A bird of two hemispheres: an examination of Swainson's hawk (*Buteo swainsoni*) ecology across a landscape of increasing wind energy development

by

Katheryn Watson, M.S.

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Approved

Clint Boal
Chair of Committee

Mark Wallace

Brent Bibles

Sarah Fritts

Carlos Portillo

Mark Sheridan
Dean of the Graduate School

August, 2021

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CHAPTER I

INTRODUCTION AND SUMMARY OF FINDINGS

The purpose of this study was to expand knowledge on the life history of Swainson's hawks (*Buteo swainsoni*), including aspects of breeding, juvenile periods, migration, and risks posed by the wind energy industry. Data presented in this dissertation was collected in northern Texas (Armstrong, Carson, Hale, Hockley, Lubbock, Potter, Randall, and Swisher counties) from 2012 to 2018 and from satellite transmitters attached to hawks from 2012 to 2021. Information has been formatted to facilitate future publication of results and is presented here in discrete chapters grouping similar categories of information; some redundancy exists among chapters, but the bulk of each chapter contains unique analyses, results, and conclusions. Each document is formatted as a mix between guidelines required by Texas Tech University (Thesis-dissertation formatting guidelines 2013) and guidelines for publishing with the Journal of Wildlife Management (Cox et al. 2018). Analyses, interpretation, and presentation of data are the responsibility of the author; however, data collection was a collaboration, and each publication produced from chapters will have multiple authors and, hence, the text contains the plural form of 'we' throughout.

Species Information

Swainson's hawks are a Neotropical migratory raptor species that breed in western North America and spend the austral summer season in Argentina and Uruguay (Houston and Schmutz 1995*b*, Fuller et al. 1998, Canavelli et al. 2003, Bechard et al.

2010, Kochert et al. 2011). Swainson's hawks have been considered a declining species of conservation concern in California (Bloom 1980), Oregon (Littlefield et al. 1984), Nevada (Herron et al. 1985), and western Canada (Houston and Schmutz 1995*a*), but may have stable and increasing populations in other regions across the breeding range (Bechard et al. 2010, Sauer et al. 2013). Similar to most other new world *Buteo* species, Swainson's hawks form monogamous pairs, build large stick nests on structures such as trees and utility poles, use soaring flight, and use open country as habitat (Schmutz et al. 1980, Giovanni et al. 2007, McConnell et al. 2008, Bechard et al. 2010, Nishida et al. 2013). This species preys on small vertebrate and large invertebrate animals, such as rodents, lizards, snakes, and grasshoppers, during the breeding season (Rodríguez-Estrella 2000, Giovanni et al. 2007, Bechard et al. 2010, Nishida et al. 2013). However, unlike most raptorial species that maintain similar diets year-round, Swainson's hawks switch to primarily invertebrate prey, such as grasshoppers, beetles, and dragonflies, prior to migration and maintain that diet throughout the nonbreeding season (Woffinden 1986, Johnson et al. 1987, Kirkley 1991, Tiranti 1996, Canavelli et al. 2003). Migration is a common trait among raptor species that inhabit temperate regions; due to seasonal resource availability, Swainson's hawks migrate long distances (typically > 10,000 km per trip) and spend the majority of their year in summer grasslands where food is plentiful and temperatures are warm (Kerlinger 1989, Kirkley 1991, Bildstein 2006, Bechard et al. 2010, Kochert et al. 2011). Additionally, unique from most New World raptor species that spend significant time as solitary individuals or in pairs, Swainson's hawks are gregarious and relatively tolerant of conspecifics throughout life (Bechard et al. 2010). Though pairs are territorial near nests, it is common for multiple adults to use the same hunting grounds with no aggression (Bechard et al. 2010). Prior to full migration, hawks gather in large groups while gorging on outbreaks of insects (Woffinden 1986, McGrath 1988, Houston 1990, Bechard et al. 2010, Littlefield and Johnson 2013). Migration is made en masse, with thousands of hawks flocking together along with other soaring species generally travelling the same route (Fox 1956, Smith 1985, Bechard et al. 2010). Swainson's hawks continue a gregarious lifestyle during their nomadic non-breeding season (Canavelli et al. 2003, Sarasola and Negro 2006, Bechard et al. 2010). Swainson's hawks are a long-lived species, surviving up to (and possibly beyond) 24 years (Houston and Schmutz 1995*b*, Woodbridge et al. 1995, Bechard et al. 2010); known threats to this species include pesticides, electrocution, vehicular collisions, human persecution, and collision with wind energy structures (Kerlinger 1989, Yosef 1996, Goldstein et al. 1999*a*, Bildstein 2006, Bechard et al. 2010). An abundance of research and observations exist from the breeding season, particularly focused on reproduction (e.g., Dunkle 1977, Bechard 1983, Bednarz 1988, Houston and Zazelenchuk 2004, Briggs 2007), diet (e.g., Bechard 1982, Bechard et al. 1990, Rodríguez-Estrella 2000, Giovanni et al. 2007, Behney et al. 2010), and habitat associations (e.g., Green and Morrison 1983, Schmutz 1987, Babcock 1995, England et al. 1995, Bosakowski et al. 1996). In this research, I chose to expand our knowledge on reproductive observations from the northern Texas population, migratory details, such as speed of travel and habitat use, juvenile ecology from post-fledging through first reproduction, and risks posed by the wind energy industry throughout the species global range.

