ dnorm(0,0.001)
    md ~ dnorm(0,0.001)
    stb ~ dnorm(0,0.001)
    tb ~ dnorm(0,0.001)
    stm ~ dnorm(0,0.001)
    tw ~ dnorm(0,0.001)
    nd ~ dnorm(0,0.001)
    tpw ~ dnorm(0,0.001)
    tpm ~ dnorm(0,0.001)
    pcw ~ dnorm(0,0.001)
    nd2 ~ dnorm(0,0.001)
    tpw2 ~ dnorm(0,0.001)
    tpm2 ~ dnorm(0,0.001)
    pcb ~ dnorm(0,0.001)
    pcmc ~ dnorm(0,0.001)
    pcmr ~ dnorm(0,0.001)

    tau1 <- pow(sig1, -2)
    tau2 <- pow(sig2, -2)
    sig1 ~ dunif(0, 1)
    sig2 ~ dunif(0, 1)
    }
    ",fill = TRUE)
sink()
```

```
# Bundle data

jags.data <- list(breed=breed, nstop=nstop, temp_br=temp_br, storm_br=storm_br,
temp_mig=temp_mig_s, precip_w=precip_w_s, precip_mig_c=precip_mig_c_s,

                precip_mig_r=precip_mig_r_s, migdur=migdur, storm_mig=storm_mig_s,
temp_w=temp_w_s, mtwd=mtwd_s, ndvi=ndvi_s, precip_br=precip_br, N = nrow(dt))



# Initial values

inits <- function (){list(alpha = 0)}


# Parameters monitored

parameters <- c("ns","md", "stb", "tb", "nd","nd2", "tw", "tpw","tpw2","tpm", "tpm2",
"stm", "stb", "pcw", "pcb", "pcmc","pcmr", "sig1", "sig2", "alpha", "alpha1", "alpha2")


# Call jags from R

m10 <- jags(data=jags.data, inits=inits, parameters.to.save=parameters,
model.file="m10.jags",

          n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb, parallel=T)

print(m10)
```

APPENDIX II

Supplementary information for Chapter 2

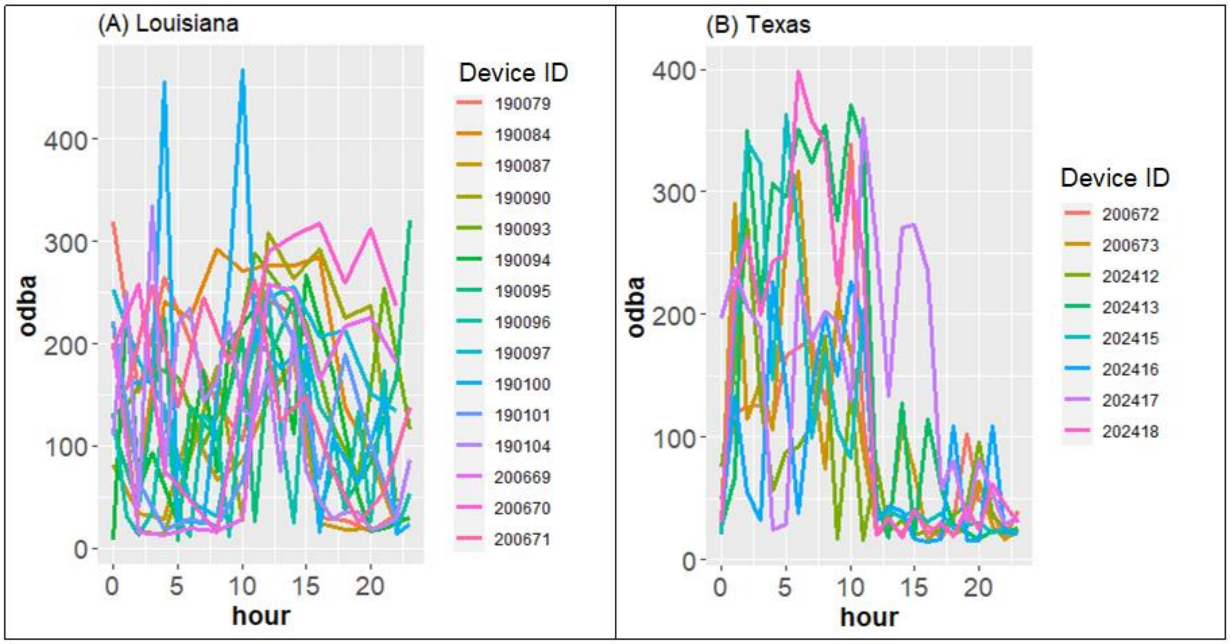

Figure A2.1. Mean ODBA for each hour of the day (in UTC) for (A) Louisiana and (B) Texas birds. Each colored line represents one individual.

Model Code for Chapter 2

```
# Code: Energy Landscape Model
library(boot)
library(jagsUI)
ni <- 5000
nt <- 5
nb <- 2000
nc <- 3

