

ABSTRACT

Title of Dissertation: TIME IS ENERGY: DRIVERS OF MIGRATORY
AND NON-MIGRATORY MOVEMENTS BY
SOARING BIRDS

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Vultures are obligate scavengers and search over large areas for carrion, which is ephemeral. To profit from carrion, they are also obligate soarers that rely on the availability of environmental updrafts to subsidize flight. This restricts their flight spatially and temporally to where and when strong updrafts are available. In this dissertation, I investigate how Turkey Vultures (*Cathartes aura*) use stopovers to both avoid inclement weather and to replenish spent fuel reserves, as well as how the timing of movement activity differs according to flight mode.

Using GPS-tracking data from four migratory Turkey Vulture populations, I evaluated how Turkey Vultures respond to changing weather conditions. During stopovers, movement activity was positively correlated with conditions that promote thermal development, suggesting not all stopovers are used for

weather-avoidance. Turkey Vultures began stopovers immediately in response to deteriorating weather conditions but their departure from stopovers was delayed relative to improvements in weather, behavior that is consistent with an energy-minimization strategy.

I estimated total energetic costs for each migration and identify probable refueling stopovers. Only long-distance Turkey Vulture migrants regularly stop to feed. Overall migratory costs are driven by migration duration, and therefore are lower in the spring when vultures migrate faster, which may contribute to seasonal differences in flight behavior.

Last, I compared the non-migratory movements of 49 avian species to test for the influence of flight mode on the timing of movement activity. Terrestrial soaring birds began activity later and stopped activity earlier than other birds. This study demonstrates that flight mode influences temporal patterns of daily movement activity of birds.

This dissertation enhances our understanding of how soaring birds cope with the temporal and spatial restrictions on their movements. During non-migration, soaring birds are active for longer proportions of the day to search for food over greater spatial areas than flapping birds. During migration, total energetic costs are driven more by migration duration than by behavior. Therefore, an energy minimization strategy for Turkey Vultures is also a time minimization strategy and vultures are expected to optimize their migration so that they spend the fewest days migrating as possible.

TIME IS ENERGY: DRIVERS OF MIGRATORY AND NON-MIGRATORY
MOVEMENTS BY SOARING BIRDS

by

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Preface

This dissertation contains three chapters, written in manuscript form, and appendices to chapters 1 and 3. This dissertation includes a previously published work (chapter 3).

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Chapter 3: Diurnal timing of nonmigratory movement by birds: the importance of foraging spatial scales.

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Dedication

To Eric, Graham, John, Michael, Terry and Terry: for their thoughtful discourse on the physical limitations on avian flight.

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I am grateful for all the people I have had the pleasure to know and work with over the last several years. They have all contributed to this dissertation in some way. In particular, I would like to acknowledge:

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List of Abbreviations

GPS, global positioning system

BMR, basal metabolic rate

FPT, first passage time

MR, metabolic rate (specific to behavior; kJ/h)

d , Days fasted

β , energy savings of 4% per day

ACT , metabolic expenditure for activity (kJ/day)

W , daily body mass (g)

t , total duration of behavior (h/day)

DEE , Daily energy expenditure (kJ/day)

e , energetic equivalent of the catabolism of fat (39.7 kJ/g)

AM , daily body mass change (g)

Kg_{start} , starting body mass (g)

Chapter 1: Inclement weather prevents migratory progress for obligate soaring migrants

1.1 Abstract

Migrating birds experience weather conditions that change with time, which affect their decision to stop or resume migration. Soaring migrants are especially sensitive to changing weather conditions because they rely on the availability of environmental updrafts to subsidize flight. We used satellite tracking data from four migratory Turkey Vulture (*Cathartes aura*) populations, paired with local weather data to determine how frequently the vultures use stopovers and to evaluate how they use stopovers to avoid inclement weather. We analyzed 174 migrations of 33 individuals from 2006 - 2019 and identified 590 stopovers. Stopover duration ranged from 2 h to more than 11 days, with 51% of stopovers lasting < 24 h. Stopover use increased with migration distance and was more frequent during fall than spring migration. Turkey Vultures began stopovers immediately in response to deteriorating weather conditions but their departure from stopovers was delayed relative to improvements in weather, behavior that is consistent with an energy-minimization migration strategy. During stopovers, the proportion of activity was positively correlated with conditions that promote thermal development,

suggesting not all stopovers are used for weather-avoidance. As revealed by our results, birds are capable of responding rapidly to their environment; therefore, for studies interested in external drivers of stopover use it is essential that stopovers be identified at fine temporal scales.

1.2 Introduction

As birds migrate, they pass through a variety of habitats and experience variable environmental conditions. Locally, migrating birds experience weather conditions that change with time, which are known to influence their flight behavior, especially the likelihood of stopping and resuming active migration. Passerines avoid departing stopovers during precipitation (Smith and McWilliams 2014) and are more likely to resume active migration during low wind speeds and decreasing surface pressure (Matthews and Rodewald 2010). Migratory raptors also avoid migrating under poor weather conditions, where they are rarely observed migrating during cold fronts but are observed in peak numbers immediately following a passing cold front (Allen et al. 1996, Inzunza et al. 2005). Similarly, the likelihood of soaring birds stopping over increases on days with cloud cover and rain (Goodrich 2010), and when thermal updraft strength is weak (*sensu* Dodge et al. 2014).

Soaring birds, like condors (Poessel et al. 2018), are especially sensitive to changing weather conditions because they rely on the availability of environmental updrafts to subsidize flight. Although terrestrial birds can soar using orographic (Bohrer et al. 2012) or turbulent updrafts (Mallon et al. 2015) to subsidize flight, thermals (Dodge et al. 2014) are the most important type of updraft for most soaring migrants because thermals are widely distributed across the landscape (Pennycuick 1975), allow birds to reach altitudes necessary for fast cross-country soaring, and allow for straight, efficient flight paths (Duerr et al. 2012). Thermals (i.e., vortices of ascending hot air surrounded by descending cooler air) (Pennycuick 1975, Kerlinger 1989) are generated by differential heating of the earth's surface. Thermals are, therefore, an uncertain resource that only form under appropriate weather conditions (Kerlinger 1989). Poor weather conditions slow or prevent the development of updrafts, thereby forcing birds to switch to energetically expensive flapping flight (Spaar and Bruderer 1997, Ferland-Raymond et al. 2005) or grounding them.

Despite recognizing the relationship between migratory flight behavior and changing weather conditions, stopover use by large, soaring birds has been understudied. This is in part due to challenges around defining what constitutes a stopover - rule selection varies depending on the species ecology and desired behavior. Some of the definitions of stopovers include: ≤ 150 km/day (Kochert

et al. 2011), < 100 km/day (Hake et al. 2001, Crawford and Long 2017), < 50 km/day of directed flight (Sergio et al. 2017), \leq 25 km/day (Vansteelant et al. 2015), >24 h in an area <30 km in diameter (Shiu et al. 2006), and spending more than 24 h in an area (Monti et al. 2018). These definitions pose two problems. First, all of these definitions consider the durations of stopovers to be \geq 24 h, due in part to the assumption that stopovers are primarily used to refuel. If we define stopovers based on the movement behavior of individuals, however, stopovers occur whenever individuals do not engage in fast, directed flight but are otherwise expected to do so. Using this movement-based definition of stopovers, the duration of stopovers may be much shorter than 24 h as local weather conditions can change rapidly and may only prevent birds from flying for short periods of time (i.e., hours). Second, identification at the daily scale may underestimate the duration of stopovers that are > 24 h. For example, birds may actively migrate for several hours before stopping over and exceed the distance threshold. The following day would be identified as the start of the stopover, several hours after the bird ceased directed flight. Alternatively, a bird that is refueling may travel 10's of kilometers in a day searching for food and would exceed these distance thresholds although they are not engaged in directed flight. Clearly, standardized measures of movements that constitute what are and are not stopovers are warranted.

Stopover behavior is ideal to study using Turkey Vultures (*Cathartes aura*) because vultures are obligate soaring birds (Ruxton and Houston 2004) and cannot sustain themselves aloft using flapping flight (Rosser and George 1986). Hence, Turkey Vultures should be more sensitive to changes in weather than other soaring migrants and stopover more frequently than other migratory soaring species. We anticipated some stopovers may be quite short if they were responding to passing weather fronts in the late afternoon or early morning that overlapped with their daily roosting patterns. Therefore, we chose to be highly conservative with our selection of stopovers and identified the start and end of stopovers at the hourly scale. We sought to determine how extensively Turkey Vultures depend on stopovers, and how the birds use stopovers. To this end, we used satellite tracking data from four migratory Turkey Vulture populations, paired with local weather data. As a first step, we identified stopovers using first passage time (FPT). We automated identification of stopovers by selecting the radius and FPT threshold based on the structure of the data, to avoid under- and over-selection of stopovers, and to avoid selection biases. We explore general patterns of stopover use by comparing the frequencies of stopover use between seasons and across populations.

Next, we sought to determine if Turkey Vultures migrated with a time or energy minimization strategy, and to evaluate when Turkey Vultures began their

stopovers, relative to the onset of inclement weather. Birds that minimize energetic costs should fly as long as weather conditions allow for energy-efficient soaring flight; therefore energy-minimizers would not switch to flapping flight and instead would stop as soon as weather conditions deteriorate. Birds that minimize time would fly as long as possible, switching to flapping flight and stopping after weather conditions deteriorate. Alternatively, birds may not be time or energy minimizers but instead may be risk-averse and stop flying before weather conditions deteriorate. As obligate scavengers, Turkey Vultures have several behavioral and physiological adaptations to minimize energetic costs (Hatch 1970, Mallon et al. 2015, Grilli et al. 2017); therefore, we hypothesized that Turkey Vultures would use an energy minimization strategy.

Last, we evaluated if average weather conditions affected movement activity during stopovers, or only the decision to stop and resume migration.

1.3 Methods

1.3.1 Study Species

We used GPS-GSM tracking data collected between 2006 - 2019 from four migratory populations that represent three of the seven subspecies of Turkey Vulture (*C. aura aura*, *C. aura meridionalis*, and *C. aura ruficollis*). These populations range across most of the species' distribution – from Canada to

southern South America (Figure 1.1). Tracking data were provided by Hawk Mountain Sanctuary (Pennsylvania, USA) and accessed via Movebank (Wikelski and Kays 2018).

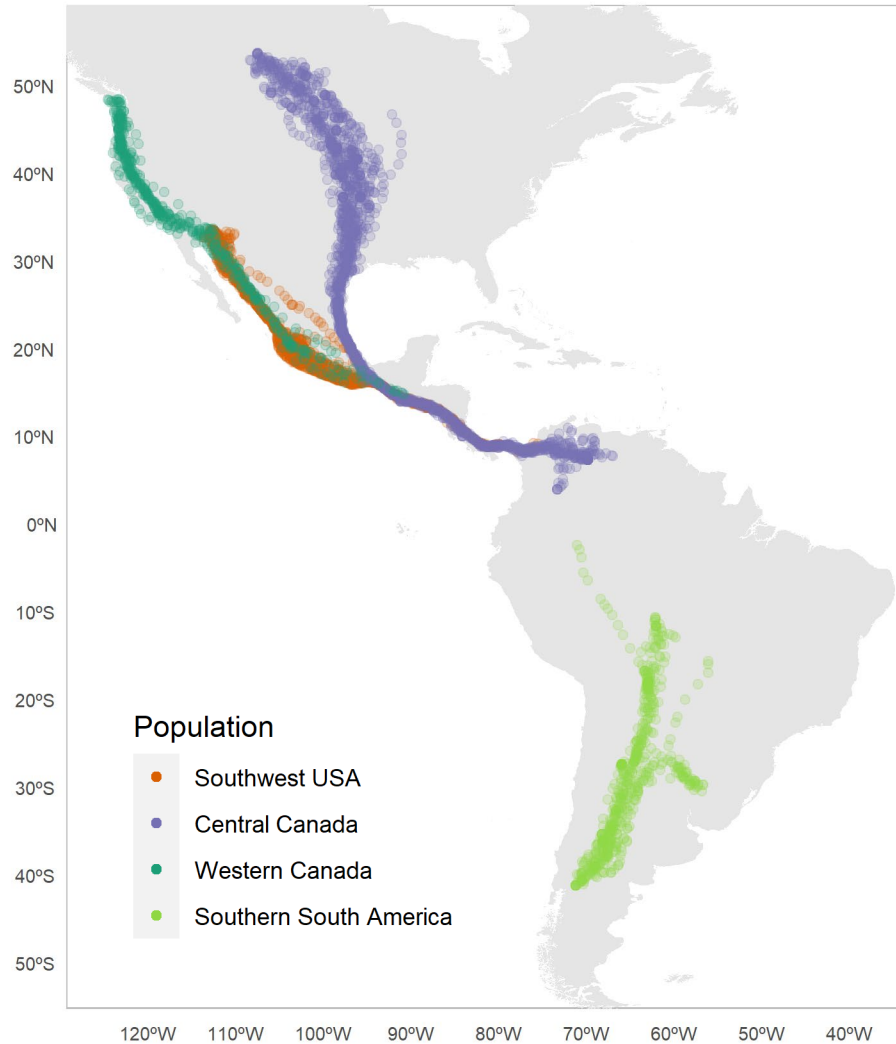


Figure 1.1. Map of daily migration locations for 33 individuals across four populations and three subspecies: Southwest USA (orange; *C. aura aura*), Central Canada (purple; *C. aura meridionalis*), Western Canada (dark green; *C. aura meridionalis*), Southern South America (light green; *C. aura ruficollis*).

1.3.2 Weather Predictors

We accessed weather data using Movebank Env-data annotation (Dodge et al. 2013). Several weather variables were selected (Table 1.1), which were considered important to the use of thermal or orographic soaring by Golden Eagles (Duerr et al. 2015). To evaluate the behavioral response of Turkey Vultures to changing weather conditions, we excluded any static variables (e.g. NDVI, landcover).

Table 1.1. Definitions of weather variables used. For variables that have units, units are provided in parentheses. Weather data were sourced from European Centre for Medium-Range Weather Forecasts (ECMWF) or Movebank.

Weather variable	Source	Definition
Air temperature (C)	ECMWF	Air temperature 2 m above the ground
Boundary height (m)	ECMWF	The depth of air next to the earth's surface which is most affected by the resistance to the transfer of momentum, heat, or moisture across the surface.
Downward longwave thermal radiation (j m ⁻²)	ECMWF	Amount of downward thermal (longwave) radiation (heat emitted by the earth's surface and atmosphere) at the earth's surface
Downward shortwave thermal radiation (j m ⁻²)	ECMWF	Amount of downward incident solar (shortwave) radiation at the earth's surface
Latent heat flux (j m ⁻²)	ECMWF	Exchange of latent heat with the surface through turbulent diffusion (accumulated)
Precipitation fraction	ECMWF	The accumulated fraction of the model grid cell that was covered by large-scale precipitation.
Orographic updraft velocity (m/s)	Movebank	The velocity of upward air movement caused when rising terrain forces air to higher elevations

Sensible heat flux (j m ⁻²)	ECMWF	Exchange of heat with between the earth's surface and the atmosphere through turbulent air motion, excluding any heat transfer resulting from condensation or evaporation (accumulated)
Thermal updraft velocity (m/s)	Movebank	Velocity of thermal updrafts (air that rises as it is heated by the sun near the earth's surface)
Total atmospheric water (kg m ⁻²)	ECMWF	Total water in the entire atmospheric column (water vapor + cloud water + cloud ice)
Windspeed (m/s)	ECMWF	Calculated from wind u and v components

1.3.3 Stopover Classification

We used only migrations with regularly collected data (i.e., mean data interval <3 hours). We manually annotated migrations from continuous tracks using first passage time (FPT) (R package `adehabitatLT`; Calenge 2006). For the purposes of annotating migration and stopover locations, we interpolated any gaps within the movement trajectories to get hourly fixes.

To find potential stopovers using FPT, we selected the radius that minimized log-variance of FPT (between 2500 and 6000 m). The radii we selected were based on patterns of activity and inactivity in our dataset and will vary among species. To find the start and end times of each stopover, we used a threshold relative to the structure of the data to reduce under-selection of stopovers from tracks with high FPT variance and over-selection of stopovers from tracks with low FPT variance. Stopovers selected from FPT were rejected if <25% of the data was during daylight hours or if the duration was <2 hours. To find non-

stationary stopovers that were missed with this approach, we considered groups of >30 points within a 15km buffer to be a 'stopover'. To improve the precision of the start and end times of stopovers in our dataset, we removed the first and last observations if those speeds exceeded 95% of all the speeds during the stopover. If an individual ceased activity during normal roosting hours, we considered 0800 the following morning to be the start of the stopover.