Summary of Findings

My collaborators and I began studying this species because it is a common breeding raptor in the High Plains of Texas. Our interests began with monitoring nesting activity east of Amarillo, Texas (Walker 2013, Groen 2015, Watson et al. 2017), but this is a relatively understudied species, so my interests quickly to expanding the ecological knowledge for this species throughout its life, especially for information-poor aspects, such as migration, the juvenile period, and mortality risks. To do so, we attached satellite transmitters to adult hawks from 2012 to 2013, and later equipped fledglings with transmitters from 2016 to 2018 (Walker 2013, Groen 2015, Watson et al. 2017). We monitored transmitter data from 2012 to 2021.

To our knowledge, this is the third transmitter study on this species. The first was a range-wide effort encompassing multiple research groups that revealed the most detailed migratory information to date (Fuller et al. 1998, Bechard et al. 2006, Kochert et al. 2011) and helped discover the now-famous mass mortality problems related to pesticide use on the wintering range (Woodbridge et al. 1995, 1996, Goldstein et al. 1999*a, b*). The second study focused on northern California Swainson's hawks, which are a unique population that follow different migratory pathways, have different season lengths, and use unique wintering areas (Airola et al. 2019). This study differs from the first with updated technology, including significantly lower locational error (using GPS rather than Doppler estimates) and multiple locations per day. This study also differs from both previous efforts in using hawks captured from a unique area at the eastern edge of the breeding range (around 650 km southeast from the nearest previous capture location), and this also is the first to include data from fledgling hawks.

In Chapter 2, collaborators and I monitored nesting across the study area in Armstrong, Carson, Hale, Hockley, Lubbock, Potter, Randall, and Swisher counties, Texas, from 2014 to 2018. This study expanded in space and effort over time, and the study area went through several periods of drought, producing variable results. In compiling data, I found this population had lower average nesting success and fledglings produced compared to other studies. However, my extensive literature review coupled with the results from this chapter suggest that the population was likely stable and adaptable to annual variation in weather conditions.

In Chapter 3, I presented location and movement data from transmittered hawks to add to the body of knowledge on Swainson's hawk migration. This is the first chapter presenting transmitter data; I therefore presented details on adult hawk survival, filtering data prior to analyses, and the advantages and caveats of using transmitters for such research. This chapter involved both a re-examination of migration data described by previous researchers (primarily Fuller et al. 1998, Kochert et al. 2011, and Airola et al. 2019) and novel observations and analyses. I examined the migration route, timing, distance travelled, speed of travel, staging and stopover behaviors, if breeding status affected or was affected by migration, and whether migration differed by sex of bird. My conclusions mostly supported the conclusions of previous research, and many discrepancies were explained by the breeding location of birds in this study (e.g., northern Texas hawks had a shorter distance to travel, and therefore had shorter spring migrations and began nesting earlier than hawks captured by Fuller et al. 1998 and Kochert et al. 2011). Importantly, my study expanded our understanding of plasticity in migratory behaviors among individuals of this species, which likely aids in individual survival and persistence of migratory behaviors over time.