# model #1
#interaction of landcover and tide, with individual random effect
```

```
sink("el8_all.jags")
cat("
   # likelihood


   model{
   for (i in 1:N){
   odba[i] ~ dnorm(mu[i],tau)
   mu[i] <- lc[landcover[i]] + n[night[i]] + t*tide[i] + yd*yday[i]
+txlc[landcover[i]]*tide[i]
   + id*individual[i] + alpha
   }
   #alpha ~ dnorm(0, 0.001)
   t ~ dnorm(0,0.001)
   n[1] <- 0 # [1] is day
   lc[4] <- 0 # [4] is beach
   txlc[4] <- 0
   yd ~ dnorm(0,0.001)
   id ~ dnorm(0,tau.id)
   lc[5] ~ dnorm(0, 0.001)
   txlc[5] ~ dnorm(0, 0.001)
   for (k in 1:3) {lc[k] ~ dnorm(0, 0.001)}
   for (j in 2:4) {n[j] ~ dnorm(0, 0.001)}
   for (p in 1:3) {txlc[p] ~ dnorm(0, 0.001)}


   tau.id <- pow(sig, -2)
   sig.id ~ dunif(0, 10)


   tau <- pow(sig, -2)
   sig ~ dunif(0, 10)
   }
```

```
    ",fill = TRUE)
sink()



# Bundle data
jags.data <- list(landcover=landcover, night=night, tide=tide_s,
                odba=log_odba, yday=yday_s,individual=individual, N = nrow(birds1))