1.3.4 Analysis

To determine if Turkey Vultures migrated with a time- or energy-minimization strategy, we looked for any evidence of lagged responses to changing weather variables. As not all stopovers were expected to be in response to weather, we sought to remove noise from the dataset by ranking stopovers by their proportion of activity. We used the 33% of stopovers characterized as the least active for these analyses. We subset each weather variable from 7 hours before to 7 hours after the start of each stopover. To facilitate comparison across populations with different climates and across years, we used the hourly change of each weather parameter as our response variables. For each hour, we then averaged the rate of change across all stopovers. For each variable, we used a generalized linear model with a loess smoother to visually inspect the average rate of change over time relative to the start of stopovers. We then determined if the start of stopovers lagged relative to the minima and maxima for each weather variable. To determine if the decision to depart from stopovers

lagged relative to changing environmental conditions, we repeated this analysis using the end of stopovers as the model predictor. We report the population-specific responses to changing weather variables at the start and end of stopovers in Appendix A.

To compare movement behavior during stopovers, we used FPT and proportion of activity as response variables. FPT at a small radius (250 m) is a measure of sedentariness while proportion of activity within a fixed radius is a measure of tortuousness. Proportion of activity was calculated during non-roosting hours, and activity was defined as > 1 km/h. For predictors, we selected the top eight variables with the strongest link to the start or end of stopovers. To evaluate the effect of mean weather conditions during a stopover on movement behavior, we used generalized linear mixed models (GLMM) with individuals as the random effect. We repeated this analysis instead using linear regressions where we averaged the response and predictor values to the individual-level. We found no difference in the results between the GLMM and linear regression, so we only report the results of the linear regression here. All analyses were done using R version 4.0.2 (R Core Team 2020).

1.4 Results

1.4.1 Description of Stopover Use

We analyzed 174 migrations of 33 individuals from 2006 - 2019 and identified 590 stopovers. Frequency of stopover use varied among population (Figure 1.2). In spring, Southwest USA used 1.1 stopovers per migration (n = 44 total stopovers) with a mean distance between stopovers of 2690 ± 1022 km. Central Canada used 6.7 stopovers per migration (n = 128) with a mean distance between stopovers of 1409 ± 1295 km. Western Canada used 2.9 stopovers per migration (n = 32) with a mean distance between stopovers of

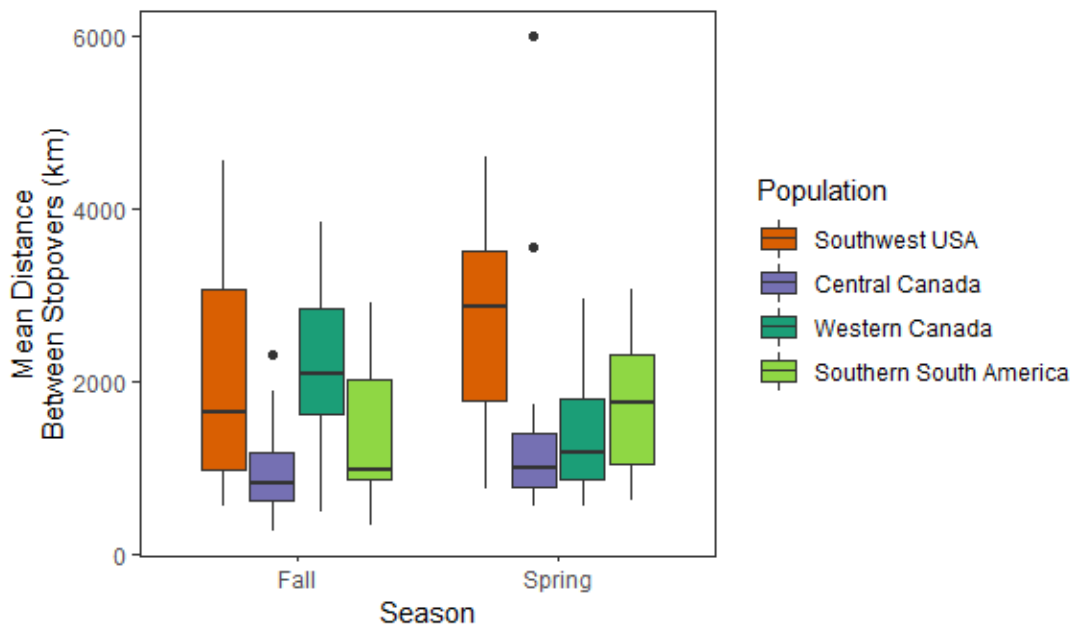


Figure 1.2. Mean distance between stopovers, per population. All populations except Western Canada, travel farther between stopovers in spring than fall. With the exception of 1 migration, no migrations traveled farther than 5000 km without stopping.

1371 ± 730 km. In austral spring, Southern South America used 2 stopovers per migration (n = 22) with a mean distance between stops of 1735 ± 771 km. In fall, all populations except Western Canada used stopovers more frequently (Figure 1.2). Southwest USA used 2.3 stopovers per migration (n = 103 total stopovers) with a mean distance between stopovers of 1993 ± 1157 km. Central Canada used 8.2 stopovers per migration (n = 188) with a mean distance between stops of 960 ± 507 km. Western Canada used 2 stopovers per migration (n = 22) with a mean distance between stops of 2187 ± 942 km. In austral fall, Southern South America used 3.4 stopovers per migration (n = 51) with a mean distance between stopovers of 1382 ± 824 km.

Movement behavior during stopovers varied from highly sedentary to highly tortuous (Figure 1.3). Total distances moved during stops ranged from 0 km to 601 km. Duration of stopovers ranged from 2 hours to more than 11 days. Fully 51% of stopovers (n=301) were < 24 h in duration. 58% of stopovers (n=342) started or ended on a day where birds migrated > 100 km. All stopovers > 24 h (n=289) had at least one stopover day where the bird travelled a total distance <100 km. Most of these (n=260) had at least one stopover day where the bird travelled a total distance <25 km.

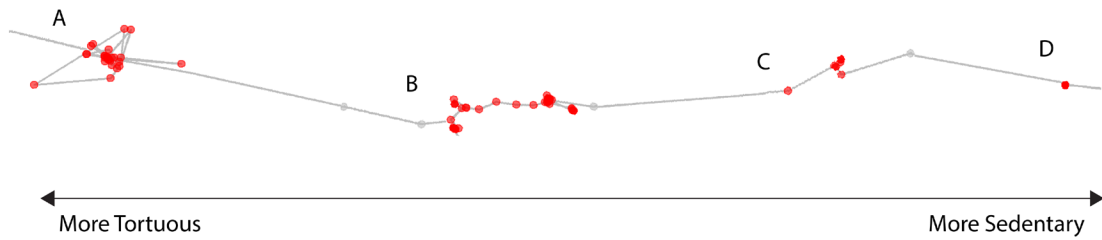


Figure 1.3. Examples of four stopovers, ranked from most tortuous (A) to most sedentary (D). More tortuous stopovers have a lower first passage time and a higher proportion of activity. More sedentary stopovers have a higher first passage time and a lower proportion of activity.

1.4.2 Onset of Stopovers

Stopovers typically began in the midafternoon (Supplemental Figure A.1). At the species-level, Turkey Vultures responded to changing weather variables immediately and showed no lag in response at the species-level. Several weather variables (Table 1.1) had peak rates of increase within one hour of the start of stopovers, including downward longwave thermal radiation, downward shortwave thermal radiation, precipitation fraction, and total atmospheric water (Figure 1.4).

Latent heat flux and thermal updraft velocity had a maximum rate of decrease within one hour of the start of stopovers. There was no predictable response to change in surface pressure. Other weather variables showed no peak in the rate of change but a gradual change over time, including boundary height, sensible heat flux, and temperature. The peak rate of increase for wind speed

was more than one hour before the start of stopovers, suggesting either a lagged response by vultures, or that the decision to stop was correlated with the decrease in wind speed. Responses were similar across three of four populations; however, the Western Canada population showed a delayed response to several variables (Supplemental Figure A.2c).

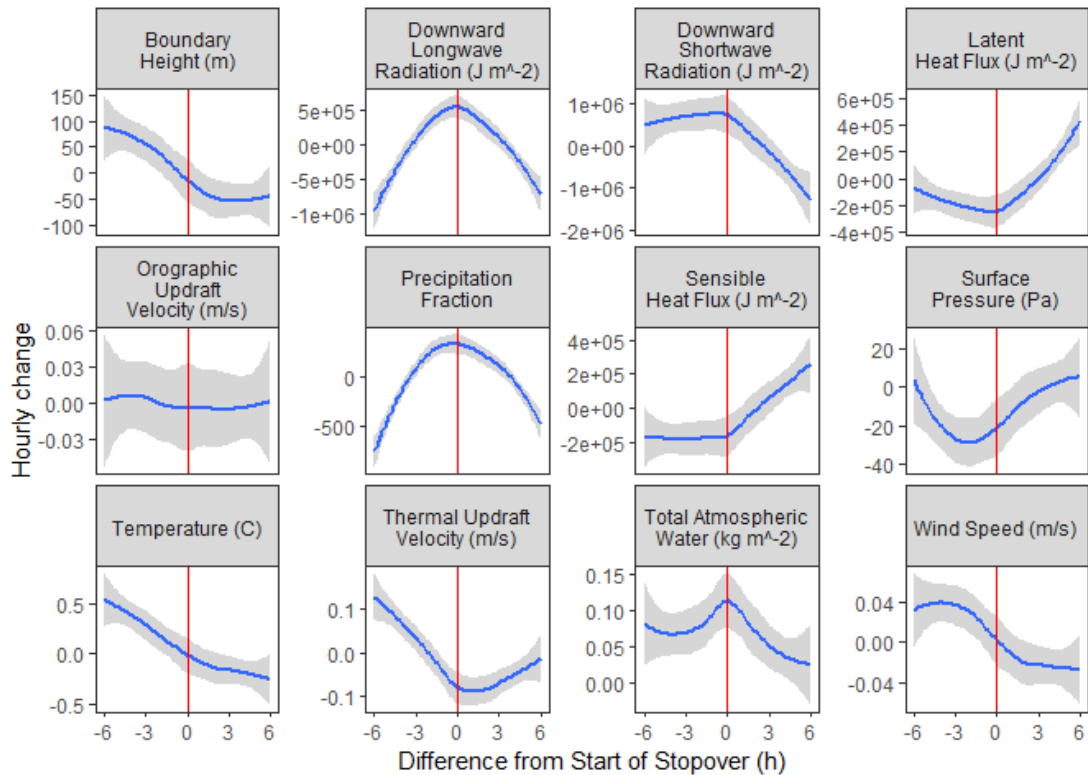


Figure 1.4. Average weather conditions relative to the start of identified stopovers (red line) for $n = 539$ stopovers. The labels on each plot indicate the name of the y-axis. The average hourly change in each weather variable is shown in blue and the error around this estimate is shown in gray. Peaks of several variables (i.e., downward longwave radiation, downward shortwave radiation, latent heat flux, precipitation fraction, thermal updraft velocity, and total atmospheric water) are within 1 hour of the start of stopover, indicating rapid response by Turkey Vultures to deteriorating weather conditions. Several other variables are declining at the start of stopover, i.e., boundary height, temperature, and wind speed.

1.4.3 Departure from Stopovers

Stopovers typically ended in the early morning (Supplemental Figure A.1). At the species-level, Turkey Vultures showed a delayed response to changing weather variables when departing stopovers and resuming migration. Overall, the departure from stopovers was less predictable than the onset of stopovers, indicated by larger confidence intervals (Figure 1.5). Several weather variables had a maximum rate of increase more than one hour before the end of stopovers, including boundary height, orographic updraft velocity, surface pressure, temperature, thermal updraft velocity, and wind speed.

Other weather variables that had a maximum rate of decrease within one hour of the end of stopovers, including downward longwave radiation, precipitation fraction, and sensible heat flux. There was no predictable response to change in orographic updraft velocity, latent heat flux, or total atmospheric water. Only downward shortwave thermal radiation had a peak rate of change after the end of the stopover. Responses were similar across three of four populations; however, the Western Canada population departed from stopovers during increasing rates of precipitation and downward longwave radiation (Supplemental Figure A.3c).

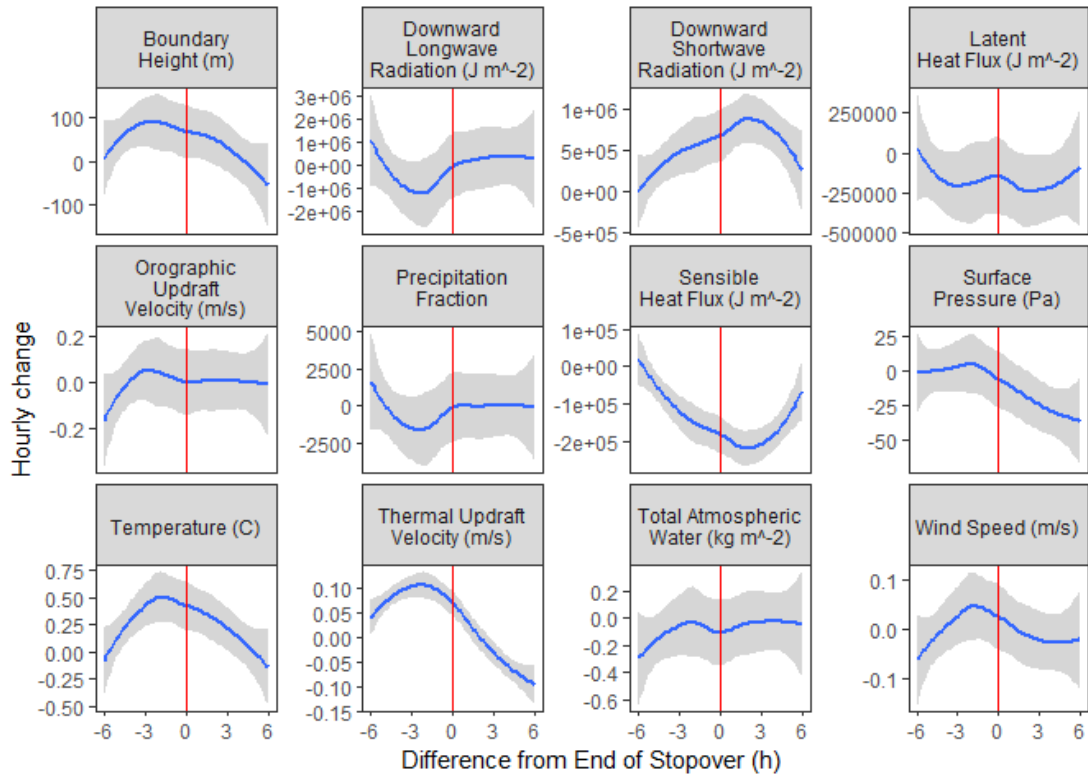


Figure 1.5. Average weather conditions relative to the end of identified stopovers (red line) for $n = 539$ stopovers. The labels on each plot indicate the name of the y-axis. The average hourly change in each weather variable is shown in blue and the error around this estimate is shown in gray. Peaks of several variables (i.e., boundary height, orographic updraft velocity, surface pressure, temperature, thermal updraft velocity, and wind speed) are > 3 hours before the end of stopover, indicating a delayed response by Turkey Vultures to improving weather conditions. Several other variables have little to no change at after the end of stopover, suggesting these variables negatively affect flight performance (i.e., downward longwave radiation, precipitation fraction, and total atmospheric water).