In Chapter 4, I used transmitter location data to explore habitat use and selection during migration. I used Manly's selection ratios to describe landscape use at the second order with a Design III analysis. I divided data into sets representing fall (outbound or southward) and spring (return or northward) migration, active (daytime) or roosting hours, moving or stopped data, and the two types of stops observed (pre-migratory staging or mid-migration stopover). I found that habitat for migrating birds mostly reflected breeding- and nonbreeding-range habitat (open landscapes), with some additional use of forests, and almost complete avoidance of large bodies of water. These habitat uses and selection presumably aid hawk survival during migration.

In Chapter 5, I used transmitter data from fledgling hawks to provide novel observations of the first several years of Swainson's hawk life, an area of research that the body of literature was significantly lacking. I described survival and mortalities during the juvenile period. One of the original goals of this research was to follow hawks through the first breeding attempt to determine natal philopatry or dispersal, but most (16 out of 17) hawks presumably perished before recruitment, and the one remaining hawk I have continued tracking through the end of writing this dissertation had not yet attempted to breed. I described behaviors (particularly locations and frequency of movements) observed during each season, comparing juvenile migration to adult migration data from Chapter 3 and previous research where possible. I found that juveniles often deviated from known migratory routes during the first migration attempt, which usually resulted in mortality. I found that some juveniles spent the nonbreeding season 400 km north of the main nonbreeding areas used by adults. Summer behaviors on the breeding range were nomadic and transitory, and while some hawks visited natal territories, others never returned to the study area. I tracked a few pairs of siblings, which separated and became independent by the end of the post-fledging period, prior to first migration attempts. Overall, the juvenile period was a time of exploration, learning, and low survival, and I found no evidence that hawks recruit into the population by three or four years of age, even though hawks gain adult plumage around their second year.

Last, in Chapter 6 I examined the risk posed to Swainson's hawks from the wind energy industry. Wind turbines are a known hazard for flying animals and may be especially important as a hazard for raptorial species due to their hunting behaviors, low fecundity, and low population sizes compared to smaller bird species. To my knowledge, the body of wind energy risk literature lacked analyses of Swainson's hawks, even though this species heavily overlaps the industry throughout North America. I, therefore, used adult and juvenile transmitter data to compare hawk locations to locations of wind energy facilities in the United States to assess risk. I could not find wind energy information for international regions, so I used satellite imagery and other resources to find facilities to further evaluate overlap with hawk locations throughout the global range. I additionally used resource selection functions and resource selection probability functions to model hawk occupancy and likelihood of finding wind energy facilities throughout the global range, to further evaluate risk to this species. I found that Swainson's hawks were at the highest risk on the breeding range, due to the density of facilities in the United States. Few reports of mortality range-wide and low risk of encountering wind turbines outside of the breeding range may indicate that Swainson's hawks are less vulnerable to this hazard than other species. This may perhaps be due to behavioral and dietary differences, such as perching on the ground to eat insects and Neotropical migration. However, the lack of data transparency within the industry clouded my ability to draw strong conclusions.

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CHAPTER II

SWAINSON'S HAWK REPRODUCTION IN THE HIGH PLAINS OF TEXAS

Abstract

Reproduction plays an important role in population dynamics, and there is value in describing reproductive parameters from understudied populations, especially in those regions that may differ in climate dynamics. Swainson's hawks (*Buteo swainsoni*) are migratory raptors that breed across western North America and are common breeding raptors in the High Plains of northern Texas. These hawks build large, conspicuous stick nests in trees and occupy territories for three to five months during the North American summer. We monitored High Plains nests over five years to report reproductive parameters and compare to populations occupying other regions of the breeding range. Over the course of the study, we monitored 171 nests to determine occupancy by Swainson's hawks and fate. Swainson's hawks were the most common breeding raptor outside of urban areas, and usually the only occupant of large stick nests throughout the study. We estimated Swainson's hawks occupied one nest for every 33 km^2 surveyed. We observed 29 to 76% nesting success each year, with successful nests producing 1 to 4 fledglings. Our average nesting success and fledglings produced were lower than reports from across the breeding range, with high interannual variability. Nest survival ranged from 22 to 79% and was likely affected most by winter drought. However, the consistent occupancy of nesting territories and nesting attempts each year suggested that this population of Swainson's hawks adjust well to variable environmental conditions, possibly aided by their generalist, and highly insectivorous, diet.