# Initial values
inits <- function (){list(lc=c(0,0,0,NA,0), txlc=c(0,0,0,NA,0),n=c(NA,0,0,0), alpha = 0)}


# Parameters monitored
parameters <- c("lc","t","n", "yd","txlc","id","odba","alpha","sig")


# Call jags from R
el8_all <- jags(data=jags.data, inits=inits, parameters.to.save=parameters,
model.file="el8_all.jags",
              n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb, parallel=T)
```

APPENDIX III

Supplementary information for Chapter 4

Categorical Light Model

Model Structure

The categorical light regression used all locations collected by all devices (battery level was recorded each time the device collected a location) and light was a categorical variable according to treatment to evaluate the effects of three levels of duty cycle and shade treatments on device battery charge over a period of seven days. This provided us with data at intervals in which devices collected positions and was intended to show variation in the effects of light and duty cycle on battery level throughout an entire day rather than focusing on the net gain or loss of battery among days. We formed a regression was such that $B_{ijklmn} = \alpha + \beta_1 T_i + \beta_j S_i + \beta_k D_i + \beta_l T_i S_i + \beta_m T_i D_i + \varepsilon_n$, in which we estimated battery level (*B*) on a logit scale as a function of time (*T*), light treatment (*S*) and duty cycle (*D*) and time (*T*) for each collected point (*i*) with each reduced light treatment (*j*), duty cycle (*k*) and combinations of shade and time (*l*) and duty cycle and time (*m*), with a random effect for individual device (*n*).

Results

Model Summary Tables

Table A3.1. 10-g device posterior means and 95% CIs for the three levels of the interactions of shade and time (txs), and duty cycle and time (txd) for the categorical light model. The first levels (txs[1] and txd[1]) are reference conditions, so the effect sizes of other terms are in reference to the means and CIs of 0 for txs[1] and txd [1].

	Mean	2.50%	97.50%
txs[1]	0	0	0
txs[2]	-0.37	-0.46	-0.29
txs[3]	-0.87	-1.06	-0.67
txd[1]	0	0	0
txd[2]	0.01	-0.12	0.13
txd[3]	-0.54	-0.68	-0.40

Table A3.2. 15-g device posterior means and 95% CIs for the three levels of the interactions of shade and time, and duty cycle and time for the categorical light model.

	Mean	2.50%	97.50%
txs[1]	0	0	0
txs[2]	-0.15	-0.20	-0.09
txs[3]	-0.53	-0.59	-0.47
txd[1]	0	0	0
txd[2]	-0.09	-0.16	-0.01
txd[3]	-0.03	-0.10	0.03

Table A3.3. 35-g device posterior means and 95% CIs for the three levels of the interactions of shade and time, and two levels of duty cycle and time for the categorical light model.

	Mean	2.50%	97.50%
txs[1]	0	0	0
txs[2]	-0.17	-0.27	-0.10
txs[3]	-0.86	-0.92	-0.79
txd[1]	0	0	0
txd[2]	0.03	-0.02	0.09

Table A3.4. Table of expected fix capacity for 90% solar exposure provided by Lotek (A. Marsh, July 2019) based on the approximate migration route of an American avocet (*Recurvirostra americana*), which aided in our decisions of duty cycles to test. Red boxes indicate that the amount of data collected will outpace the amount that can be transmitted though the Argos satellite system, and therefore will result in remaining data being stored in the tag's memory.

Please beware: Estimate ONLY.

	Unknown Region [29, -98]	Unknown Region [29, -98]	Unknown Region [29, -98]	Unknown Region [31, -98]	Unknown Region [41, -101]	Unknown Region [41, -101]	Unknown Region [41, -101]	Unknown Region [41, -101]	Unknown Region [31, -98]	Unknown Region [31, -98]	Unknown Region [29, -98]	Unknown Region [29, -98]