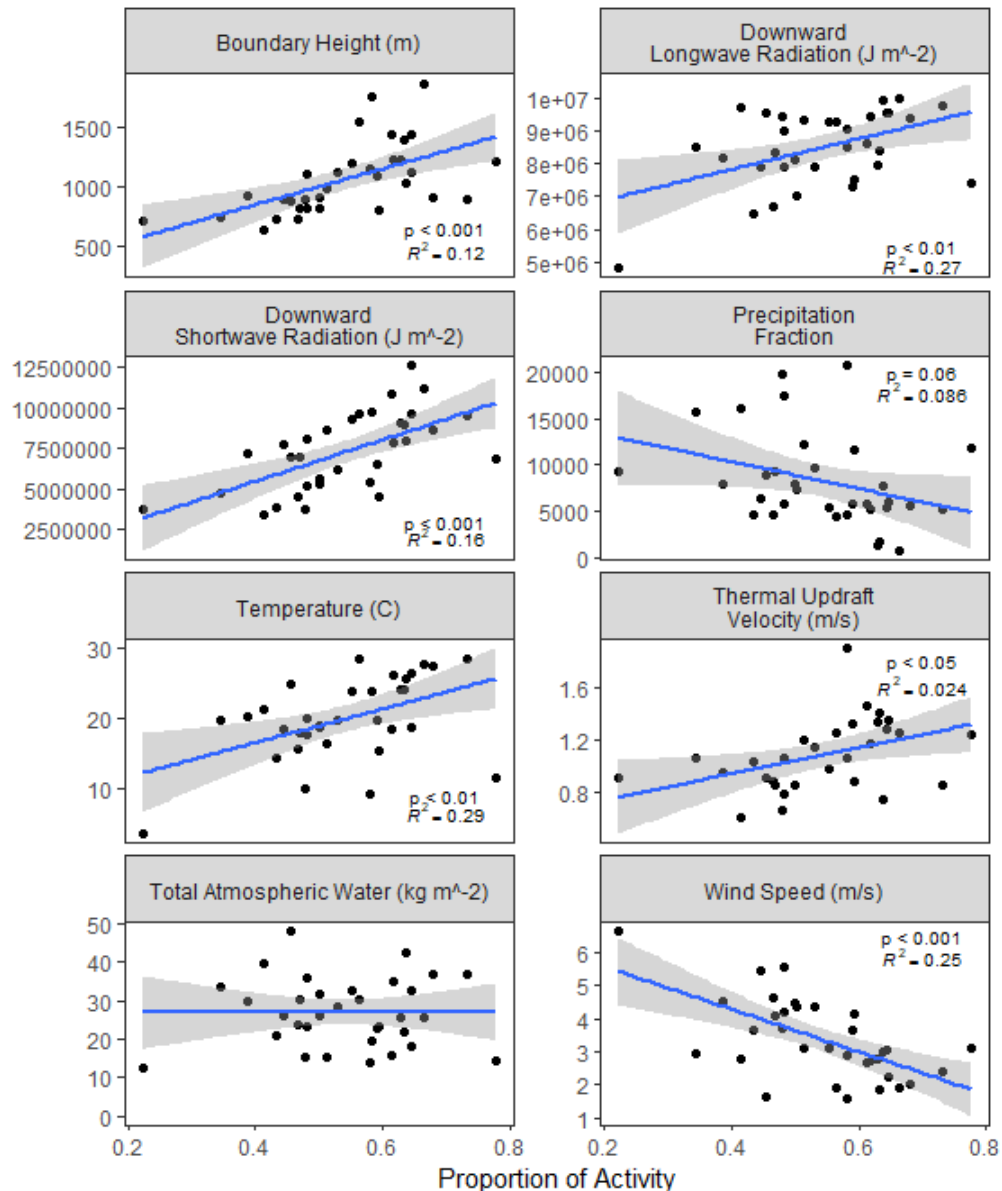


Figure 1.6. Average values for several weather variables as a function of mean proportion of activity during stopovers (a measure of tortuosity). All variables were significant except total atmospheric water. P value and R^2 are reported if $p < 0.1$. Several variables (i.e., boundary height, downward longwave radiation, downward shortwave radiation, temperature, and thermal velocity) were positively associated with greater amounts of activity during stopovers. Other variables (i.e., precipitation fraction and wind speed) were negatively associated with greater amounts of activity during stopovers, indicating that Turkey Vultures avoid moving during high levels of precipitation and high wind speeds.

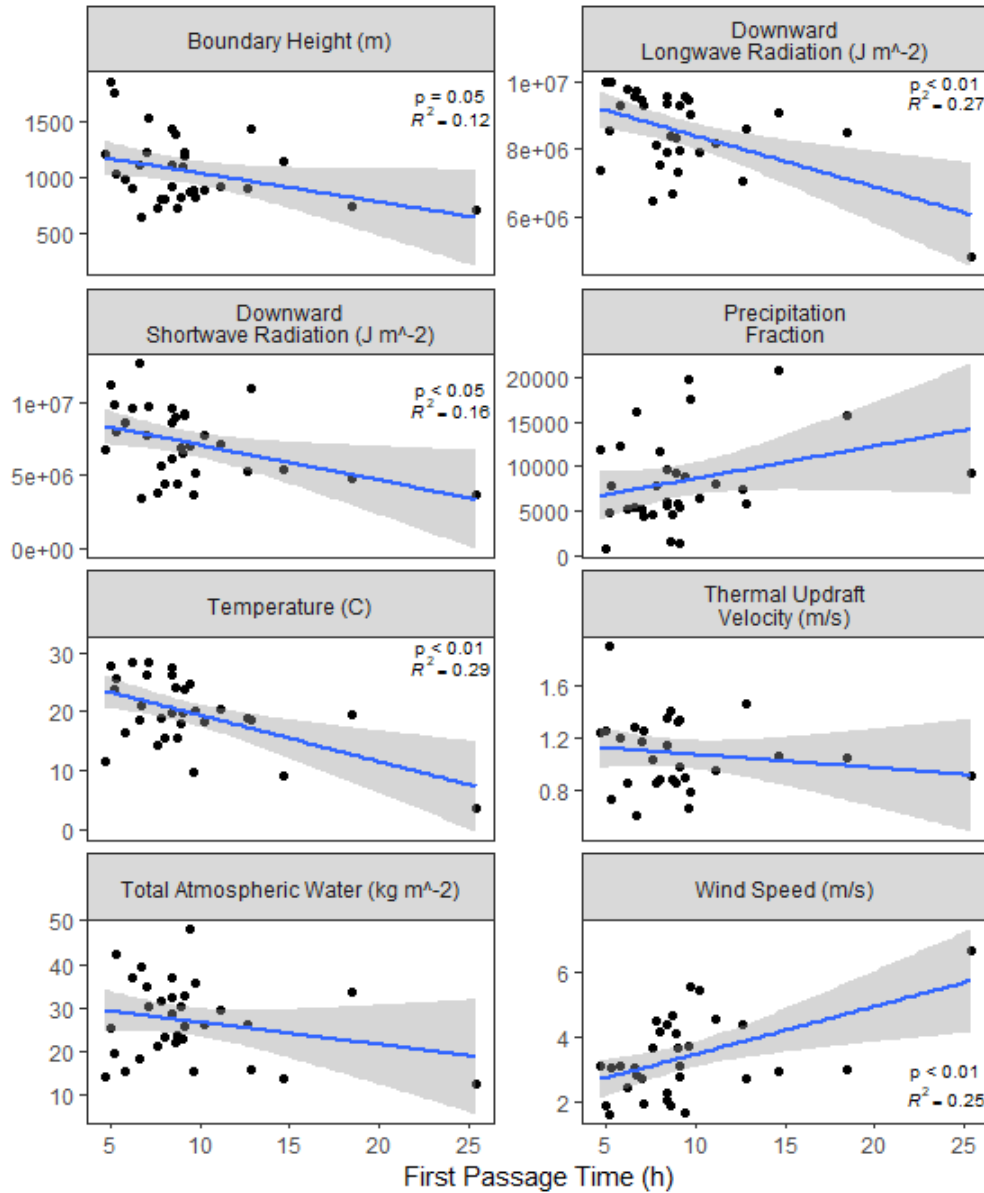


Figure 1.7. Average values for several weather variables by mean first passage time during stopovers with a radius of 250 m (a measure of sedentariness). All variables were significant except total atmospheric water and thermal updraft velocity. P value and R^2 are reported if $p < 0.1$. Several variables (i.e., boundary height, downward longwave radiation, downward shortwave radiation, and temperature) were negatively associated with longer first passage times during stopovers. Other variables (i.e., precipitation fraction and wind speed) were positively associated with longer first passage times during stopovers, indicating that Turkey Vultures avoid moving during high levels of precipitation and high wind speeds.

1.4.4 Movement Behavior and Weather

At the individual level, proportion of activity (Figure 1.6) and first passage time (Figure 1.7) were correlated with several weather variables associated with soaring. Birds had more tortuous stopovers at higher values of boundary height, downward longwave thermal radiation, downward shortwave thermal radiation, temperature, and thermal updraft velocity. Birds had less tortuous stopovers at higher values of precipitation and wind speed but had no relationship with total atmospheric water.

Birds were more sedentary during stopovers when temperature, boundary height, downward longwave thermal radiation, and downward shortwave thermal radiation decreased (Figure 1.7). Birds were more sedentary at higher values of precipitation and wind speed but had no relationship with total atmospheric water or thermal updraft velocity.

1.5 Discussion

We found that Turkey Vultures frequently stop during migration to avoid flying during poor weather conditions, adding to the growing literature recognizing weather avoidance as an important driver of stopover use by migrating birds (Calvert et al. 2009, Arizaga et al. 2011, Clipp et al. 2020). Turkey Vultures ceased directed flight quickly in response to changes in several weather

variables, indicating Turkey Vultures migrate using an energy-minimization strategy. As obligate soaring birds, vultures are highly sensitive to changing weather conditions that affect the availability of updrafts. The variables they responded to are broadly associated with thermal updraft strength (Duerr et al. 2015, Poessel et al. 2018), which is the most important type of updraft for these migratory populations (Bohrer et al. 2012). The lack of response to orographic updraft velocity suggests that this was not an important updraft source for these populations, which largely avoid areas of high topographic relief in their migration routes.

1.5.1 Weather Avoidant Stopovers

Although Turkey Vultures responded rapidly to changing weather when choosing to stopover, they showed a delayed response when choosing to take-off and resume migration. The most frequent time for take-off for vultures to resume migration was in the morning. At early hours, there is rapid change in variables such as temperature and thermal updraft velocity, which occur before thermals are fully formed. Therefore, this delayed response to changing conditions at the end of the stopover is likely an important part of their energy minimization strategy, as vultures wait until thermal updrafts have fully formed to avoid energetically expensive flapping flight (Harel et al. 2016a).

Interestingly, Egyptian Vultures, which are also obligate soaring migrants, rarely stop for more than 24 h during migration (López-López et al. 2014,

Buechley et al. 2018). Compared to Turkey Vultures (Dodge et al. 2014), Egyptian Vultures migrate much shorter distances and migrate for fewer days (López-López et al. 2014). In addition to having shorter migrations, Egyptian Vultures also migrate through more arid landscapes than most of the populations in our dataset, which suggests Egyptian Vultures generally migrate during better soaring conditions than Turkey Vultures.

We did not see a strong response to wind speed when Turkey Vultures began or departed the stopovers. Ospreys are also soaring migrants that frequently use stopovers and their decision to switch between active migration and stopover is not influenced by winds (Thorup et al. 2006). However, we did see that the proportion of activity during stopovers decreased with wind speed. In addition, first passage time during stopovers increased with wind speed. Although winds may not be a determining factor in the decision to actively migrate, vultures appear to be more likely to refuel during stopovers with only low wind speeds, which are correlated with conditions that promote the development of thermal updrafts (Bohrer et al. 2012).

1.5.1 Movement Behavior during Stopovers

Although we did not see support at the species-level for Turkey Vultures being risk-averse and stopping before the peak rate of change in weather, the Western Canada population showed a delayed response to the peak rate of change in weather, suggesting some individuals may have used risky flight

behaviors (Horvitz et al. 2014). Across all populations, we found several stopovers where vultures were slow moving, which could support the aversion of a Turkey Vulture to stopping by attempting to make migratory progress while its progress was slowed by weak updrafts.

Alternatively, such movements could represent migrants foraging en route. Several raptor species use a fly-and-forage strategy on migration, including Montagu's Harriers *Circus pygargus* (Klaassen et al. 2017), Ospreys *Pandion haliaetus* (Strandberg and Alerstam 2007), and Eleonora's Falcons *Falco eleonora* (Mellone et al. 2013). Fly-and-forage results in lower daily migration distances (Klaassen et al. 2017) and in slower, more tortuous movements (Mellone et al. 2013), but allows migrants to continue in the direction of their goal. These movements are quite similar to Figure 1.2B, where Turkey Vultures continually move in the direction of their goal, but at a very slow pace. While vultures do not capture live prey like other fly-and-forage migrants, vultures search over large areas for carrion. Turkey Vultures specialize in flying at low altitudes over forested landscapes, searching for carrion odors (Mallon et al. 2015).

The strong linear relationship between movement activity during stopovers and weather conditions that promote the development of thermals further suggests not all stopovers are used for weather-avoidance. Although we are unable to comment on how many stopovers are used for weather-avoidance or refueling,

the use of stopovers clearly increased with migration distance. The Central Canada population migrates > 2000 km farther than the other populations, indicating a greater energetic burden that likely requires some refueling stops. Although Turkey Vultures are expected to complete most of their migrations while fasting (Bildstein 2006), this finding suggests that some vultures do stop to feed during migration. While weather-avoidance stopovers are important for an energy-minimization strategy, frequent stops may increase their energetic costs and require additional refueling stops. As climate change is expected to increase the frequency of storms (Webster et al. 2005), further investigation is required to fully understand how the energetic cost of migration is impacted by stopovers used for weather-avoidance.

1.5.1 Short Stopovers

Half of the stopovers we identified did not meet the < 100 km and > 24 h criteria commonly used by other studies. Interestingly, of the stopovers that met the < 100 km criteria, 90% also met the < 25 km criteria. However, these stopovers do not necessarily align with the calendar day (i.e., 0000 - 2400 h). Only 4% of stopovers we identified started and ended during normal roosting hours (approx. 1700 - 0900 h), where the timing of movement activity would match with the normal daily activity patterns of diurnal migrants (Mallon et al. 2020). Stopovers identified at the daily scale, therefore, would have incorrectly identified the start and end times for 96% of stopovers. As revealed by our

results, birds are capable of responding rapidly to their environment; therefore, for studies interested in external drivers of stopover use it is essential that stopovers be identified at fine temporal scales.

1.6 Conclusion

This study is the first to attempt to determine the function of stopover use by migrant Turkey Vultures. We used a data-driven approach to identify short-duration stopovers < 24 h, which are primarily used to avoid poor weather conditions. Movement behavior during stopovers was driven by local weather conditions, where individuals moved more frequently during conditions that promote thermal updraft development, likely in search of carrion. Future studies may apply our approach to other species to investigate stopover use in relation to environmental drivers.

Chapter 2: Time is energy: optimal migration of an obligate soaring migrant

2.1 Abstract

Migration is an energetically expensive endeavor that requires significant fuel stores to complete. It has long been suspected that Turkey Vultures (*Cathartes aura*) fast during migration due to competition for carrion and their inability to pursue prey. Here we show evidence confirming that not all Turkey Vultures need to feed during migration and that most go long distances without feeding.

Using GPS-trajectories of 33 Turkey Vultures over 174 migrations, we evaluated daily migration costs based on time spent in three behaviors: active migration, stopover, or roosting. We estimated total energetic costs for each migration assuming the birds were fasting with reduced metabolic rates. We compared body mass stores required to fuel migrations for four populations, which differed in migration distances and body mass. We identified probable refueling stops for migrations where energetic costs exceeded 25% of their starting body mass.

Total migration costs were directly proportional to migration duration. Fall migration lasted on average 5 to 8.6 days longer than spring migration. For the longest distance migratory population, at least 95.2% of migrations required refueling stops whereas for the other migratory populations, only 25% of migrations required refueling stops. When controlling for migration duration, spring migrants complete their migration with greater body condition than fall migrants due to energy savings associated with fasting. Spring migrants delay feeding until after passing through the Mesoamerican migratory bottleneck, whereas fall migrants feed throughout the migration route.

Our results indicate that only long-distance Turkey Vulture migrants regularly stop to feed, but spring migrants avoided feeding within the Mesoamerican passage bottleneck, as expected. Overall migratory costs were driven by migration duration, and therefore are lower in the spring when vultures migrate faster, which may contribute to seasonal differences in flight behavior.

2.2 Introduction

Seasonal migration is one of the most energetically expensive activities an organism can undertake. The energetics of migration by passerines and shorebirds has been well studied (Gudmundsson et al. 1991, Gómez et al. 2017), indicating frequent use of stopovers to feed and replenish spent fat

reserves. For many bird species, the time and energy spent at stopovers exceeds the amount of time and energy spent in active flight (Hedenström and Ålerstam 1997, Wikelski et al. 2003). Frequent refueling allows birds to avoid carrying excess body mass and can be an important strategy that allows for minimizing energetic expenditure during migration (Ålerstam 2001). Birds that anticipate changes in food abundance later along their migration route will alter their fuel deposition rates (Houston 1998), to minimize excessive time and energy costs associated with refueling.

In contrast to passerines and shorebirds, refueling behavior by migrating raptors remains a knowledge gap concerning the theory of optimal migration (Ålerstam 2011). While empirical data is lacking on the refueling behavior of many migrating raptor species, studies of a small number of species indicate that raptors can afford to use a variety of fueling strategies during migration. For example, Swainson's Hawks (*Buteo swainsoni*) require frequent or long stopovers to complete their migration (Bechard et al. 2006, Kochert et al. 2011). Some species differ in feeding strategy between sexes (Ålerstam et al. 2006) or among age classes (Restani 2000). Most raptor species cannot complete their migration while fasting; some are observed to regularly feed during migration (Goodrich 2010) and others are known to carry insufficient fat stores (Gorney and Yom-Tov 1994). Among migrating raptors in Israel, stopovers are not used *en masse* and individuals hunt opportunistically (Yosef 1996). Other

short-distance migrants may not carry significant fat stores because they can afford to spend time at stopovers (Strandberg et al. 2009).

The findings of these studies are broadly applicable to migrating raptors but are less useful for understanding the energetics of migrating vultures. Although also a member of the order Accipitriformes, vultures differ from other birds of prey in that they are obligate scavengers. Turkey Vultures (*Cathartes aura*) cannot pursue prey due to the lack of powerful flight muscles for pursuit flight and the lack of grasping talons to kill and carry prey. While they have occasionally been reported to take small, live prey (Platt and Rainwater 2009), they must otherwise find carrion, which is highly ephemeral. Vulture diets, therefore, prevent the broadscale use of stopovers (Bayly et al. 2018, Monti et al. 2018). Moreover, in some migratory bottlenecks, the quantity of carrion available in the environment is insufficient to sustain the vast numbers of other migrating and residential vultures (Bildstein 2006) as over 2 million vultures migrate through the Mesoamerican land corridor seasonally (Bildstein and Zalles 2001, Inzunza et al. 2010, Cabrera-Cruz and Villegas-Patracá 2016).