Swainson's hawks (*Buteo swainsoni*) are migratory raptors that breed in grasslands, croplands, shrublands, and deserts across western North America (Smallwood 1995, Rodríguez-Estrella 2000, Bechard et al. 2010, Nishida et al. 2013). This species has been noted as declining and of conservation concern in the past in California (Bloom 1980), Oregon (Littlefield et al. 1984), Nevada (Herron et al. 1985), USA, and in western Canada (Houston and Schmutz 1995*a*), but more recent research suggests populations may be stable in some parts of its range including Colorado, Idaho, Montana, and Washington, USA (Bechard et al. 2010), and annual breeding bird surveys from 1966 to 2011 suggested all *Buteo* species showed increasing trends across most regions (Sauer et al. 2013). Annual Swainson's hawk migration counts at locations such as Veracruz, Mexico, and Panama City, Panama, where most of the worldwide population presumably passes through, vary so substantially (e.g., 175,000 – 846,000) that Bechard and colleagues (2010) suggest they cannot be used to reliably assess population status. The variability of regional reports across time and a lack of studies aimed at population assessment of Swainson's hawks range-wide leaves open the questions of population status and dynamics (Nishida et al. 2013). Monitoring reproductive success and annual nest-site occupancy may provide some indication as to population stability in understudied regions and adds to the body of knowledge for the entire North American population.

Similar to most other *Buteo* species, Swainson's hawks build large stick nests in trees and on other tree-like structures, such as yuccas and utility poles (Fitzner 1980, Rodríguez-Estrella 2000, Bechard et al. 2010, Nishida et al. 2013). Nest site is typically a solitary tree or the largest tree within a small patch or along a planted or natural tree line, near an open landscape to facilitate hunting (Fitzner 1980, Giovanni et al. 2007, Bechard et al. 2010, Behney et al. 2010, Nishida et al. 2013). Pair formation is thought to occur when adult birds return to the breeding range in April, and nest building or refurbishing occurs within 7 to 15 days of arrival (Bechard et al. 2010). Fitzner (1980) reported that about half of Swainson’s hawk pairs in Washington, USA, reused nests that were previously built or used by Swainson’s hawks, red-tailed hawks (*Buteo jamaicensis*), black-billed magpies (*Pica hudsonia*), American crows (*Corvus brachyrhynchos*), and common ravens (*Corvus corax*). In addition to those species, Swainson’s hawks share breeding areas with many raptors, such as northern harriers (*Circus hudsonius*), Mississippi kites (*Ictinia mississippiensis*), Harris’s hawks (*Parabuteo unicinctus*), ferruginous hawks (*Buteo regalis*), American kestrels (*Falco sparverius*), Prairie falcons (*Falco mexicanus*), barn owls (*Tyto alba*), short-eared owls (*Asio flammeus*), great horned owls (*Bubo virginianus*), and burrowing owls (*Athene cunicularia*) (Schmutz et al. 1980, Bednarz 1988, Bechard et al. 1990, Bosakowski et al. 1996, Sibley 2003, Giovanni et al. 2007). Swainson’s hawks are well known for having a highly insectivorous diet when staging prior to migration and during the nonbreeding season (Woffinden 1986, Johnson et al. 1987, Kirkley 1991, Tiranti 1996, Canavelli et al. 2003), but, during the breeding season, adults consume and feed small vertebrate animals, including ground squirrels, lizards, and snakes, to nestlings (Rodríguez-Estrella 2000, Giovanni et al. 2007, Bechard et al. 2010, Nishida et al. 2013). Across the breeding range, reported nesting success (number of nesting attempts that fledged ≥ 1 young) ranged from 49 to 87% and number of young produced per successful pair ranged from

1.5 to 2.5 fledglings, with a maximum of 5 fledglings observed per nest (Table 2.1). The entire nesting period lasts about 73 days, and nestlings fledge at 38 to 46 days post-hatching (Bechard et al. 2010). Mean date of fledging ranges from July to August across the entire breeding range, with generally earlier fledging dates in more southerly populations (Bechard et al. 2010)

Swainson's hawks' reproductive information has been reported across the breeding range, from northern Mexico to Canada (Table 2.1). To our knowledge, however, little published information exists for the population breeding in the High Plains ecoregion of northern Texas. Although this region is a common overwintering location for many raptor species, breeding season diversity is much reduced. During summer in this region, Swainson's hawks are one of the few, and the most commonly encountered, diurnal breeding raptor outside of urban areas. We studied a population nesting near Amarillo and Lubbock, Texas, across seven years to compare reproductive success to other reports. We additionally used collected information to speculate on population status and the question of why Swainson's hawks may be the most common breeding raptor across the High Plains of Texas.