V0.01	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Exposure	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%
Year 1	17 fixes per Day	19 fixes per Day	23 fixes per Day	23 fixes per Day	26 fixes per Day	26 fixes per Day	26 fixes per Day	24 fixes per Day	19 fixes per Day	14 fixes per Day	11 fixes per Day	8 fixes per Day
Year 2	8 fixes per Day	10 fixes per Day	12 fixes per Day	15 fixes per Day	15 fixes per Day	17 fixes per Day	5 fixes per Day	4 fixes per Day	3 fixes per Day	2 fixes per Day	2 fixes per Day	1 fix per Day
Year 3	2 fixes per Day	2 fixes per Day	3 fixes per Day	3 fixes per Day	4 fixes per Day	4 fixes per Day	4 fixes per Day	3 fixes per Day	3 fixes per Day	2 fixes per Day	2 fixes per Day	1 fix per Day
Year 4	1 fix per Day	2 fixes per Day	2 fixes per Day	3 fixes per Day	3 fixes per Day	4 fixes per Day	4 fixes per Day	3 fixes per Day	3 fixes per Day	2 fixes per Day	1 fix per Day	1 fix per Day
Year 5	1 fix per Day	1 fix per Day	2 fixes per Day	3 fixes per Day	3 fixes per Day	3 fixes per Day	3 fixes per Day	3 fixes per Day	2 fixes per Day	2 fixes per Day	1 fix per Day	1 fix per Day

Table A3.5. Table of expected fix capacity for 50% solar exposure provided by Lotek (A. Marsh, July 2019) based on a realistic location for a Northern bobwhite (*Colinus virginianus*), which aided in our decisions of duty cycles to test.

Please beware: Estimate ONLY.	Unknown Region [37, 94]	Unknown Region [37, 94]	Unknown Region [37, 94]	Unknown Region [37, 94]	Unknown Region [37, 94]	Unknown Region [37, 94]	Unknown Region [37, 94]	Unknown Region [37, 94]	Unknown Region [37, 94]	Unknown Region [37, 94]	Unknown Region [37, 94]	Unknown Region [37, 94]
V0.01	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Exposure	50%	50%	50%	50%	50%	50%	50%	50%	50%	50%	50%	50%
Year 1	11 fixes per Day	14 fixes per Day	16 fixes per Day	18 fixes per Day	18 fixes per Day	17 fixes per Day	15 fixes per Day	13 fixes per Day	11 fixes per Day	9 fixes per Day	6 fixes per Day	5 fixes per Day
Year 2	5 fixes per Day	7 fixes per Day	8 fixes per Day	10 fixes per Day	10 fixes per Day	9 fixes per Day	2 fixes per Day	2 fixes per Day	2 fixes per Day	1 fix per Day	1 fix per Day	1 fix per Day
Year 3	1 fix per Day	1 fix per Day	2 fixes per Day	2 fixes per Day	2 fixes per Day	2 fixes per Day	2 fixes per Day	2 fixes per Day	1 fix per Day	1 fix per Day	1 fix per Day	1 fix per Day
Year 4	1 fix per Day	1 fix per Day	1 fix per Day	2 fixes per Day	2 fixes per Day	2 fixes per Day	2 fixes per Day	2 fixes per Day	1 fix per Day	1 fix per Day	1 fix per Day	6 fixes per Week
Year 5	1 fix per Day	1 fix per Day	1 fix per Day	2 fixes per Day	2 fixes per Day	2 fixes per Day	1 fix per Day	1 fix per Day	1 fix per Day	1 fix per Day	1 fix per Day	5 fixes per Week

Figures

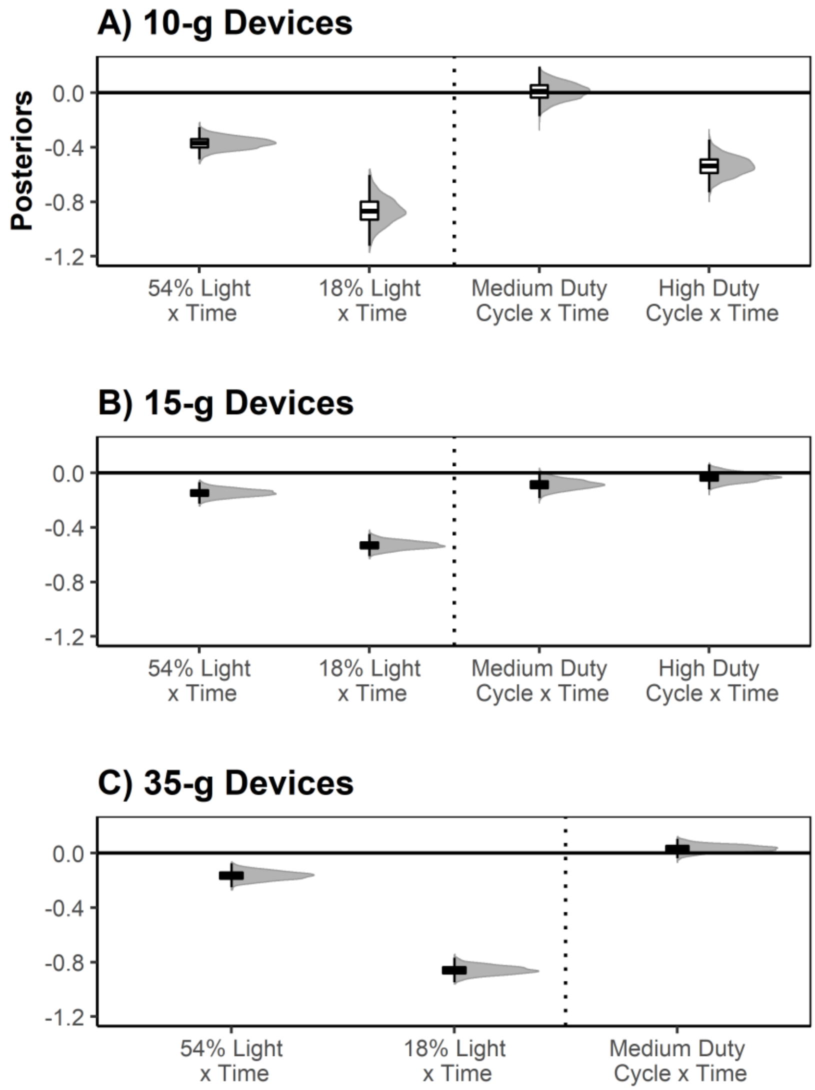

Figure A3.1. Effect sizes based on posterior samples for the interactions of light and time and the two greatest-frequency duty cycles in relation to the lowest duty cycle level for each of the device types (10-g Ornitrack-10, 15-g Ornitrack 15, and 35-g Ornitrack N35) tested in the categorical light model. The horizontal line indicates 0 and the dotted vertical line separates light from duty cycle within each device type.

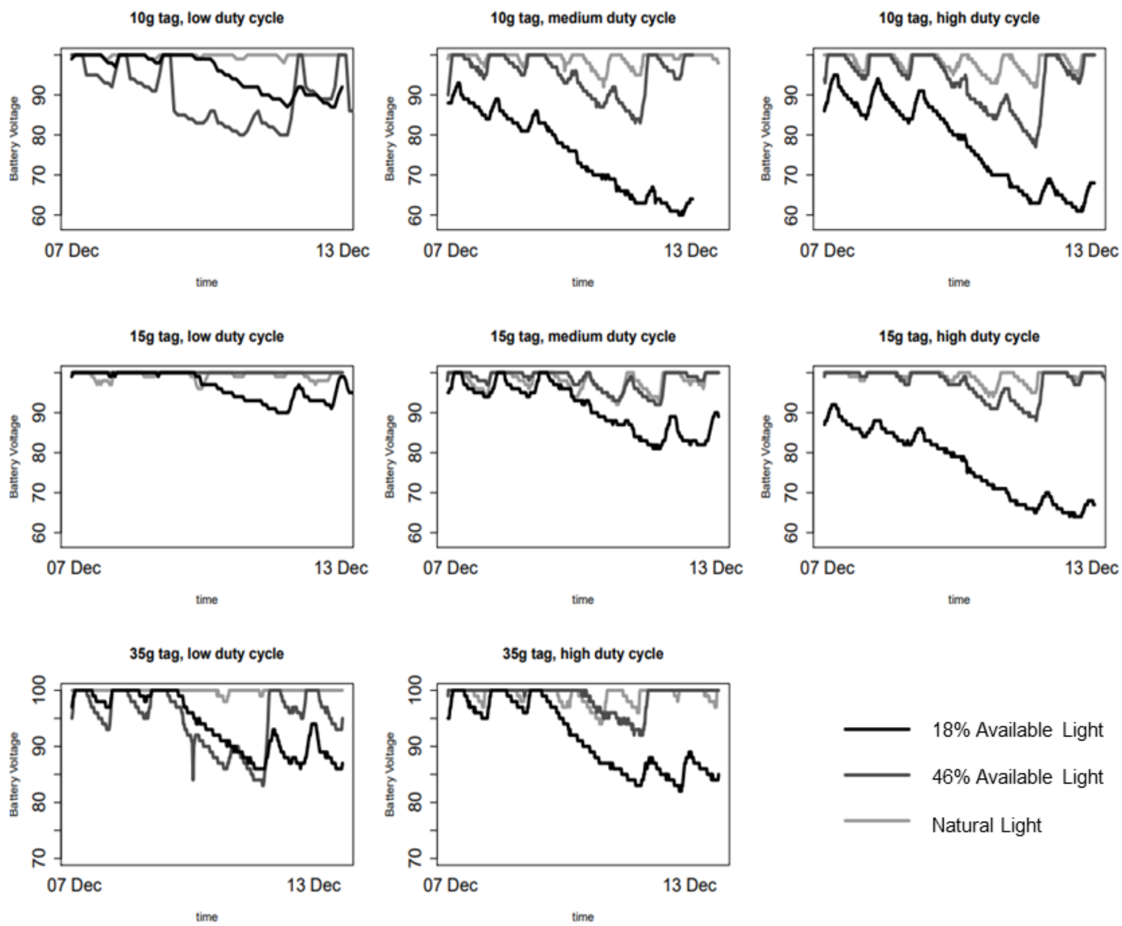

Figure A3.2. Raw data of battery voltage over time for tracking devices (10-g Ornitrack-10, 15-g Ornitrack 15, and 35-g Ornitrack N35) under natural light, 46% available light, and 18% available light and low, medium, and high duty cycles.

Example code for cumulative and categorical light models