Turkey Vultures have been assumed to not feed during migration (Bildstein 2006) due to high competition for food during their migration. For example, vultures migrating from North America reach a bottleneck in the Isthmus of Tehuantepec, Mexico (hereafter the Mesoamerican migratory bottleneck), where migrants following each of Mexico's coasts converge, en route to their

wintering grounds (Figure 2.1). This creates a highly competitive system as migrants overlap with birds from different flyways and with resident cathartid vultures. Furthermore, carrion is ephemeral by nature, and is haphazardly distributed in space and time throughout the landscape, making it difficult to find without deviating from the migration route. Migratory vultures may arrive at their wintering grounds in poor condition (Kirk and Gosler 1994), further suggesting that not all individuals feed during the journey. Observations of migratory vultures arriving at their wintering grounds in poor condition (Kirk and Gosler 1994) and a lack of observations of pellets at roosts (Smith 1980) further suggests that feeding is uncommon during migration.

This presents a unique research opportunity: vultures are well-adapted to minimize energetic expenditure (Ruxton and Houston 2004), yet it is unknown how they cope with energetic costs during migration. Turkey Vultures frequently stop during migration, but the primary driver of such stops appears to be changing weather conditions (so-called “fire escape” stopovers; Bayly et al. 2018, Chapter 1). Here, we use mathematical and statistical models to evaluate if Turkey Vultures can successfully migrate while fasting. Considering the total energetic costs of migration, we identify probable stopovers used for feeding based on analyses of movement of four migratory vulture populations, three migrating from North America and one migrating within South America. We specifically test to see if vultures appear to feed within the Mesoamerican

migratory bottleneck. Last, we test if there are optimal stopover areas for migrating Turkey Vultures that would minimize their energetic costs.

2.3 Methods

2.3.1 Study Species

Turkey Vultures (*Cathartes aura*) are habitat generalists and occur from southern Canada to the Falkland Islands (Bildstein 2006). There are several subspecies of Turkey Vulture, three of which (*C. aura aura*, *C. aura meridionalis*, *C. aura ruficollis*) are studied here. We studied four populations in all: each population's body mass, subspecies, maximum migration distance, and region are shown in Table 2.1.

Table 2.1. Descriptions of the breeding grounds, body mass, and migration distance by population.

Population	Subspecies	Body Mass (kg)	Maximum Migration Distance (km)
Southwest USA	<i>C. aura aura</i>	1.2	6427
Central Canada	<i>C. aura meridionalis</i>	1.5	8915
Western Canada	<i>C. aura meridionalis</i>	1.7	5959
Southern South America	<i>C. aura ruficollis</i>	1.7	5191

2.3.2 The physiological model

Using heart rate data of a single migrating Turkey Vulture, we first estimated the relative metabolic costs of three behaviors: soaring, resting, and roosting. Using annotated Turkey Vulture GPS tracks, we then used time spent in each behavior per day to calculate daily energetic costs during migration. Vultures were assumed to fast during migration unless otherwise noted.

From heart rate data to behavior-specific metabolic rates

Diurnal migrants such as vultures roost at night and are typically active during daytime hours when environmental updrafts are available for soaring. During daytime hours, birds may either be soaring (i.e., actively migrating) or resting (i.e., stopped). To determine the costs associated with these three behavioral states (i.e., roosting, soaring, and resting) during migration, we used heart rate data from one focal bird during fall migration in 2003. Mandel et al. (2008) reports the methods used to capture and tag the focal bird. After being fitted with telemetry, the focal bird was then fed and released at 2003-11-06 18:30:00 EST. Using heart rate data, we calculated the increase in metabolic rate over the expected metabolic rate at rest (Calder 1968, Arad and Bernstein 1988) and calculated the mean increase in heart rate by each behavior. We found no difference between active flight and daytime activity during stopovers, so we used $1.5 \times \text{BMR}$ (Duriez et al. 2014) for both behaviors. Turkey Vultures drop their body temperature while roosting (Hatch 1970) and drop the body

temperature of their extremities when ambient temperature is outside their thermal neutral zone (Arad et al. 1989). To reflect this energy saving adaptation and avoid underestimating energetic costs across a variety of climatic regions, we chose to use 1.1 x BMR as our multiplier for roosting.

Estimating total migration costs

Typical fuel loads for migrating raptors are 4 - 18%, and body fat is higher in the spring than fall (DeLong and Hoffman 2004). However, these estimates may be low if hungry individuals have a greater likelihood of being trapped on migration (DeLong and Hoffman 2004). To be conservative, we allow for a body fat range up to 25%, considering that metabolism of fuel stores during migration involves a combination of fat and muscle tissues (Piersma 1990). We do not account for water loss in our model, as water is a product of the catabolism of lipids (Blem 1980) and soaring migrants are not shown to be water stressed during migration (Gorney and Yom-Tov 1994)

The basal metabolic rate (BMR) for Turkey Vultures is 4.1 Watts/kg (Arad and Bernstein 1988). Metabolic costs of migration were calculated each day at hourly intervals using three behavioral states (α_j): actively migrating (1.5 x BMR), stopped over/resting (1.5 x BMR), and roosting (1.1 x BMR). We assumed that energy savings due to fasting were the same as for Old World vultures (Prinzinger et al. 2002). This assumption is reasonable because Old World and New World vultures have convergently evolved similar behaviors

and morphologies as obligate scavengers even though they are not closely related (Johnson et al. 2016). Both groups of birds must fast for days at a time and should have similar metabolic minimization strategies to compensate for irregular food intake. Days fasted (d) were calculated where day 0 (non-fast) occurred the day before departure. For days 1 - 7, an energy savings of 4% per day (β ; Prinzinger et al. 2002) was subtracted from the hourly metabolic cost (where day 1 = 4%, day 2 = 8%, ... day 7 = 28%), but beyond this we assumed no further benefit from fasting. To account for fasting, metabolic rate specific to each behavior (MR , kJ/h) was calculated as:

$$MR(t_h) = \alpha_j \cdot BMR \cdot (1 - \beta d) \quad (1)$$

where

$$d = \begin{cases} x: x \in [0,7] \\ 7: x > 7 \end{cases} .$$

For each day, metabolic expenditure for activity (ACT , kJ/day) was calculated for each of the three behavioral states. ACT was estimated from daily body mass (W), total duration of behavior (t , h/day), and MR . Unless otherwise stated, we assumed that the bird is fasting and not excreting feces or pellets. On day 1, we set W equal to the starting body mass in Table 2.1. After day 1, W from the previous day is used (Eq. 5).

$$ACT = W \cdot \sum_h MR(t_h) \quad (2)$$

Daily energy expenditure (DEE , kJ/day) was the sum of ACT across the three behavioral states: soaring, resting, and roosting, yielding

$$DEE = \sum_{day} ACT \quad (3)$$

Catabolism of fat yields 39.7 kJ/g (Ricklefs 1974), which is the energetic equivalent of body mass change (e). We calculated daily body mass change (AM , g) from daily energy expenditure (DEE) and e , yielding

$$AM = DEE/e \quad (4)$$

Body mass (W) was calculated as the starting body mass (Kg_{start} , Table 2.1) minus the sum of daily body mass changes (AM), specifically

$$W = Kg_{start} - \sum_{i=1}^n AM_i \quad (5)$$

When simulating a feeding stop, birds feed on the first day of stopover where d is set to 0 and 200 g is added to the body mass (W). Fasting begins the following day, where $d=1$.

2.3.3 Quantifying feeding stops

To identify which migrations required feeding stops, we determined how many days a Turkey Vulture could migrate using less than 25% of its body mass. We also estimated how many additional days of migration could be afforded per feeding day, assuming they assimilated 200 g. For each migration, we determined if the total duration was longer than these thresholds. When the

total duration was longer, we calculated how many feeding stops would be required to complete the migration with no less than 75% of its starting body mass.

Using stopovers identified from Chapter 1, we assigned likelihood scores that each stopover was used for feeding, depending on its tortuosity and duration. Tortuousness is associated with the search and capturing of prey (Fauchald and Tveraa 2003) and was positively associated with weather conditions that favored soaring flight, indicating highly tortuous stops were not used for weather avoidance (Chapter 1). We also assumed longer durations were more likely to be associated with the search and handling of food items. We made this assumption based on the rapid response by Turkey Vultures to changing weather conditions (Chapter 1), suggesting the duration of weather-avoidance stopovers are as short as possible.

To calculate likelihood scores, we first calculated tortuosity of each stopover as the ratio of total distance of all locations within a stopover to straight line distance between the first and last stopover locations. We then increased the likelihood of stopovers if their durations with increasing total duration. Stopovers that largely overlapped with roosting and < 24 h were given the lowest likelihood scores.

To identify how many feeding stops were necessary for an individual to complete its migration successfully, we first calculated the total amount of body

mass consumed for each migration, assuming the bird had fasted. Then we calculated the number of feeding stopovers needed to complete their migration while losing no more than 25% of their initial body mass. For migrations with several stopovers, the stopover with the highest likelihood score was selected as the feeding stopover.

To estimate the number of feeding stops used, we modeled the minimum number of feeding stopovers that would allow all individuals to successfully migrate while consuming < 25% of their starting body mass. To evaluate the robustness of our estimates, we compared the number of days between successive feeding stops to the number of days it took Turkey Vultures to use 25% of their body mass. We assumed the last day before migration and the first day post-migration were also days when vultures fed.

Optimal timing of feeding

We assumed that a vulture assimilated 200 g of mass from each refueling stop. In the wild, *C. aura meridionalis* consumes an estimated 228.5 g of carrion each day, based on their field metabolic rate (Grilli et al. 2019). Vultures regularly go several days without food (Hatch 1970), and therefore likely eat larger meals than their daily intake requirement when they find carrion. At least 80% of the mass of carrion is available for assimilation (Barton and Houston 1993) and Turkey Vultures have a metabolic efficiency of > 87% (Tabaka et al. 1996), suggesting 70% or more of the mass of carrion consumed can be assimilated

into tissue. However, it is unknown whether fasting would negatively affect this assimilation efficiency.

We then explored if there were optimal times along the migratory route for refueling stopovers to be used. We simulated 30 different 30-day migrations, with one feeding stopover on every migration day. Each day consisted of 13 h

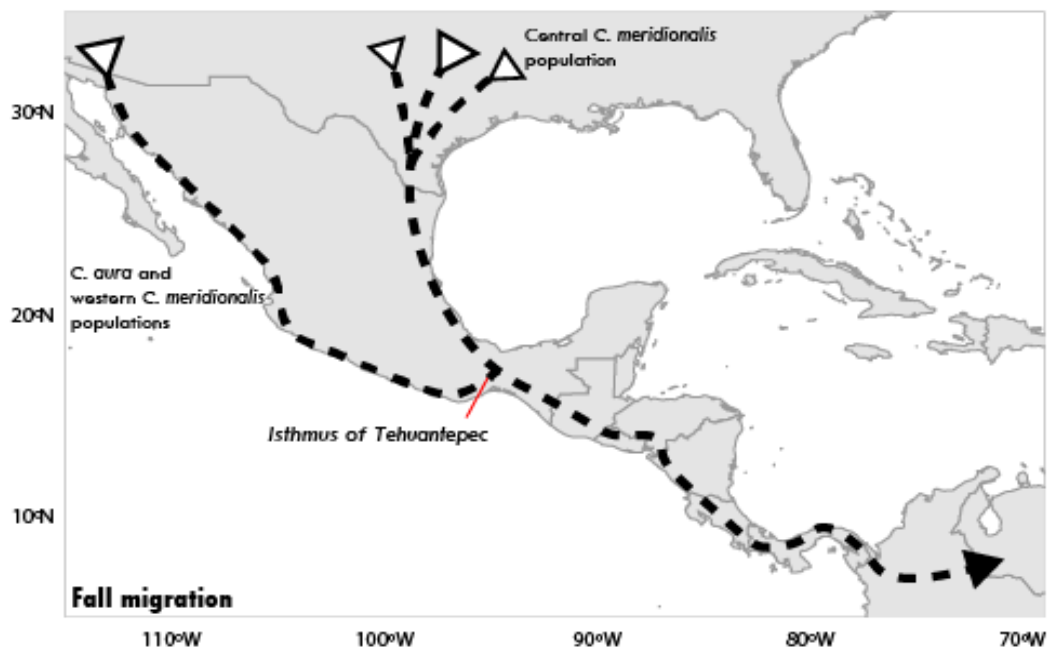


Figure 2.1. Map of Turkey Vulture fall migration through Central America. Migrants from the central USA converge and follow the Gulf coast of Mexico to the Isthmus of Tehuantepec, where they converge with migrants from the western USA. Migrants then follow the narrow Mesoamerican migratory corridor to their overwintering grounds in northern South America.

of roosting and 11 h of either active migration or resting. We report the results as final body mass on day 30.

To estimate the spatial distribution of feeding stops used, we assigned the stopovers with the highest likelihood scores as feeding stops. The number of feeding stops per migration was determined from migration duration. Due to the Mesoamerican migratory bottleneck (Figure 2.1), we expected North American Turkey Vulture populations to feed north of 30N latitude. During fall migration, vultures were expected to feed before reaching the bottleneck but during spring migration, vultures would feed after passing the bottleneck.

2.4 Results

2.4.1 Total migration costs

We calculated the energetic costs for 94 fall and 80 spring migrations for 33 birds. Total migration costs had a positive, linear relationship with migration duration ($\beta = 0.8581$, $p < 0.001$), and was not affected by population or starting body mass (Figure 2.2). Differences in proportion of body mass required among populations were due to relative differences in maximum migration distances (Table 2.1).

2.4.2 Migrations requiring feeding stops

We predicted that fasting Turkey Vultures used 25% of their body mass in 23 days. Each feeding day that assimilated 200 g of mass afforded a vulture an extra 12 days of migration before reaching the 25% limit. 95.2% of the long-

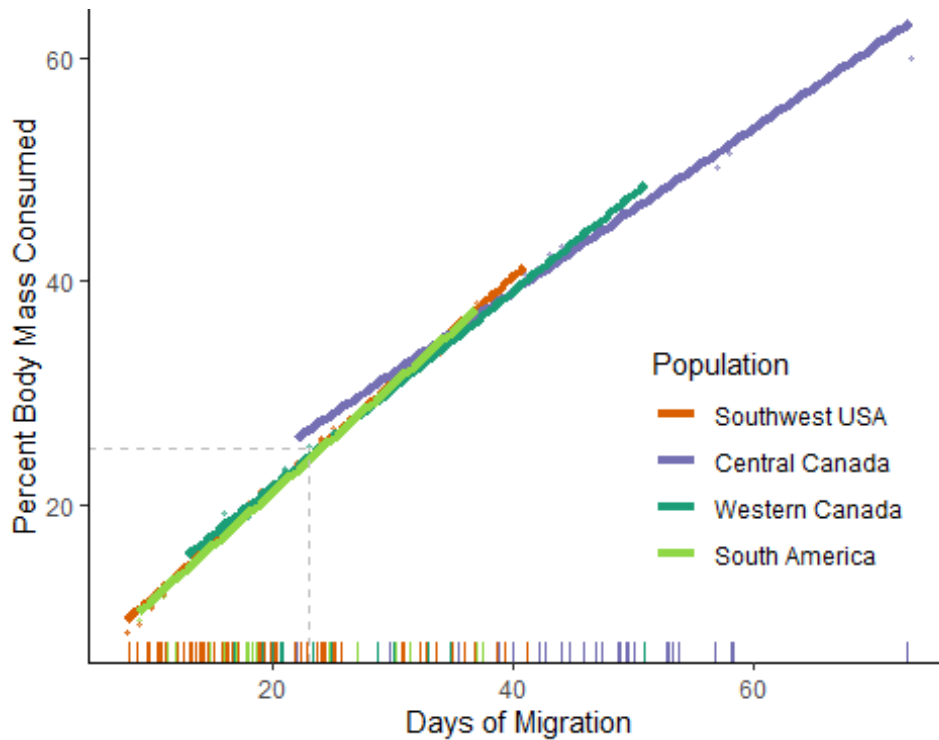


Figure 2.2. Modeled results for percent body mass consumed during migration while fasting, with separate models for each population. Results from $n = 174$ fully completed migrations between 2003 - 2019. Percent body mass consumed, regardless of starting body mass, had a positive, linear relationship with migration duration. The dashed line indicates the 25% body mass threshold. 97.0% of the Central Canada population's migrations (green) exceed this threshold and would require feeding stops, whereas most migrations from the other three populations are below this threshold and no more than 29.9% would require feeding stops. Differences in slopes between populations are attributable to decreasing rate of body mass loss over time. The rug plot shows the distribution of migration durations for each population.

distance Central Canada population's migrations exceeded the 25% body mass threshold (Figure 2.2) and required at least one feeding stop. Most migrations from the other three populations were below this threshold and only 25.0% required at least one feeding stop. 87.9% of the Central Canada population required 2 or more feeding stops, compared to only 8.5% migrations

from the other three populations. Only 4.8% of the Central Canada population’s migrations and 75.0% of the other three population’s migrations did not require any feeding stops. The proportion of migrations that required feeding stops was greater overall in fall than spring (fall: 51.1%; spring: 31.2%). However, only short-distance populations required more feeding stops during fall than spring (Table 2.2).