Methods

We conducted nest monitoring in Armstrong, Carson, Hale, Hockley, Lubbock, Potter, Randall, and Swisher counties, Texas from 2014 to 2018 (Fig. 2.1). Originally, this study was focused on the Pantex Plant and a 25-km radius around the plant; the Pantex Plant is a facility for the final assembly, dismantlement, and maintenance of nuclear weapons, and is operated by Consolidated Nuclear Security, LLC under contract from the U.S. Department of Energy and National Nuclear Security Administration (https://pantex.energy.gov/about) (Fig. 2.2). The Pantex Plant is actively supportive of conservation of natural resources on the property and contains a consistent breeding population of Swainson's hawks. We later included nests around the city of Lubbock, Texas, and those located along the I-27 highway between Lubbock and Amarillo (Fig. 2.2); this expansion was to increase the sample of nests for components of a related study (Chapter 5). The study area was a mosaic of natural and conservation reserve program (CRP) grasslands, irrigated and dryland crops (primarily cotton [*Gossypium* sp.], sorghum [*Sorghum bicolor*], and corn [*Zea mays*]), and urbanized spaces (Walker 2013, Watson et al. 2017).

We searched for large stick nests that might be used by Swainson's hawks in February and March (prior to deciduous tree leaf out) on the Pantex Plant property and along public roadways throughout the study area. We used public roadways for surveying and monitoring, because other than the Pantex Plant, we had no access to private property in the area; we later obtained permission to access nests on some private lands when young hawks were fledging for a related study (Chapter 5). We added additional nests to monitoring efforts later in the season as they were discovered. We used a Global Positioning System (GPS) to record the Universal Transverse Mercator (UTM) coordinates for each nest location, or the coordinates from the observation point combined with distance and bearing to nest to later estimate coordinates of each nest., which was our estimate of the distance we were able to consistently and reliably spot nests from roadways. Based on the furthest distance of nests from roadways that we found during the study, we assumed that we could only locate nests up to 500 m from a public roadway. We estimated the total area surveyed for nests by adding a 500-m buffer and used the surveyed area to estimate the density of nests for the year 2017, when our survey effort was highest (Fig. 2.2).

When Swainson's hawks returned from migration in mid-April, we began weekly nest checks from the location of best view to determine occupancy and nest fate. In some cases, nests were not visible due to leaf cover; in these situations, we watched for Swainson's hawk presence and activity. If Swainson's hawks were immediately visible and clearly using the nest (e.g., perching on or near the nest, carrying sticks to the tree, incubating eggs, or interacting with nestlings), we left the area to minimize disturbance. If no Swainson's hawk adults or nestlings were visible, we monitored the nest or tree for 10 to 20 minutes before moving on. If adult Swainson's hawks were witnessed using the nest, we marked the nest as "occupied". If a nest had no recorded activity for at least three consecutive checks, we declared the nest "vacant" and stopped monitoring for the remainder of the season, unless a later incidental observation indicated missed activity or occupancy by a late-nesting pair. We considered nesting efforts to be successful when nestlings reached at least 32 days old (80% of fledging age; Steenhof and Newton 2007), which we estimated by plumage characteristics described by Gossett and Makela (2005). In the cases of poor nest visibility, we continued to monitor nests for presence of fledglings as an indication of success. We considered nesting attempts as having failed when all activity at the nest ceased prior to nestlings reaching the 32nd day of age, deceased nestlings or abandoned eggs were found at the nest or tree, the nest was destroyed, or the nest appeared vacant during three consecutive checks after known occupancy. In some cases, we could not determine the fate of a nest (e.g., private land access restricted) or we failed to monitor the nest sufficiently to determine activity, and we left the occupancy and/or fate labeled as “unknown”. We used Excel and ArcMap 10.7 to examine these data.