```
# Cumulative Light Model
#  Trade-offs in performance of six lightweight automated tracking devices for birds
# Clements, Ballard, Eccles, Sinnott, Weegman 2021
b_data<-read.csv('cul10_072820.csv', header=T)
b_data$date <- as_date(b_data$date)

batt<-(b_data$battery)/100
```

```
light<-as.numeric(b_data$culight)
light <- (light-mean(light))/sd(light)
duty<-as.numeric(as.factor(b_data$dutycycle))
device<-as.numeric(as.factor(b_data$id))
time <- rep(1:length(unique(b_data$date)), times=length(unique(b_data$id)))
time<-as.numeric(time)
time <- (time-mean(time))/sd(time)
logit_batt <- logit(batt*0.99)

ni <- 5000
nt <- 5
nb <- 2000
nc <- 3


sink("bat10_d_l_cul.jags")
cat("
   # likelihood

   model{
   for (i in 1:N){
   batt[i]~dnorm(mu[i], tau)
   mu[i] <- l*light[i] + d[duty[i]]
   + t*time[i] + alpha
   }
   alpha ~ dnorm(0, 0.001)
   t ~ dnorm(0,0.001)
   l ~ dnorm(0,0.001)
   txl ~ dnorm(0,0.001)
   d[1] <- 0
   txd[1] <- 0
   for (k in 2:3) {d[k] ~ dnorm(0, 0.001)}
   for (m in 2:3) {txd[m] ~ dnorm(0, 0.001)}

   tau <- pow(sig, -2)
   sig ~ dunif(0, 10)
   }
   ",fill = TRUE)
sink()


# Bundle data
jags.data <- list(light=light, duty=duty,
              batt=logit_batt, time=time, N = nrow(b_data))
```

```
# Initial values
inits <- function (){list(alpha = 0, d=c(NA, 0, 0))}

# Parameters monitored
parameters <- c("l","t", "d","alpha","sig")

# Call jags from R
bat10_d_l_cul <- jags(jags.data, inits, parameters, "bat10_d_l_cul.jags",
                    n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb)

# Summarize posteriors
print(bat10_d_l_cul, digits = 3)

# Categorical Light Model
b_data<-read.csv('bat10_cat_090320.csv')
head(b_data)
batt<-b_data$battery
shade<-as.numeric(as.factor(b_data$shade))
duty<-as.numeric(as.factor(b_data$dutycycle))
device<-as.numeric(as.factor(b_data$id))
time <- as.numeric(b_data$timeindex)
time <- (time-mean(time))/sd(time)
logit_batt <- logit(batt*0.99)

ni <- 5000
nt <- 5
nb <- 2000
nc <- 3

#

## shade[1] duty[1] and tagid[1] are reference conditions

sink("batt_txd_txs_10.jags")
cat("
   # likelihood

   model{
   for (i in 1:N){
   batt[i] ~ dnorm(mu[i],tau)
   mu[i] <- s[shade[i]] + d[duty[i]]
   + t*time[i] + txs[shade[i]]*time[i] + txd[duty[i]]*time[i] + alpha
   }
   alpha ~ dnorm(0, 0.001)
   t ~ dnorm(0,0.001)
   d[1] <- 0
```

```
    s[1]<-0
    txs[1]<-0
    txd[1] <- 0
    for (j in 2:3) {s[j] ~ dnorm(0, 0.001)}
    for (k in 2:3) {d[k] ~ dnorm(0, 0.001)}
    for (m in 2:3) {txs[m] ~ dnorm(0, 0.001)}
    for (p in 2:3) {txd[p] ~ dnorm(0, 0.001)}

    tau <- pow(sig, -2)
    sig ~ dunif(0, 10)
    }
    ",fill = TRUE)
sink()