Table 2.2. Model estimates of the number of fall and spring migration that require feeding stops, by population. For each population, the total number of migrations and stopovers are reported by season. We also report the minimum number of non-fasting migrations and the predicted number of feeding stops used.

Season	Population	Total Migrations	Non-fasting Migrations	Total Stops	Feeding Stops
Fall	Southwest USA	45	16	103	20
	Central Canada	23	22	188	58
	Western Canada	11	4	22	6
	Southern South America	15	6	51	11
Spring	Southwest USA	39	3	44	3
	Central Canada	19	18	128	36
	Western Canada	11	2	32	2
	Southern South America	11	2	22	2

2.4.3 Quantifying feeding stops

Of 590 stopovers, 23% were estimated to be used for feeding. These occurred during 42% of migrations (n = 174; Table 2.2). Feeding stops represented a marginally greater proportion of all stopovers during fall (26%; n=364) than spring (19%; n=226). Like the proportion of migrations that required feeding

stops, only short-distance populations required more feeding stops during fall than spring (Table 2.2).

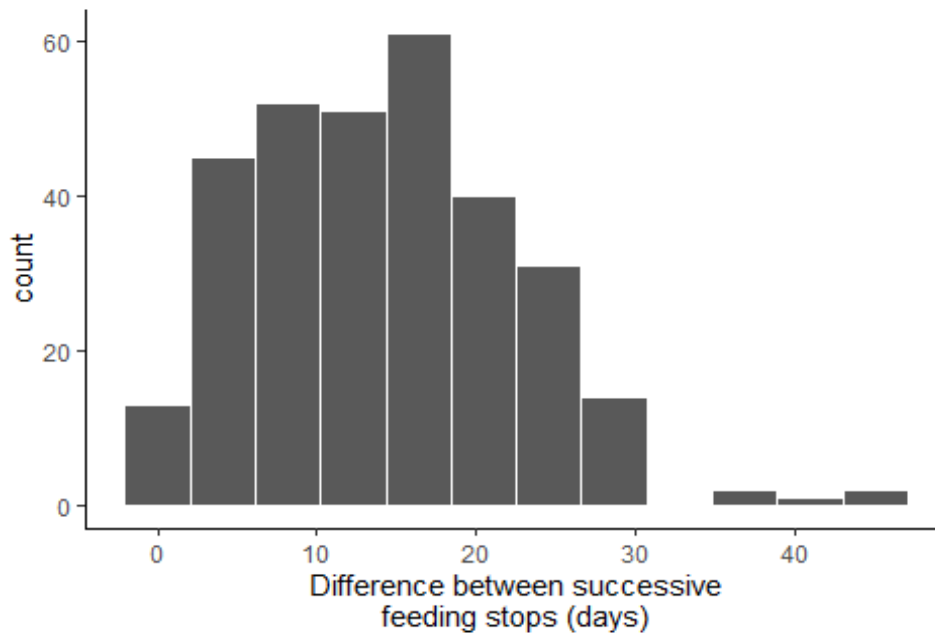


Figure 2.3 The difference in days between successive feeding stops. We assumed that the day before the onset of migration and the first day after migration were also feeding stops. Our estimates of which stops are used for feeding, using the 25% body mass rule, were very robust with 84% of feeding stops occurring < 23 days since the last feeding stop, indicating we underestimated the frequency of feeding stops 16% of the time.

If our estimate of 23 days correctly represents the capacity of most Turkey Vultures to withstand fasting, then our estimates are robust as 84% of the feeding stops occurred < 23 days since the last feeding stop (Figure 2.3). For

16% of stops, we either underestimated the number of stops or incorrectly identified which stops were used for feeding.

2.4.4 Optimal temporal and spatial patterns of feeding

The spatial distribution of feeding stops used by *C. aura meridionalis*, differed slightly by season (Figure 2.4). Fall migrants infrequently stopped between 20N - 30N, while spring migrants completely avoided using feeding stops between 20N - 30N. Spring migrants stopped to feed above 30N more often than fall migrants. The Western Canada population was less likely to stop to feed than the Central Canada population, regardless of season.

The birds we predicted to finish migration with the best body condition and greatest total body mass were the birds that stopped as late as possible (Figure 2.5). We predicted these birds finished migration with 3.4% greater final body mass than the birds that fed during the first days of migration.

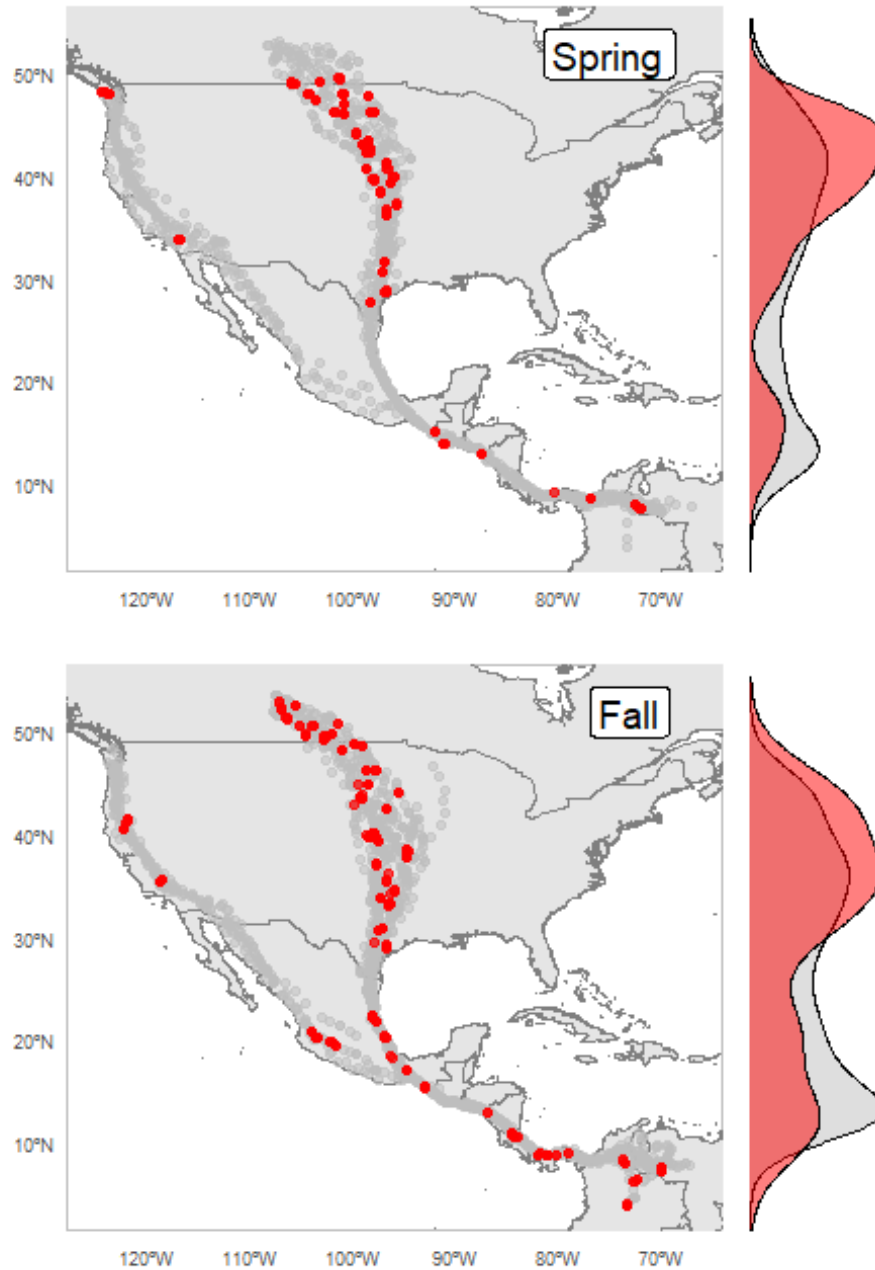


Figure 2.4. Distribution of probable feeding stopovers (red) and active migration points (grey) for western and central *C. aura meridionalis* populations. The majority of feeding stopovers occur between 30 - 55 N latitude, regardless of the direction of migration. Feeding stops occur at any latitude during fall migration but near-exclusively above 30 N during spring migration. There was no difference in the distribution of active migration points between seasons. The central population, which migrates farther, fed more extensively than the western population.

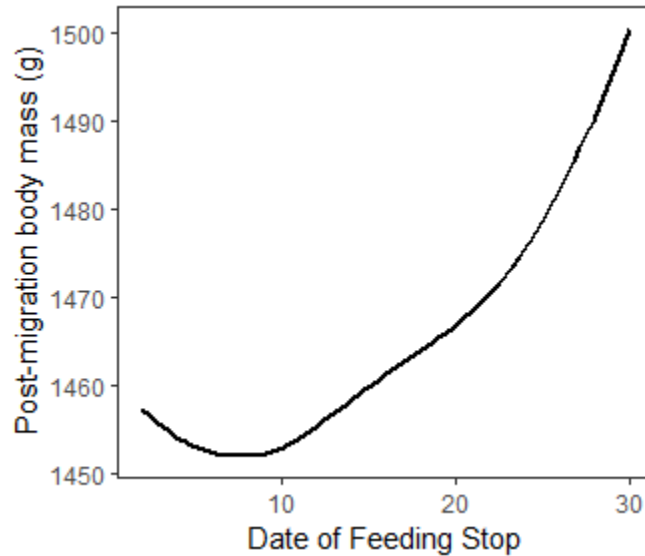


Figure 2.5. The effect of the timing of feeding on post-migratory body mass (g). We considered a 30 day migration and simulated the effect that a single 48 hour feeding stopover had on final body mass (g). The bird started at 1500 g body mass on day 0 and used the same relative amounts of energy each day (i.e., 11 hours of activity and 13 hours of roosting). During the stopover, the bird assimilated 200 g of body mass. Energy savings of 4% per day due to fasting (up to 28%) were applied from the start of migration and reset at the start of the stopover. Final body mass was lowest when stopovers occurred on days 5 - 10 and increased each day thereafter. Final body mass was greatest when the stopover was nearest to the end of the migration (i.e., day 28 - 30).

2.5 Discussion

Our research reveals a unique optimal migration strategy, not seen in other migrants. Vultures minimize energy expenditure as they require the use of soaring flight to reduce search costs so that they can profit from carrion (Ruxton and Houston 2004) and the durations of their flapping bouts are limited (Ferland-Raymond et al. 2005, Mallon et al. 2015). This results in total energetic costs that are driven more by migration duration than by behavior.

Therefore, an energy minimization strategy for Turkey Vultures is also a time minimization strategy. While vultures cannot sustain themselves aloft using active (i.e. flapping) flight, they can optimize their migration so that they spend the fewest days migrating as possible.

Although the literature has considered Turkey Vultures to be fasting migrants, our results indicate this is only true for some individuals. The expected number of feeding stops is directly related to migration duration, and is higher for longer distance migrants (i.e., Central Canada population). Shorter distance migrants rarely need to feed more than once, if at all. However, our results did confirm that even for long-distance migrants that regularly feed, feeding stops are infrequent within the passage bottleneck and feeding is largely restricted to the continental United States, regardless of season.

For Turkey Vultures that feed during migration, when they feed matters. Birds with the lowest energetic costs were birds that fed later. The difference in energetic costs is due to both the metabolic savings vultures have while fasting (Prinzinger et al. 2002) and that metabolic costs increase proportionally with body mass. If birds were able to optimize the timing of their feeding stops during both fall and spring migrations, we would find no difference in total energetic cost between seasons. However, due to avoidance of feeding within the Mesoamerican migratory bottleneck, the timing of feeding stops during migration results in a seasonal difference in energetic costs. Spring migrants

optimize their feeding stops by refueling after the Mesoamerican migratory bottleneck and maximize the energy savings associated with fasting. Fall migrants, in contrast, refuel before reaching the Mesoamerican migratory bottleneck and lose the metabolic savings due to fasting, when their body mass is relatively high. Fall migrants, therefore, complete their migration with lower body mass than spring migrants.

Seasonal differences in the duration of migration, like that observed in our dataset (Chapter 1), is a well-known phenomena among migrating birds (Nilsson et al. 2013, Schmaljohann 2018). Non-breeding golden eagles have a shorter migration duration, only flying when conditions were optimal in order to minimize energy expenditure (Duerr et al. 2015). This suggests that conditions in spring are more favorable for soaring flight than during fall migration. In fall, they experience lower levels of downward solar radiation (Duerr et al. 2015), which generates weaker thermals and limits migration speed, contributing to longer and more energetically expensive fall migrations. Seasonal differences in migration speed of Turkey Vultures has been linked to longer migration days and greater thermal updraft strength in spring than in fall (Mellone et al. 2012, Dodge et al. 2014).

The shorter duration of spring migration, combined with the directional effect on energetic gains associated with feeding, may result in large energetic savings for spring migrants. Consequently, spring migrants should arrive at

their breeding grounds with greater body condition, in preparation for the breeding season. Alternatively, empirical investigation of the energetic costs of migrations may reveal that Turkey Vultures use less energetically efficient flight behaviors, such as more flapping or more risky flight behaviors (Harel et al. 2016a) to arrive at breeding grounds faster (Duerr et al. 2015). Although Turkey Vultures cannot maintain flight altitude using flapping flight due to a lack fast-twitch muscle fibers (Rosser and George 1986), they still flap for take-off and landing, and may flap while soaring if the updrafts are weak (Ferland-Raymond et al. 2005), which would increase energetic costs.

Without empirical data on where and when vultures feed, our estimates were largely restricted to identifying which migrations required feeding stops and how much carrion they need to consume. Our models serve as minimum estimates because vultures should feed opportunistically if a carcass were found along the migration route. We also expect that vultures will seek food before consuming all of their fuel stores, so some may stop to feed even though they could complete their migration while fasting. Our estimate of fasting for 23 days exceeds the currently known longest period of fasting a vulture has survived (16 days; Hatch 1970). However, the study had a limited sample size and used residential Turkey Vultures from the *C. aura septentrionalis* population, which may not fast for extended periods of time. The author also conducted the experimental fasting in January outside of any phenological cues that may

affect metabolism and while the vultures were exposed to temperatures outside their thermal neutral zone (Arad et al. 1989). Therefore, we expect vultures to be able to withstand longer periods of fasting than previously reported.

Considering the number of days between feeding stops, 84% of the identified feeding stops agreed with our 23 day fasting limit. The other 16% of stops were either incorrectly identified, leading to large temporal gaps between consecutive feeding stops, or we underestimated the number of feeding stops used. Future studies of the movements of New World vultures, combined with stomach temperature data and accelerometry will help identify which stops are used for feeding with greater certainty and fill in gaps in our current understanding of how frequently New World vultures feed. As New World and Old World vultures are not closely related, it is important to study the effect of fasting on the metabolism of New World vultures. Documenting this energy efficient adaptation will confirm our findings that predict there is an effect of season and migration direction on the optimal migration strategies of Turkey Vultures.

Further investigation using empirical data on energetic expenditure may reveal other interesting optimization strategies, such as energy minimization outside of the passage bottleneck and time minimization within the passage bottleneck (*sensu* Efrat et al. 2019). Similar energetic patterns may be found in other migrating vultures that also rely on ephemerally available carrion. Egyptian

Vultures (*Neophron percnopterus*) migrate through migratory bottlenecks (Buechley et al. 2018) where competition for carrion is expected to be high, if they feed during migration. Both Egyptian and Griffon Vultures (*Gyps fulvus*) cross ecological barriers and may have better flight performance (Harel et al. 2016a) and greater energetic gain by feeding after crossing.

2.6 Conclusion

We concluded that many Turkey Vultures must feed during migration. Birds that migrate greater distances generally need to feed more often, but some individuals from the Central Canada population were able to complete their migrations quickly enough to avoid stopping to feed, especially in the Spring. Migration speed (Nilsson et al. 2013), therefore, is the most important factor to determine energetic costs. Consequently, season (Schmaljohann 2018), conditions experienced during migration (Duerr et al. 2015) and experience (Mueller et al. 2013) are all major contributing factors that influence energetic costs of soaring migrants.