# Bundle data
jags.data <- list(shade=shade, duty=duty,
              batt=logit_batt, time=time, N = nrow(b_data))


# Initial values
inits <- function (){list(txs=c(NA,0,0), txd=c(NA,0,0), alpha = 0, s=c(NA, 0, 0), d=c(NA,
0, 0))}

# Parameters monitored
parameters <- c("s","t","txs", "txd", "d","alpha","sig")

# Call jags from R
batt_txd_txs_10 <- jags(data=jags.data, inits=inits, parameters.to.save=parameters,
model.file="batt_txd_txs_10.jags",
                  n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb, parallel=T)
```

APPENDIX IV

Supplementary information for Chapter 5

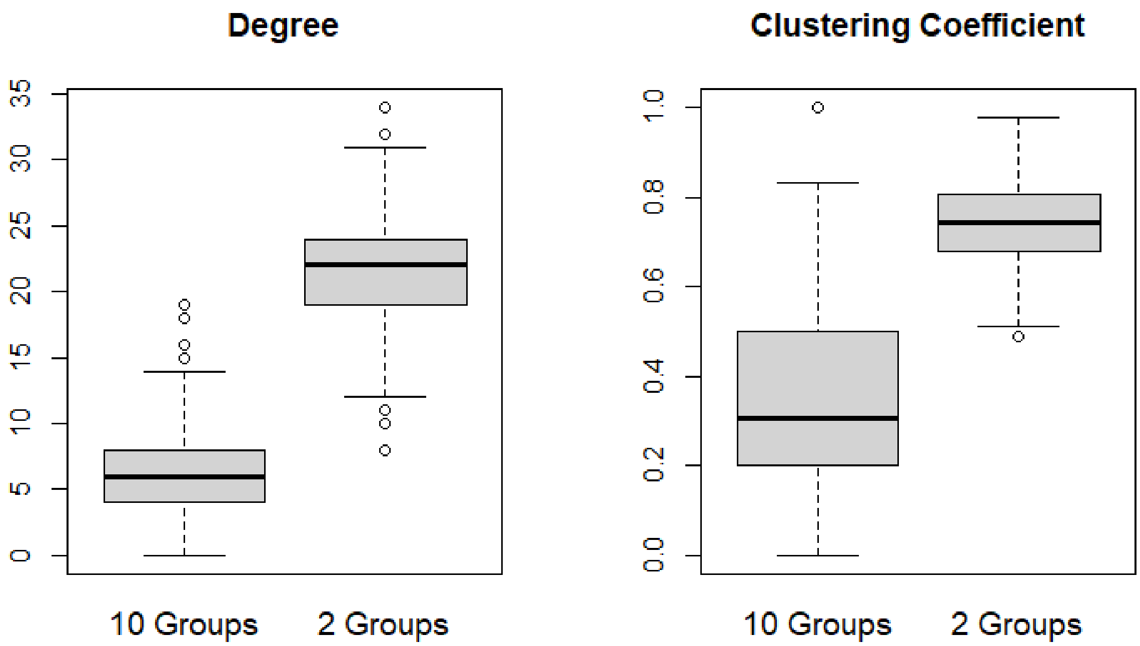

Figure A4.1. Boxplot of individual degree and clustering coefficient for networks created for 10-group populations and 2-group populations of 50 individuals, across 50 runs of the simulation. Both degree and clustering coefficient are substantially higher for the 2-group populations.

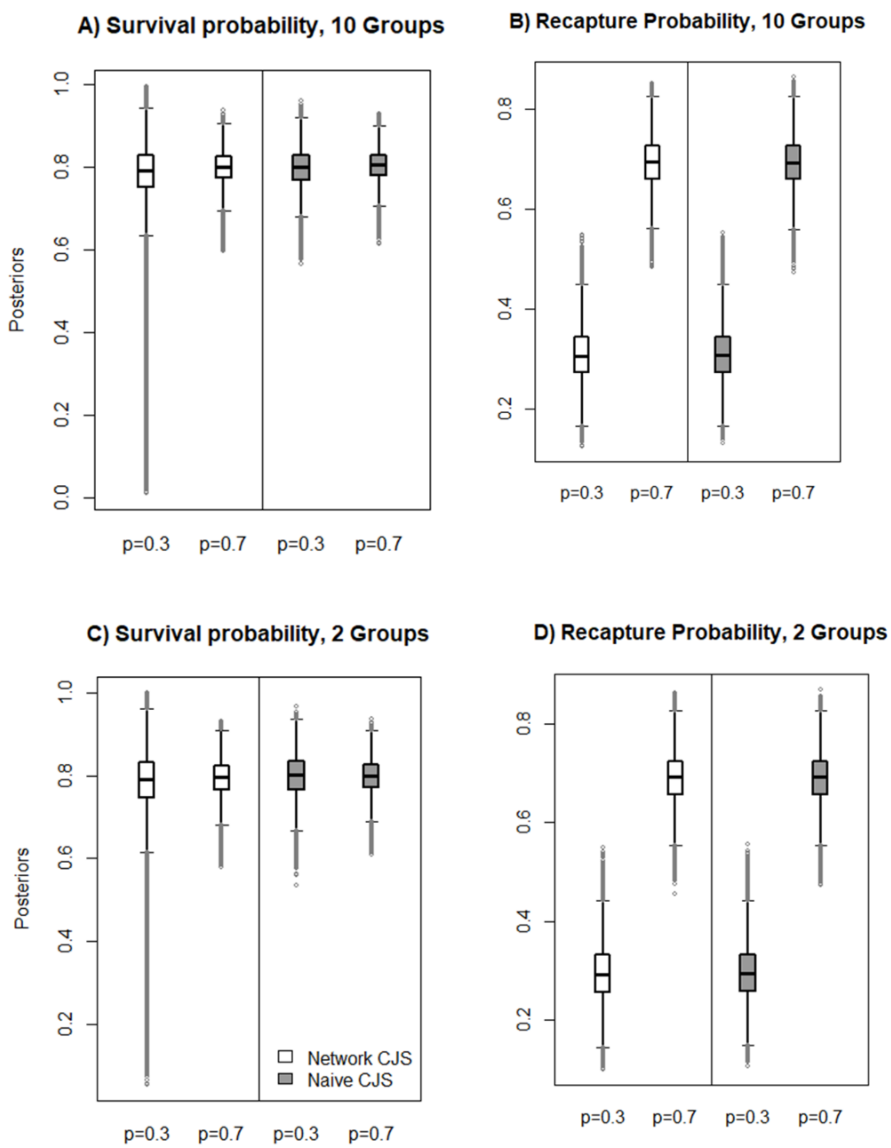

Figure A4.2. Posterior values for survival and recapture probability for all simulated populations using our social network CJS model and a traditional, naïve CJS model without network information.

Simulation Code

The following code can be used to run our simulation combining social network analysis and a Cormack-Jolly-Seber (CJS) survival model. This simulation requires Jags to be installed (https://sourceforge.net/projects/mcmc-jags/).

Number of simulations (nsim), number of individuals (nind), and number of years (nyrs) provide a basic structure for the data and simulation and can be modified.

Recapture probability (pcap) can also be modified, and increasing the recapture probability will increase the number of encounters on which the social network and survival models are constructed.

Number of groups (ngrp) determines the number of social groups individuals in the simulation are assigned to, and changing the number of groups will provide networks with different structures and therefore different values of degree and clustering coefficient.

Covariate and network effects can also be modified to reflect specific study systems.

```
# Packages
library(jagsUI)
library(boot)

#==============
# Basic values
#==============
nsim <- 1 # number of simulations (we used 50)
# Values
nind <- 50 # number of individuals in the true network
pcap <- .7 # capture probability, 0.3 or 0.7
ngrp <- 2  # number of groups, 2 or 10
nyrs <- 10  # number of years

# Probability of internal and external edges
pei <- 0.70 # probability of edge within group
pee <- 0.02 # probability of edge outside group

# Covariate effects on internal and external edges
x1_pei_eff <- 0.8
x1_pee_eff <- 0.8
x2_pei_eff <- 1.8
x2_pee_eff <- 1.8

# Network effects on survival
```

```
omega_mean <- .8 # mean survival
omega_alpha <- logit(omega_mean) # intercept of survival regression
omega_deg <- .5 # slope, effect of degree on survival
omega_clu <- .3 # slope, effect of clustering coefficient on survival

for (s in 1:1) {
#==================
# Simulate network
#==================
# Initial network
groups <- rep(1:ngrp, each=nind/ngrp) #vector of groups
x1 <- rnorm(nind, 0, 1) #x1 for each individual, normal distribution
x2 <- sample(c(0,1), nind, replace=T) # x2 for each individual, 0 or 1

# Create empty network to fill
net_pi <- net <- matrix(0, nind, nind)

#Fill network matrix
for(i in 1:(nind-1)) {
for(j in (i+1):nind) {
# probability of edges between individuals in the same group, from regression using x1
and x2
      if(groups[i] == groups[j]) {
          net_pi[i,j] <- inv.logit(
            logit(pei) +
              (x1_pei_eff * x1[i] + x1_pei_eff * x1[j]) / 2 +
              (x2_pei_eff * x2[i] + x2_pei_eff * x2[j]) / 2)
          #probability of edges between individuals in different groups, from
      regression using x1 and x2
        } else if (groups[i] != groups[j]) {
          net_pi[i,j] <- inv.logit(
            logit(pee) +
              (x1_pee_eff * x1[i] + x1_pee_eff * x1[j]) / 2 +
              (x2_pee_eff * x2[i] + x2_pee_eff * x2[j]) / 2)
        }
        net[i,j] <- rbinom(1, 1, net_pi[i,j])
      } # j
    } # i

    for (i in 2:nind) {
      for (j in 1:(i-1)) {
        net[i,j] <- net[j,i]
      } # j
    } # i

    for (i in 1:nind) {
```

```
    net[i,i] <- 0
  } # i

  net_sub <- array(NA, dim=c(nind, nind, nind)) # this is just for calculating
clustering coef
  for (i in 1:nind) {
    for (k in 1:nind) {
      for (l in 1:nind) {
        net_sub[i,k,l] <- ifelse(net[i,k]==1 & net[i,l]==1, net[k,l], 0)
      } # l
    } # k
  } # i

  deg <- clu <- numeric(nind) # calculate degree and clustering coefficient
  for(i in 1:nind) {
    deg[i] <- sum(net[i,])
    if (deg[i] <= 1) {
      clu[i] <- 0
    } else {
      clu[i] <- sum(net_sub[i,,]) / (deg[i] * (deg[i] - 1))
    }
  } # i

  # survival regression
  omega <- inv.logit(omega_alpha + omega_deg * (deg - mean(deg)) / sd(deg) +
omega_clu * (clu - mean(clu)) / sd(clu))

#===========================
# Simulate survival history
#===========================
  sh <- matrix(0, nind, nyrs)
  sh[,1] <- 1
  for (t in 2:nyrs) {
    sh[,t] <- rbinom(nind, 1, sh[,t-1]*omega)
  }

#==========================
# Simulate capture history
#==========================
  ch <- matrix(rbinom(nind*nyrs, 1, sh*pcap), nind, nyrs)
  for (i in 1:nind){
    for(t in 1:nyrs){
      ch[i,t] <- rbinom(1, sh[i,t], pcap)
    }
  }
```

```
#==========================
# Define CJS model in Jags
#==========================
       sink('net_cjs.txt')
       cat("
        model {
        # Priors
        pei ~ dunif(0, 1)
        pee ~ dunif(0, 1)

        x1_pei_eff ~ dnorm(0, .01)
        x2_pei_eff ~ dnorm(0, .01)
        x1_pee_eff ~ dnorm(0, .01)
        x2_pee_eff ~ dnorm(0, .01)

        omega_mean ~ dunif(0, 1)
        omega_alpha <- logit(omega_mean)
        omega_deg ~ dnorm(0, .01)
        omega_clu ~ dnorm(0, .01)

        pcap ~ dunif(0, 1)

        # Covariates with missing values
        for (k in 1:ngrp) {
          pi_group[k] <- 1 / ngrp
        } # k

        for (i in 1:nind) {
          x1[i] ~ dnorm(0, 1)
          x2[i] ~ dbin(.5, 1)
          groups[i] ~ dcat(pi_group)
        } # i