Chapter 3: Diurnal timing of nonmigratory movement by birds: the importance of foraging spatial scales

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3.1 Abstract

Timing of activity can reveal an organism's efforts to optimize foraging either by minimizing energy loss through passive movement or by maximizing energetic gain through foraging. Here, we assess whether signals of either of these strategies are detectable in the timing of activity of daily, local movements by birds. We compare the similarities of timing of movement activity among species using six temporal variables: start of activity relative to sunrise, end of activity relative to sunset, relative speed at midday, number of movement bouts, bout duration, and proportion of active daytime hours. We test for the influence of flight mode and foraging habitat on the timing of movement activity across avian guilds. We used 64570 days of GPS movement data collected between 2002 and 2019 for local (non-migratory) movements of 991 birds from

49 species, representing 14 orders. Dissimilarity among daily activity patterns was best explained by flight mode. Terrestrial soaring birds began activity later and stopped activity earlier than pelagic soaring or flapping birds. Broad-scale foraging habitat explained less of the clustering patterns because of divergent timing of active periods of pelagic surface and diving foragers. Among pelagic birds, surface foragers were active throughout the day while diving foragers matched their active hours more closely to daylight hours. Pelagic surface foragers also had the greatest daily foraging distances, which was consistent with their daytime activity patterns. This study demonstrates that flight mode and foraging habitat influence temporal patterns of daily movement activity of birds.

3.2 Introduction

An animal's movement behavior is heavily influenced by its evolutionary history, which affects movement capacity and behavior (Norberg and Norberg 1988, Tobalske 2001). An animal's movement path is based, in part, on the distribution of resources (Fryxell et al. 2004), which is determined by their environment. These interact when animals forage, as they need to traverse the landscape according to their movement capacities to locate resources distributed non-randomly in the environment (Suryan et al. 2008). To maximize energetic gains from foraging, the timing of an animal's foraging movements is expected to correspond to either the temporal availability of its resources

(Rydell et al. 1996, Lang et al. 2018) or the quantity and quality of resources required (Jetz et al. 2004, Ramesh et al. 2015, Cid et al. 2020). Alternatively, animals can reduce their energy expenditure by timing their foraging activity when their movements are most energetically efficient (Chapman et al. 2011, Shepard et al. 2013) via behavioral thermoregulation (Matern et al. 2000) and passive movement (Krupczynski and Schuster 2008). Both strategies are used by animals to forage optimally (Stephens and Krebs 1986), but these strategies have yet to be evaluated together within any group of animals.

Birds are distinct from other vertebrates because most birds are volant and most fly actively (i.e., by flapping) while a smaller number fly passively (i.e., by soaring). Soaring birds save energy by using updrafts (Baudinette and Schmidt-Nielsen 1974) to move across the landscape. One tradeoff faced by terrestrial soaring birds is that the availability of updrafts is skewed towards daylight hours (Pennycuick 1978). Switching to flapping flight can further extend the activity of soaring birds (Stark and Liechti 1993, Harel et al. 2016b) as flapping flight is self-powered and can therefore be used in a broader suite of conditions.

When animals can be flexible in the timing of their movements, their activity is expected to be driven more by ecological interactions and the need to acquire resources. These needs can manifest as temporal matching between consumers and their resources. For example, Black-legged Kittiwakes (*Rissa*

tridactyla) time their foraging concurrently with tidal cycles, when prey are most accessible (Irons 1998). Alternatively, the amount of movement activity may be due to resource quality. When high quality food items are available, animals can spend more time resting as their energetic needs are met more quickly (Saj et al. 1999, Fleischer Jr et al. 2003, Ménard et al. 2013). Despite long lasting interest in the factors that shape animal activity times, it is still poorly understood how internal traits and external conditions jointly shape the timing of movement across avian species.

Using daily movement activity data from a wide range of avian species, we tested for broad-scale differences in the temporal patterns by flight mode and foraging habitat. Temporal patterns do not only describe when individuals are moving, but they also convey information about the behaviors driving those movements (Pasquaretta et al. 2020). Therefore, temporal patterns of movement activity are best described using a suite of variables. First, we evaluated the similarity of temporal patterns among species using multivariate analyses and test for signals of foraging habitat and flight mode among clusters of species in ordinal space. Due to geographic and dietary segregation, we expected to find the greatest differences in multivariate space to be between birds from terrestrial and pelagic foraging habitats.

Second, we hypothesized that the timing of daily movement activity is more restricted for species that soar, because the flight performance of soaring birds

varies within a day (Mellone et al. 2012) due to temporal variation in availability of environmentally derived updrafts (Spiegel et al. 2013). We predicted start and end times of movement activities would differ between flight modes. Flapping birds are unrestricted in their capacity to move and therefore can be active before sunrise and after sunset; in contrast, we expected terrestrial soaring birds to be limited to daylight hours. Soaring flight is most beneficial for large-bodied birds (Hedenström 1993), which are often raptorial (Schoener 1968); consequently, the use of soaring flight covaries with trophic level and morphology (Viscor and Fuster 1987, Baliga et al. 2019). We also predicted that pelagic soaring birds would be less temporally restricted than non-soaring birds as dynamic soaring is not driven directly by solar energy but by wind and wave energy (Pennycuick 1982).

3.3 Methods

3.3.1 Data

We compiled GPS tracking data for 49 bird species whose movements were studied between 2002 and 2019. We obtained data from Movebank (www.movebank.org; Wikelski and Kays 2018) or through direct contributions by co-authors (Supplementary material Appendix B.1). For quality control, we removed anomalous locations with speeds greater than 80 kmh⁻¹ for flapping species and locations with speeds greater than 100 kmh⁻¹ for soaring species. All speeds were calculated as the speed between points. We calculated UTM

zones from coordinates. To evaluate the timing of movement relative to local sunrise and sunset, all timestamps were converted from GMT to local time.

Our dataset included movements from 49 species (Supplementary material Appendix B.1). These species represent 14 orders: Accipitriformes, Anseriformes, Bucerotiformes, Charadriiformes, Ciconiiformes, Falconiformes, Gruiformes, Otidiformes, Passeriformes, Pelecaniformes, Phaethontiformes, Phoenicopteriformes, Procellariiformes, and Suliformes. Most (n=46) species were non-Passeriformes, and all Passeriformes were from the same genus (*Corvus*).

We analyzed movement data at the daily scale. Most of the data were sampled at hourly time intervals, so we subsampled high resolution data to an hourly scale with location intervals ≥ 57 min (mean time between locations: 79.5 ± 31.1 min). To accurately assess active and inactive states while maximizing number of sampling days, we excluded sampling intervals ≥ 180 min. We did not interpolate missing points.

Days included in the analysis had a minimum of eight locations per day. We selected eight-hour minimum time periods to represent the daily scale because many telemetry units do not sample continuously and, instead, cycle on and off to save battery life. To avoid any potential bias in movements due to handling during tagging, we excluded the first day of tracking for all studies. We included

species with at least 20 days of data. Full sampling information is provided in Supplementary material (Appendix B.1).

Due to known intra-specific differences that occur in association with migration (Cagnacci et al. 2016), our analyses explore non-migratory daily foraging movements. To compare local, foraging movements of birds, we standardized the data to include only non-migratory movements by excluding migrations from individuals with range shifts > 500 km. We intentionally selected a high threshold to avoid removing exploratory and foraging movements by individuals that did not migrate in partially migratory populations.

3.3.2 Movement Characteristics

Measurement errors due to error in calculations of latitude and longitude by global positioning system (GPS) are inherent in movement tracking studies (Frair et al. 2010) and can inflate estimates of movement activity. After comparing the distributions of location errors across species, we characterized locations as either 'active' or 'inactive' according to their mean speed. Species with a mean speed < 9 kmh⁻¹ had an activity threshold of 50 mh⁻¹. This threshold was conservative relative to the distributions of mean location errors across most of the species (Supplementary material Appendix B.2). Species with a mean speed > 9 kmh⁻¹ had an activity threshold of 300 mh⁻¹.

These different thresholds allowed us to identify active versus inactive periods for terrestrial and pelagic birds, which forage at different spatial scales (Schoener 1968, Oppel et al. 2018). To confirm our results were not sensitive to spatial scale, we compared our results using a smaller threshold (25 mh^{-1}) and found no difference in the change in activity levels (Supplementary material Appendix B.2). To determine if the sampling frequency affected the activity patterns of any groups of species, we compared our results to a 20 min sampling scheme. The differences between these two sampling schemes were linear; our results are therefore robust to temporal sampling (Supplementary material Appendix B.2).

Table 3.1. Temporal variables and their definitions.

Variable	Definition
Sunrise Activity	The time difference between first activity and sunrise
Sunset Activity	The time difference between last activity and sunset
Relative Speed at Midday	Speed at solar noon relative to mean speed
Number of Movement Bouts	Number of groups with 1+ consecutive, active hours
Activity Duration	The length of time between non-active locations
Proportion of Daytime Activity	Number of daytime active locations / total number of daytime locations

Based on these daily, active hours, we summarized temporal characteristics of daily movements using six variables, defined in Table 3.1. The objective of these measures was not to reliably estimate species averages for these temporal variables, but to provide standard, relative measures that could allow

for multispecies comparisons. We included the timing of activity relative to sunrise and sunset to understand the relationship between activity and light availability, while accounting for variation in latitudes and time of year across datasets. Several sampling regimes were set to collect data between sunrise and sunset, which limit our interpretations. However, these intervals were selected by experts on the focal species' biology, so we do not expect that the true mean start and end times of activity would differ strongly from our results. We list species with limited sampling periods (i.e., mean start or end of sampling time were within the hour of local sunrise and sunset) in Supplementary material Appendix B.2. The distributions of the timing of movement activity for each species are reported in Supplementary material Appendix B.3.

To determine if movements were clustered in time or dispersed throughout the day, we defined number of movement bouts as the number of groups of consecutive active hours. We used the duration of these groups of consecutive active hours to represent activity duration. To determine how active species are at midday, for each day we calculated relative speed, which is the speed at solar noon divided by their speed averaged across all active bouts. Last, to compare activity among species, we calculated the proportion of time birds were active during the day, which was the proportion of hours between sunrise and sunset where the individual exceeded the speed threshold. We calculated

this metric using the number of hours during daytime, rather than hours during the full day, because species with limited sampling periods would have artificially high activity levels. We first calculated each temporal variable at the daily scale and then found the mean of each temporal variable at the species level (Supplementary material Appendix B.1).

3.3.3 Morphological and Ecological Characteristics

Ecological characteristic data were taken from the Elton 1.0 database (Wilman et al. 2016), which broadly describes the feeding ecology of all extant bird species in terms of the percent contribution of diet items and of different foraging habitats. We combined variables that were redundant for the species in our dataset; Table 3.2 lists the variables used and how they were derived.

Table 3.2. Ecological variables used in analysis. Data sourced from Elton database (Wilman et al. 2016). Where variables are combined, sample sizes are indicated in parentheses. Final sample size used in analyses are in column N.

Variable	Category	N	Definition
Foraging Habitat	Above Ground	7	midcanopy (6) + canopy (3) + aerial (6)
	Ground	34	ground (34) + understory (5)
	Water (other)	29	freshwater or non-obligate pelagic species that forage below (4) + around surf (18)
	Pelagic Surface	7	pelagic specialist that forage around surf
	Pelagic Diver	8	pelagic specialist that forage below surf
Diet	Herbivore	17	plant (17) + seed (14)
	Frugivore	6	fruit

	Carnivore	33	endotherms (18) + ectotherms (14) + unknown (4)
	Piscivore	25	fish
	Invertivore	32	invertebrates
	Scavenger	20	carrion
Flight Mode	Pelagic Soaring	7	pelagic birds that soar >20% of the time
	Obligate Soaring	8	terrestrial birds that cannot sustain flapping flight
	Facultative Soaring	14	terrestrial birds that soar >20% of the time
	Flapping	20	birds that flap >80% of the time

Foraging habitats were collapsed to five levels: above ground, ground, freshwater, pelagic surface, and pelagic diver. Similarly, several diet variables were collapsed to six levels: herbivore, frugivore, carnivore, piscivore, invertivore, and scavenger.

Flight mode was described as either flapping or soaring. Although many species may occasionally be observed soaring, we included only species that soar regularly. We further subdivided soaring into obligate, facultative, and pelagic soaring. All other species were categorized as flapping.

We gathered morphometric data for three variables: body mass (kg), wing span (m), and wing area (m²). Where wing area values were missing, but wing span was known, we calculated wing area using aspect ratio ($\text{wingspan}^2/\text{wingarea}$)

from a closely related species. Then, using known wingspan and estimated aspect ratio, we were able to derive wing area and relative wing loading (Pennycuick 2008). Wing spans were unknown for two species (*Anas poecilorhyncha* and *Grus nigricollis*), which we excluded from the analyses of morphological characteristics. We controlled for the effect of body size by using relative wing loading ($\text{bodymass}^{2/3}/\text{wingarea}$; Norberg and Norberg 1988). We used only relative wing loading and aspect ratio in our analyses. All species' morphological data and sources, as well as ecological character data, are provided in the Supplementary material (Appendix B.4).

3.3.4 Analysis

To determine which guilds were most similar in the timing of movement activity, we quantified dissimilarity across the suite of temporal variables (listed in Table 3.1) using non-metric multidimensional scaling (NMDS). NMDS is a distance-based ordination that maximizes rank order correlation, which is suitable for non-parametric data. Accipitriformes and Anseriformes were over-represented in our dataset, making our dataset phylogenetically uneven.

To correct for this, we bootstrapped our NMDS analysis by randomly subsampling four species (the median size of other orders with multiple individuals) within each order, iterated 100 times. For each iteration, we then tested for any significant diet, foraging, flight, and morphological correlates of the NMDS (Table 3.2). Our final analysis included only variables that were

significant predictors for at least 20% of subsampled datasets. This allowed us to exclude any predictors that would have been significant only due to the skewedness of our dataset. As many behaviors and adaptations have coevolved, we also report any highly correlated predictors.

To test our flight mode hypothesis, we used one-way ANOVAs followed by TukeyHSD post-hoc tests. We excluded one species that was an outlier with regards to daytime movement activity, Cory's shearwater (*Calonectris diomedea*), as our estimates of activity duration exceeded those of known activity budgets (Ramos et al. 2019). To explore the drivers of clustering among foraging habitats in ordinal space, we compared the distributions of active hours among foraging groups. To assess if the differences in activity level are due to physiological limitations of flight speed, we included a post-hoc analysis of the mean daily net squared displacement, a measurement of daily foraging distance, according to foraging habitat. Due to insufficient sample size, terrestrial above ground foragers were excluded from this analysis. We report summary statistics as mean and standard deviation. We performed analyses using R version 3.6.3 (2020-02-29) (R Core Team 2020); a list of R packages used can be found in the Supplementary material (Appendix B.5).

3.4 Results

We summarized 64570 days of movement data for 991 birds. For three species, movement data came from fewer than three individuals (Supplementary material Appendix B.1). Wing spans ranged from 0.71 to 2.81 m and body mass ranged from 0.44 to 9.87 kg, a range that includes the body masses of 28% of all volant non-Passeriformes.

We found several continuous covariates related to the clustering of species according to the suite of temporal variables. Variation along NMDS1 was largely attributed to terrestrial ground foragers and pelagic surface foragers (Figure 3.1a). Terrestrial ground foragers were largely comprised of Accipitriformes and were therefore correlated with obligate and facultative soaring birds, scavenging ($r=0.63$), and carnivorous diets ($r=0.71$). Pelagic surface foragers were comprised of Procellariiformes and some Suliformes (i.e., Frigatebirds), which were positively correlated with high aspect ratio wings ($r = 0.76$), pelagic soaring, and invertivores. However, there was no separation between terrestrial and pelagic foragers in ordinal space. The greatest separation between foraging groups was between pelagic diving and pelagic surface foragers (Figure 3.1b). Variation along NMDS2 was largely attributed to flapping versus soaring flight (Figure 3.1c). In our dataset, body size was related to flight mode (soaring 3.65 ± 2.76 kg, flapping 1.20 ± 0.60 kg).