        # Process model
        for(i in 1:(nind-1)) {
          for(j in (i+1):nind) {
            net_pi[i,j] <-
              ifelse(groups[i] == groups[j],
                ilogit((logit(pei) + logit(pei) + x1_pei_eff * x1[i] + x1_pei_eff * x1[j] +
      x2_pei_eff * x2[i] + x2_pei_eff * x2[j]) / 2),
                ilogit((logit(pee) + logit(pee) + x1_pee_eff * x1[i] + x1_pee_eff * x1[j] +
      x2_pee_eff * x2[i] + x2_pee_eff * x2[j]) / 2))
          } # j
        } # i

        for (i in 2:nind) {
```

```
      for (j in 1:(i-1)) {
        net_pi[i,j] <- net_pi[j,i]
      } # j
    } # i

    for (i in 1:nind) {
      net_pi[i,i] <- 0
    } # i

    for (i in 1:nind) {
      for (j in 1:nind) {
        net[i,j] ~ dbin(net_pi[i,j], 1)
      } # j
    } # i

    # calculate degree & clustering coefficient
    for (i in 1:nind) {
      for (k in 1:nind) {
        for (l in 1:nind) {
          net_sub[i,k,l] <- ifelse(net[i,k]*net[i,l]==1, net[k,l], 0)
        } # l
      } # k
    } # i

    for(i in 1:nind) {
      deg[i] <- sum(net[i,1:nind])
      clu[i] <- ifelse(deg[i]<=1, 0, sum(net_sub[i,1:nind,1:nind]) / (deg[i] * (deg[i] -
1)))
    } # i

    for(i in 1:nind) {
      omega[i] <- ilogit(omega_alpha + omega_deg * (deg[i] - mean(deg)) / sd(deg)
+ omega_clu * (clu[i] - mean(clu)) / sd(clu))
    } # i

    # predict survival with degree and clustering coefficient
    for (i in 1:nind) {
      sh[i,1] <- 1
      for (t in 2:nyrs) {
        sh[i,t] ~ dbin(omega[i] * sh[i,t-1], 1)
      } # t
    } # i

  # Observation model
  for (i in 1:nind) {
    for (t in 1:nyrs) {
```

```
    ch[i,t] ~ dbin(sh[i,t] * pcap, 1)
   } # t
  } # i
   }
  ", fill=TRUE)
  sink()

#==========
# Run Jags
#==========
  id_obs <- which(rowSums(ch) > 0)
  x1_obs <- x1
  x1_obs[-id_obs] <- NA
  x2_obs <- x2
  x2_obs[-id_obs] <- NA
  groups_obs <- groups
  groups_obs[-id_obs] <- NA

  net_obs <- net
  net_obs[-id_obs,] <- NA
  net_obs[,-id_obs] <- NA

  net_init <- matrix(sample(c(0,1),nind*nind,replace=T), nind, nind)
  net_init[lower.tri(net_init, diag=F)] <- net_init[upper.tri(net_init, diag=F)]
  diag(net_init) <- 0
  net_init[which(!(is.na(net_obs)))] <- NA

  sh_init <- matrix(, nind, nyrs)
  sh_init[,-1] <- 1

  data <- list(
   nind=nind, nyrs=nyrs, ngrp=ngrp,
   net=net_obs, ch=ch,
   groups=groups_obs, x1=x1_obs, x2=x2_obs)

  inits <-function() list(
   pei=.5, pee=.5,
   x1_pei_eff=0, x2_pei_eff=0,
   x1_pee_eff=0, x2_pee_eff=0,
   omega_mean=.5, omega_deg=0, omega_clu=0,
   net=net_init, sh=sh_init,
   pcap=.5)

  parms <- c('pei', 'pee',
        'x1_pei_eff', 'x1_pee_eff',
        'x2_pei_eff', 'x2_pee_eff',
```

```
            'omega_mean', 'omega_deg','omega_clu',
            'pcap')

  fit <- jags(data, inits, parms, 'net_cjs.txt',
             #n.chains=1, n.adapt=100, n.burnin=100, n.iter=200, n.thin=1,
             n.chains=3, n.adapt=2000, n.burnin=2000, n.iter=4000, n.thin=1,
             parallel=TRUE)

  save(fit, file=paste(c('fit_net_cjs_', nind, '_', pcap, '_', s, '.RData'), collapse=''))
  save(data, file=paste(c('data_net_cjs_', nind, '_', pcap, '_', s, '.RData'),
collapse=''))

} # s
```

VITA

Sarah Jeanne Clements was born in New Hampshire on July 9, 1995. She graduated from John Stark Regional High School in 2013 and is an alumna of 4-H. She graduated from the University of New Hampshire in 2016 with a B.S. in Wildlife and Conservation Biology, during which time she worked as a technician and undergraduate researcher on saltmarsh sparrow, shrubland songbird, bobcat, and New England cottontail projects in New Hampshire and Maine. In 2016-2017, she worked at Tin Mountain Conservation Center studying forest songbirds and brook trout. In 2017 she was awarded a National Science Foundation Graduate Research Fellowship and began PhD work at the University of Missouri in the lab of Dr. Mitch Weegman. Her fieldwork during grad school took her to Louisiana, Texas and Chile. She was the secretary and president of the Wildlife & Fisheries Sciences Graduate Student Organization as well as the funding officer and event coordinator for Science on Wheels, an outreach organization. She also has work experience as a farm hand on five different horse farms and one alpaca farm, a custodian at a middle school, the person in charge of salad at a cafeteria, and a taekwondo instructor. Her dog, Emmett, is the best dog ever.