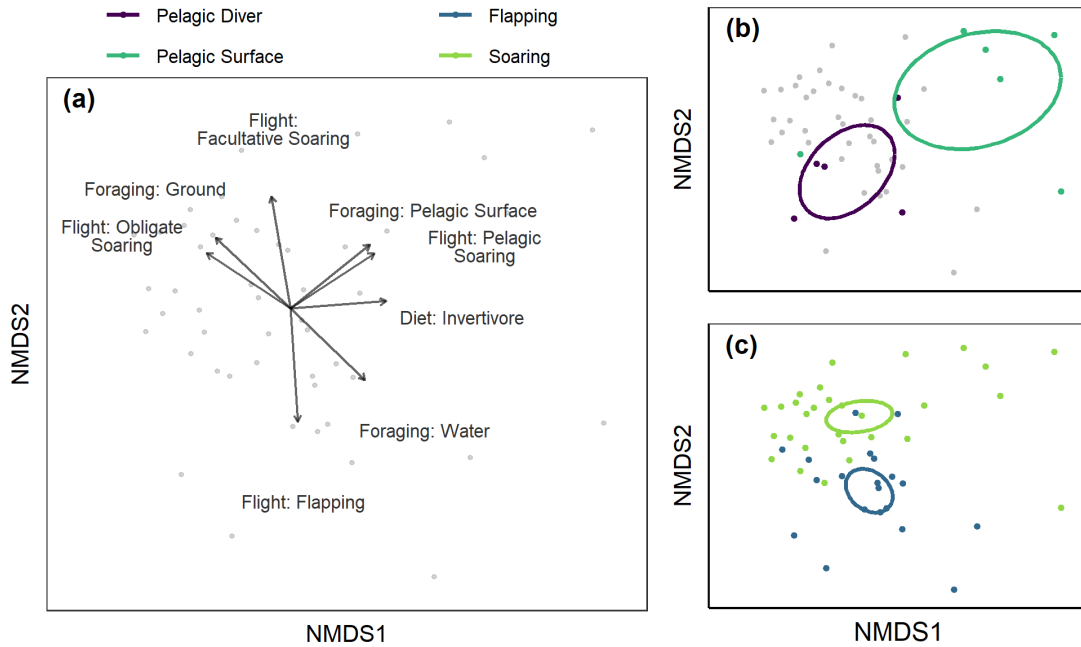


Figure 3.1. The NMDS ordination indicates inter-specific similarities within temporal activity patterns, among all 49 species. (a) NMDS annotated with environmental fit loadings (included if significant at p -value < 0.05). Environmental fit loadings were bootstrapped to correct for an uneven sample across phylogeny. Ground foragers were correlated with carnivorous diets ($r = 0.71$) and scavenging diets ($r = 0.63$) and both were omitted from the environmental loadings for clarity. Pelagic surface foragers were correlated with high aspect ratio wings ($r = 0.76$), which was removed for clarity. NMDS annotated by (b) pelagic foraging habitats and (c) flight mode. Ellipses represent 90% confidence interval around the centroid of each group. (b) There is little overlap between the pelagic foraging groups, indicating that pelagic divers (purple) have different activity patterns than pelagic surface foragers (green). Terrestrial foragers (grey) had high overlap with pelagic foragers, indicating little differences between terrestrial and pelagic foragers, overall. (c) There is little overlap between flight modes, indicating that soaring species (light green) have different activity patterns than flapping species (blue). Stress value is 0.15.

Soaring birds had higher relative speeds than flapping birds at midday (soaring: 0.901 ± 0.232 ; flapping: 0.568 ± 0.211 ; $F = 26.28$, $df = 1$, $p < 0.001$). Obligate soaring birds began activity later than flapping birds (obligate

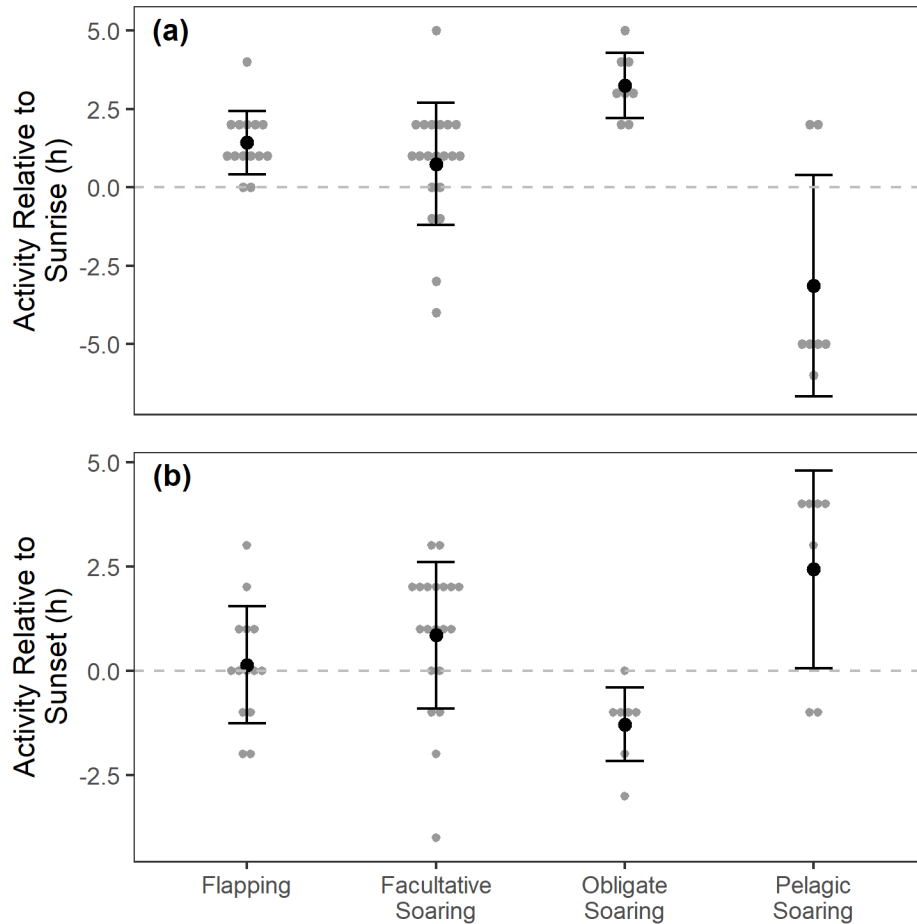


Figure 3.2. Dot plots of flapping, terrestrial (obligate and facultative), and pelagic soaring birds by (a) start of activity relative to sunrise and (b) end of activity relative to sunset, with units in hours. (a) Terrestrial soaring birds began activity after sunrise, with obligate soaring birds beginning activity later than facultative soaring birds. (b) Terrestrial soaring birds ceased activity before or at sunset, with obligate soaring birds stopping activity earlier than facultative soaring birds. Sunrise and sunset times were similar for facultative soaring and flapping birds.

soaring: 3.250 ± 1.035 h; flapping: 0.750 ± 1.943 h; $F = 14.542$, $df = 3$, $p < 0.001$; TukeyHSD $p=0.017$; Figure 3.2a). Similarly, obligate soaring birds stopped activity earlier than did flapping birds (obligate soaring: -1.286 ± 0.881

h; flapping: 0.850 ± 1.755 h; $F = 6.777$, $df = 3$, $p < 0.001$; TukeyHSD $p = 0.018$; Figure 3.2b). The same pattern was observed for pelagic soaring birds. Obligate soaring birds began activity later than pelagic soaring birds (pelagic soaring: -3.143 ± 3.532 h; TukeyHSD $p < 0.001$; Figure 3.2a) and obligate soaring birds stopped activity earlier than pelagic soaring birds (pelagic soaring: 2.429 ± 2.37 h; TukeyHSD $p < 0.001$; Figure 3.2b). Post-hoc tests did not reveal significant differences in the start or end times between obligate and facultative soaring birds (sunrise $p = 0.159$, sunset $p = 0.224$), but obligate soaring birds were active for a shorter range of hours in the day (Figure 3.2).

Activity distributions differed by foraging habitats (Figure 3.3a). Pelagic surface foragers were active most continuously throughout the day and terrestrial ground foragers had the narrowest range of active hours. Differences in the activity patterns of pelagic surface foragers and diving foragers corresponded to differences in daily foraging distances (Figure 3.3c). Daily maximum net squared displacement was greatest among pelagic surface foragers, indicating they travelled the furthest within a day of any foraging group ($F = 3.373$, $df = 3$, $p = 0.027$). These differences were not due to differences in mean flight speed (Figure 3.3b). Pelagic foragers had greater mean flight speeds than terrestrial foragers, but this was partially an artifact of our methods requiring different activity thresholds.

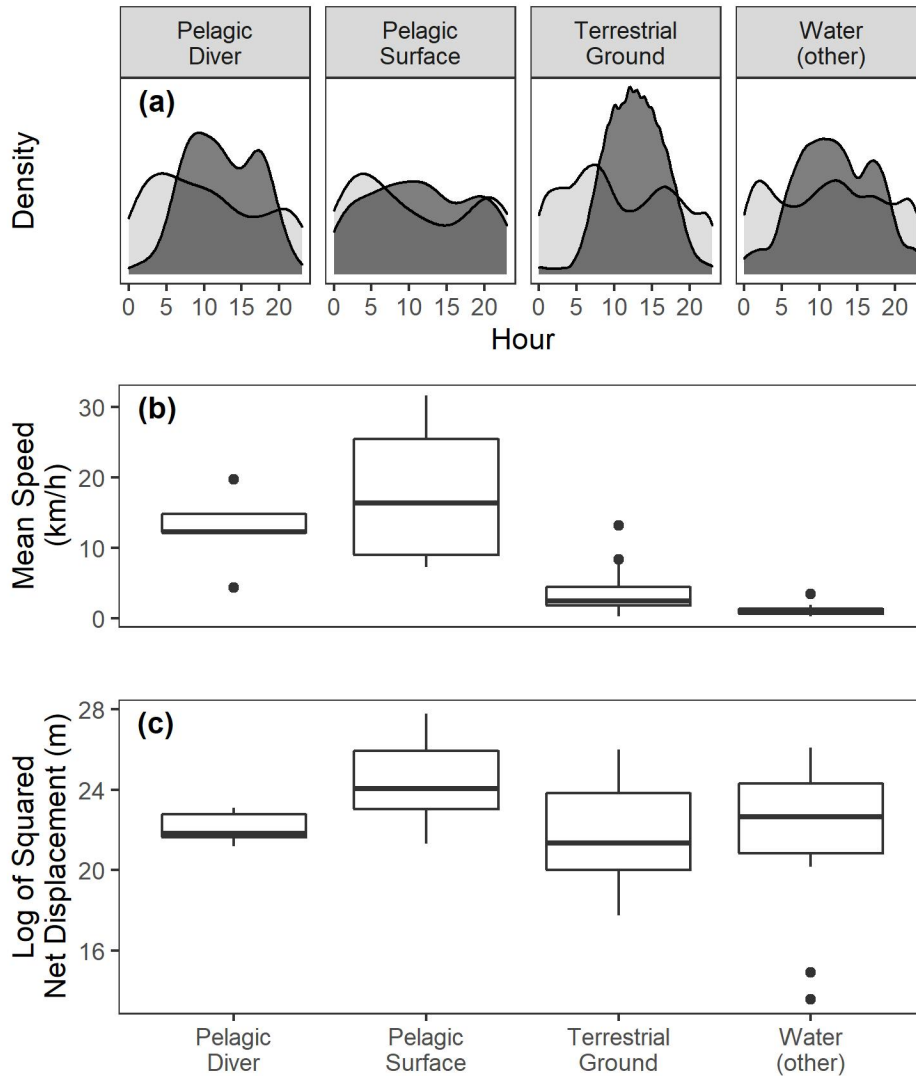


Figure 3.3. Foraging habitats by (a) active time, (b) mean speed, and (c) distance. For all plots, terrestrial above ground foragers were excluded due to small sample size ($n = 2$). (a) Distributions of active (black) and inactive (grey) hours by foraging habitat. Pelagic surface foragers were active a greater proportion of the day than pelagic diving and terrestrial foragers, whose activity was more clustered during midday. (b) Mean speed between points. There is no difference in maximum speeds among pelagic foraging habitats. (c) Post-hoc analyses of log-transformed squared net displacement (in meters) of daily foraging trips according to foraging habitat. Pelagic surface foragers travel farther than pelagic divers on daily foraging trips, suggesting differences in their activity levels is driven by their respective foraging distances.

3.5 Discussion

In this study we have combined a rich GPS tracking data set, spanning over several species and guilds, and used a multispecies comparative approach to test for intrinsic factors that shape the timing of activity by birds. We found broad-scale differences in the timing of avian daily movement activity between flight modes, supporting our hypothesis. Movements of Accipitriformes, which represent the largest proportion of soaring birds in our broad dataset, were largely restricted to daytime hours. This effect was even stronger among obligate soaring birds (i.e. Old World and New World vultures). Soaring species were further differentiated from flapping species by higher relative speeds at midday. These findings were not surprising as updrafts are stronger around midday than in the morning or late afternoon, supporting previous research suggesting their activity is more strongly linked to the temporal availability of updrafts (Mandel and Bildstein 2007, Bildstein et al. 2009, Nathan et al. 2012, Sur et al. 2017) than to their spatial availability (Mallon et al. 2015).

Flapping species were characterized by a lower percent of activity during the day. This suggests either flapping species are less active than soaring species, or they are similarly active, but on different spatial scales. Flapping species were largely represented by Anseriformes (i.e., ducks and geese) and Pelecaniformes (i.e., herons), which forage locally (e.g. < 1 km) by walking, stalking, dabbling, or grazing. These species generally feed on abundant or

localized resources (i.e., herbivores and granivores), and therefore spend greater amounts of time foraging within a given area (Mueller and Fagan 2008).

Other species either face less temporal predictability of resources or have greater spatial heterogeneity of resources and are more mobile as a consequence (Mueller and Fagan 2008). This is true of soaring species, many of which use a fly-and-forage strategy where birds spend substantial time in flight searching for food over large spatial scales (e.g. 10's of kms; Ruxton and Houston 2004). This is consistent with other findings concerning foraging space use: large-bodied birds, which tend to feed on high-quality resources and forage over large spatial scales (Schoener 1968), travel farther in homogeneous environments than heterogeneous environments (Tucker et al. 2019). Among mammals, trophic level is correlated with home range size (Jetz et al. 2004), which is positively correlated with activity levels (Cid et al. 2020), suggesting a positive relationship between space use and activity levels over large scales.

Like our results for terrestrial species, the temporal patterns we observed of pelagic species are a consequence of the spatial scale they forage over. While flight mode is related to the same morphological adaptations that allow pelagic species to specialize as surface or diving foragers (Ashmole 1971), we argue instead that the differences in timing among pelagic birds are not due to flight mode but to foraging behavior. In our dataset, pelagic surface foragers were

comprised of Suliformes (i.e. boobies and frigatebirds) and Procellariiformes (i.e. albatrosses and shearwaters), which forage over different spatial scales (Oppel et al. 2018). Although in other colonies, Suliformes respond to intraspecific competition by traveling further from the colony to forage (Oppel et al. 2015), Suliformes in our dataset forage closer to their colonies relative to the Procellariiformes, which frequently forage in open ocean. This difference in space use also likely drives the observed differences in the temporal patterns of their movement activity. To travel further, but at similar flight speeds, Procellariiformes have longer foraging trips that often extend overnight. This resulted in Suliformes appearing to be relatively less active, as their foraging trips in our dataset were always < 24 h. The predominantly diurnal activities of Suliformes contributed greatly to the overlap in temporal activity patterns between pelagic and terrestrial foragers. There was better contrast among pelagic birds when comparing foraging groups, as frigatebirds are not diving foragers like other Suliformes, but are surface foragers that behave more like Procellariiformes. Frigatebirds in our dataset did move at night but are diurnal foragers that sleep on the wing (Rattenborg et al. 2016). This, in part, explains why the differences in start times between pelagic surface and diving foragers were more distinct than between Procellariiformes and Suliformes alone.

At least for some species, the relative significance of flight mode and foraging habitat may not be clear cut. The timing of their movements may not be driven

by food availability, but instead by foraging restrictions. For example, in arid climates, some birds reduce their activity during midday as a means of behavioral thermoregulation (Silva et al. 2015, Gudka et al. 2019). Likewise, visually orienting species are limited by the availability of light. As such, although fruits and seeds are available at all hours, Passerines begin activity at dawn when there is sufficient light to detect their food resources (Roth and Lima 2007). Temporal segregation of foraging can also be driven by pressures to avoid predators or kleptoparasites (Baglione and Canestrari 2009), such as frigatebirds. Such adaptive behavior is thought to have contributed to the evolution of nocturnal foraging behaviors by some pelagic species (Hailman 1964).

Interpretation of our results is limited as we compiled our dataset from several different studies, which were biased towards larger, data-rich species that can support the weight of telemetry units. Also, sampling schemes across studies were uneven in terms of inter-location frequency and effort; this required us to use data averaged at the species level. If our data could be resolved on the scales specific to each guild, rather than standardized across species, we might have identified other ecological variables, such as diet, as important drivers of movement activity. Nevertheless, our approach provided standardized activity metrics for 49 bird species, which allowed us to compare intrinsic drivers of movement activity across a diversity of avian guilds.

Although our analyses were restricted to temporal attributes of movement, the relationship between physiological limitations on flight speed and activity duration lead us to hypothesize that the spatial scales animals forage over is an important driver of the timing of movement activity. Our results show that animals have predictable, intrinsic patterns to the timing of local movements that make up the large-scale behaviors we are interested in studying. Recognizing that spatial scale indirectly influences the timing of movement activity, future studies that focus on the spatial attributes of animal movement should consider the temporal attributes of movement as well. For example, studying spatial and temporal patterns in concert may reveal intraspecific differences due to personality influences on movement behavior (Spiegel et al. 2017, Hertel et al. 2019). With the development of smaller, high-resolution tracking devices, future research may apply analyses such as ours to the full diversity of birds, filling gaps of our knowledge on granivorous, frugivorous and insectivorous species (e.g., passerines, shorebirds, swifts, etc.), which may reveal interesting new phylogenetic or allometric predictors of movement.

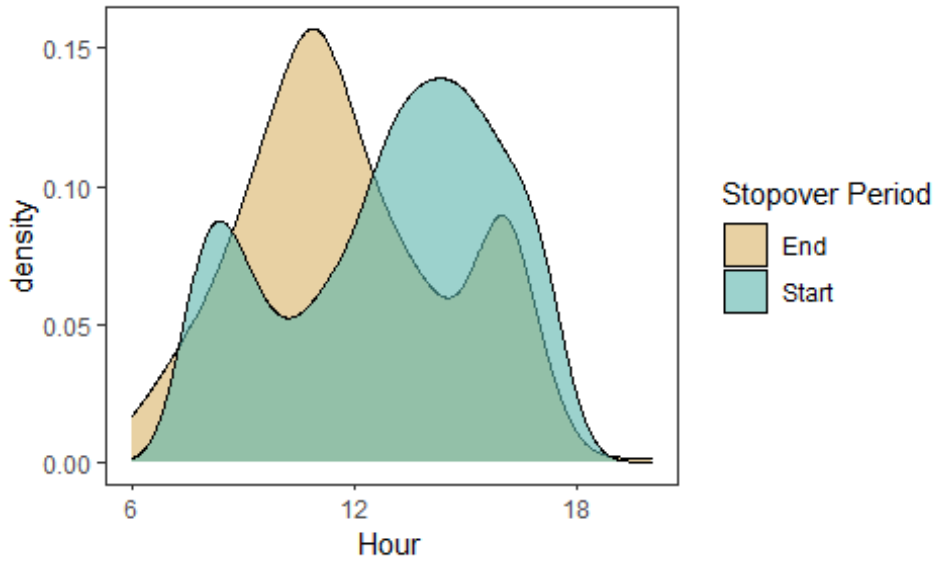
3.6 Acknowledgements

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We would also like to acknowledge those that have contributed data: Missy Braham, Annette Broderick, Adam Duerr, Sharon Poessel, and Brendan

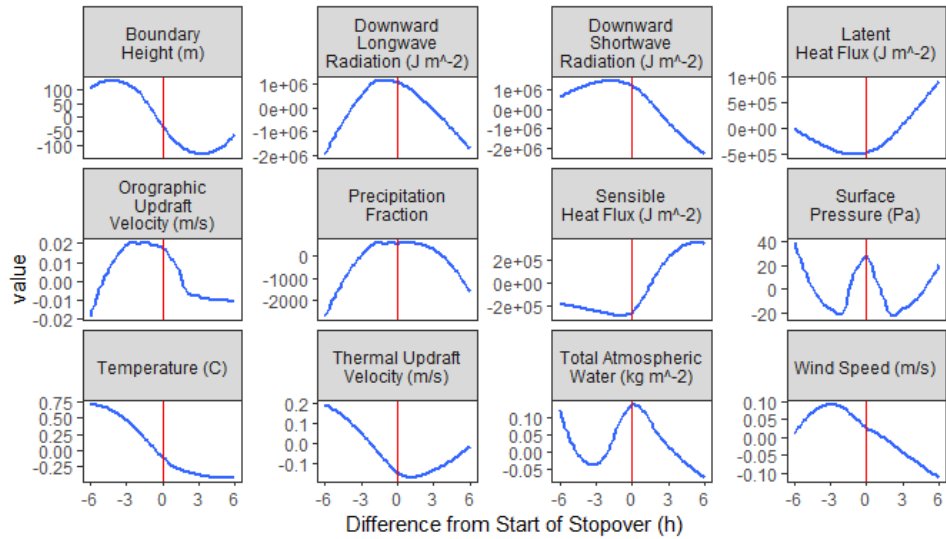
Godley. We would like to thank Jesper Madsen, Justin Calabrese, and René Janssen for their helpful comments. We would also like to acknowledge all of those that helped during data collection.

Appendix A: Supplementary Material Chapter 1

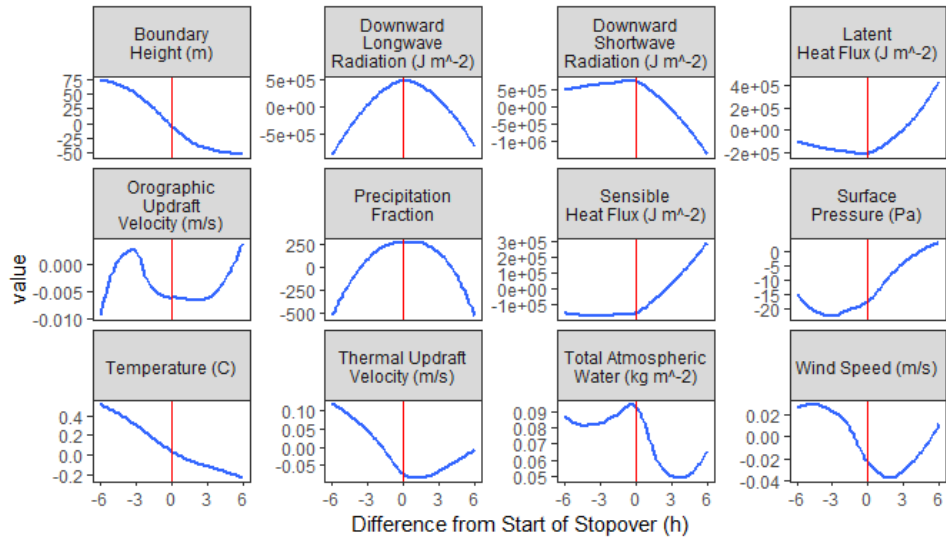


Supplemental Figure A.1. Density plots of the timing of the starts and ends of stopovers. Stopovers started most frequently around 1500 h and ended most frequently around 1000 h. Typical roosting times begin and end approximately at 1700 h and 0900 h, respectively. Due to some gaps in the data, some stopovers appeared to end before 0700 h, during normal roosting hours.

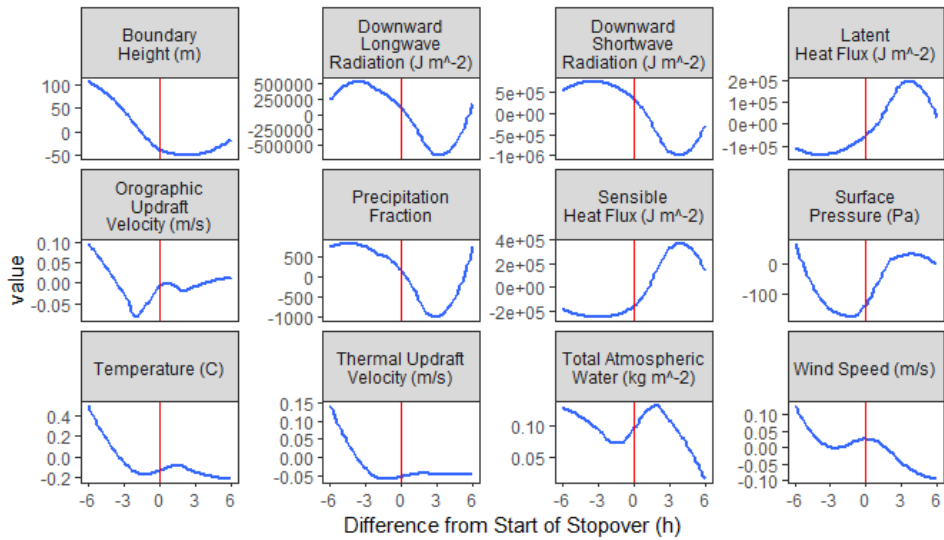
(a) Southwest USA



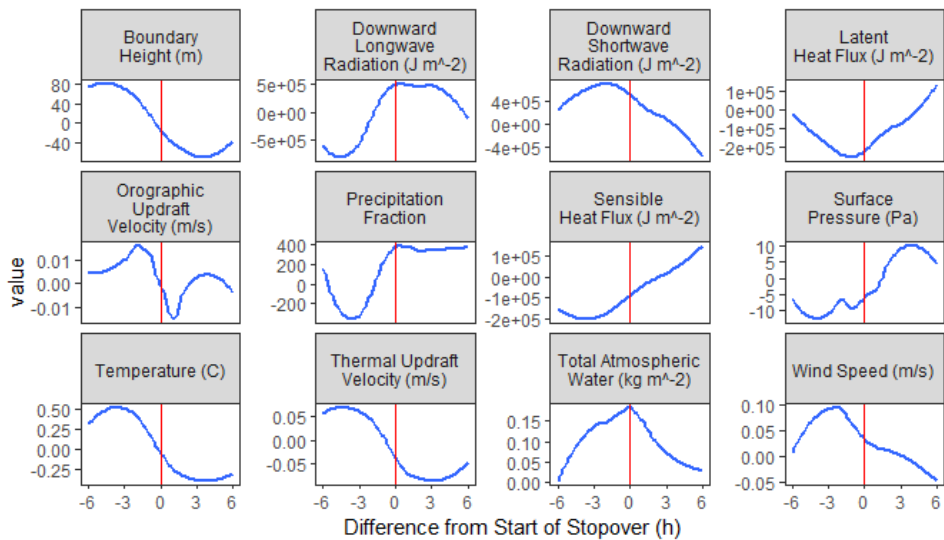
(b) Central Canada



(c) Western Canada

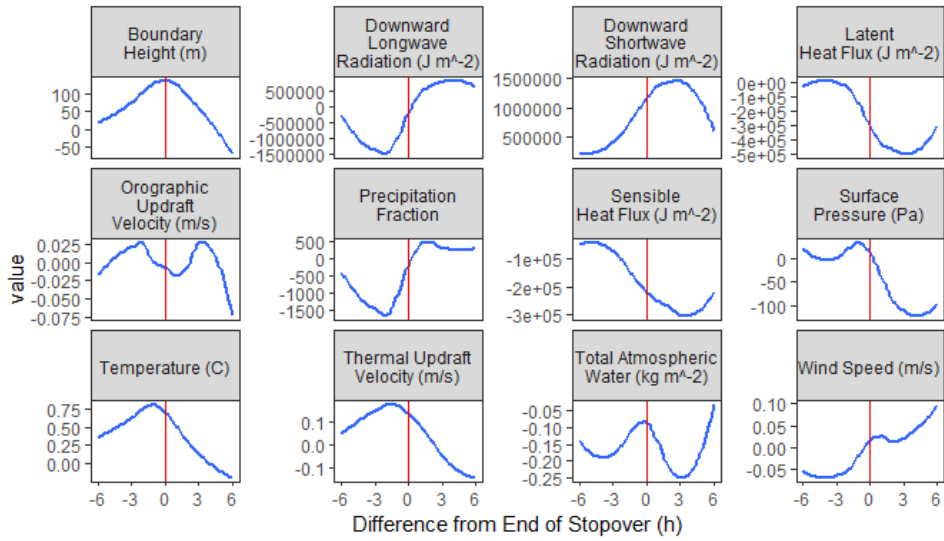


(d) Southern South America

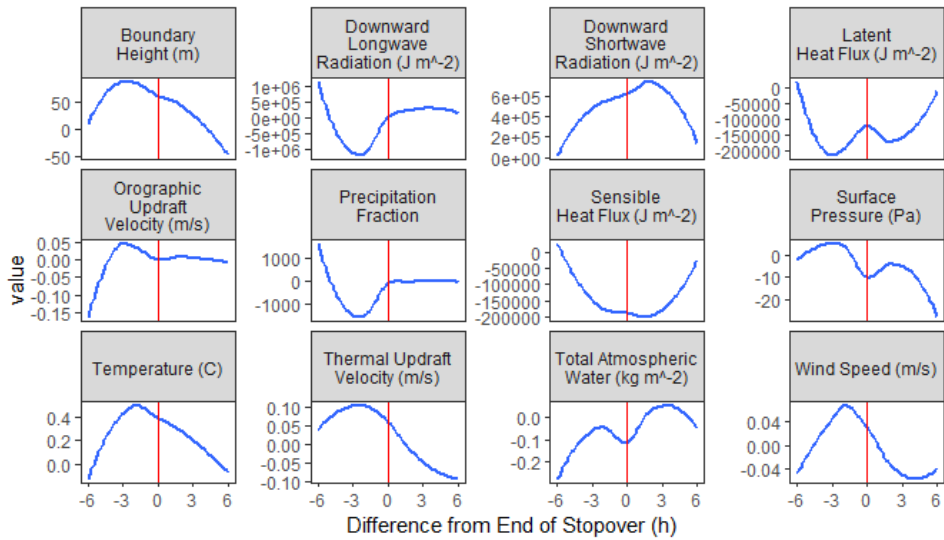


Supplemental Figure A.2. Average weather conditions relative to the start of identified stopovers (red line), by population. The labels on each plot indicate the name of the y-axis. (a) Southwest USA, $n = 138$. (b) Central Canada, $n = 283$. (c) Western Canada, $n = 49$. (d) southern South America, $n = 69$. Differences in responses across populations due to a combination of unequal sample sizes, differing weather variable interactions associated with local climates, and stopovers used for feeding.

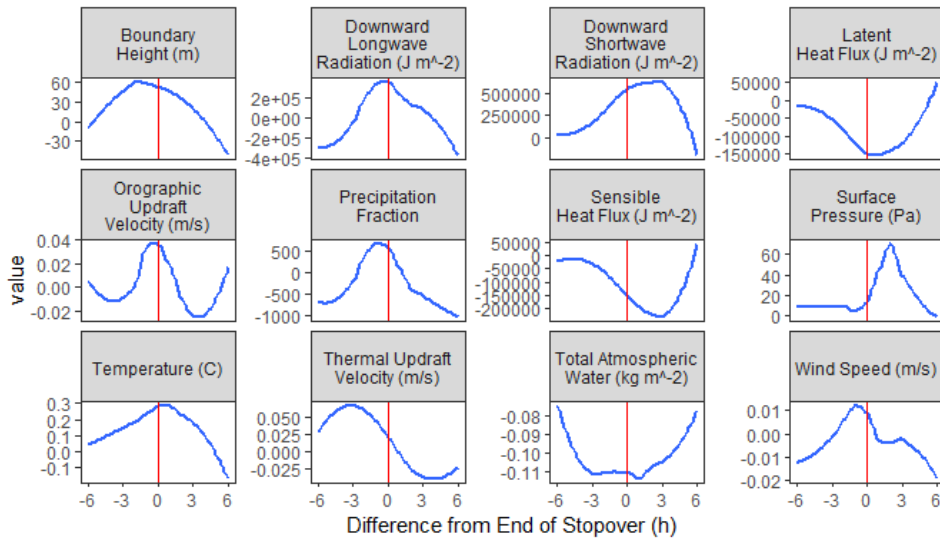
(a) Southwest USA



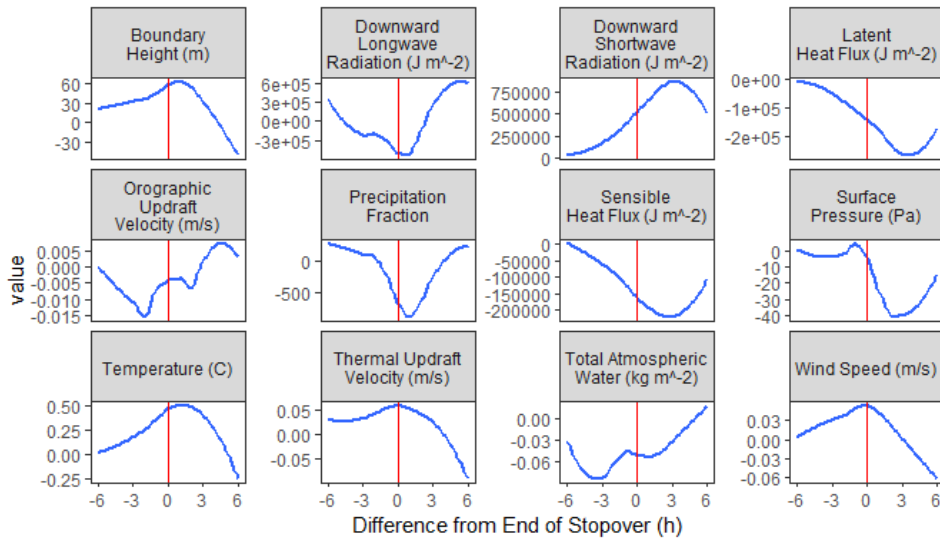
(b) Central Canada



(c) Western Canada



(d) Southern South America



Supplemental Figure A.3. Average weather conditions relative to the end of identified stopovers (red line), by population. The labels on each plot indicate the name of the y-axis. (a) Southwest USA, $n = 138$. (b) Central Canada, $n = 283$. (c) Western Canada, $n = 49$. (d) southern South America, $n = 69$. Differences in responses across populations due to a combination of unequal sample sizes, differing weather variable interactions associated with local climates, and stopovers used for feeding.

Appendix B: Supplementary Material Chapter 3

All supplemental materials for chapter 3 are available at

doi: 10.1111/jav.02612

(current url: <https://www.avianbiology.org/appendix/jav-02612>).

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