We used known fate models in Program MARK to estimate daily survival rate (DSR, or the probability of a nest surviving one day of monitoring) of nests we monitored where fate was known and we had sufficient survey data for the analysis (Dinsmore and Dinsmore 2007, Cooch and White 2019). We estimated the likelihood of any nest surviving the nesting season (approximately 75 days long; Bechard et al. 2010) as DSR^{75}. Variability was reported as standard error, estimated by MARK for DSR, and estimated using the delta method for DSR^{75} (Powell 2007). We then modeled annual DSR with several variables that might have impacted annual nesting success in MARK (i.e., modelling one explanatory variable at a time in a logistic regression with the DSR as the response variable); whether or not the National Weather Service (NWS, https://www.weather.gov) classified the year as a drought year for the main study area (weather station located at 35.22 N, 101.71722 W, within our northern nest-monitoring polygon; Fig. 2.1), amount of annual precipitation the NWS reported for Amarillo, the annual average Standardized Precipitation Evapotranspiration Index (SPEI; Global SPEI database, https://spei.csic.es) for a point within the region containing the most nests in our dataset (coordinates = -101.75, 35.25), average winter SPEI (Nov to Mar) prior to each breeding season, and average SPEI during each breeding season (Apr to July) (Table 2.2). SPEI provides an estimate of drought severity that considers precipitation, evapotranspiration of local flora, and temperature; zero represents an average month, positive numbers indicate a better than average month, and negative numbers indicate a worse than average month (i.e., drought). We used Akaiki's information criterion (AICc) to select the model that best explained variability in DSR.

Results

We located 305 large stick nests that might be suitable for Swainson's hawk use throughout the entire study, and we monitored 171 nests to determine occupancy by Swainson's hawks and fate (Table 2.3, Fig. 2.2). Effort to discover and monitor nests varied throughout the study due to logistical constraints; we focused most monitoring efforts on northern-study-area territories to consistently track occupancy over time, while we made efforts to discover, but failed to sufficiently monitor, most nests in the southern portion of the study area, and thus omitted many of those nests from analyses. We estimated the maximum area surveyed was 2,475 km^2. The estimated density of large stick nests in 2017 (our year with greatest survey effort) was 0.04 nests/km^2, or 1 nest for every 25 km^2 surveyed. The estimated density of nests occupied by Swainson's hawks was 0.03 nests/km^2, or one occupied nest for every 33 km^2 surveyed. We found few nests within and near urban areas; most nests were spread out across the rural landscape (Fig. 2.2). Few large stick nests we monitored were found to be occupied by species other than Swainson's hawks; one was occupied by a pair of red-tailed hawks, one was occupied by a pair of white-tailed kites (*Elanus leucurus*, a rare species for the region; Watson et al. 2019), and several were occupied by Chihuahuan ravens (*Corvus cryptoleucus*).

Swainson's hawks tended to place nests in lone trees or trees that were in small patches or along treelines but appeared to avoid larger wooded patches (we did not measure wooded patch size; this is our subjective impression of the landscape available to hawks). A few large stick nests were located on abandoned windmills (all confirmed to be unsuccessful nesting attempts due to nest destruction during storms) and one utility pole (occupied by Chihuahuan ravens), but our observations indicated mostly trees were used as nest substrates by Swainson’s hawks in the study area. The closest nesting pairs we found were 0.9 km apart.

From 2014 to 2018 we monitored 36 to 104 large stick nests per year, of which 17 to 79 were occupied annually (Table 2.3, Fig. 2.2); of these, we observed 29 to 75% nesting success (Tables 2.1 and 2.3). Estimated DSR for all nests where we had sufficient data to analyze was 0.993 ± 0.010, or 0.576 ± 0.117 for the entire nesting period (DSR^{75}, Table 2.3). Model selection indicated that SPEI for the months prior to breeding season (Nov – Mar) best explained the annual variation in DSR (Table 2.4); the year with the highest DSR had a positive winter SPEI (i.e., no drought and better than average rainfall), and DSR declined with increasingly negative winter SPEI (i.e., worse daily survival in years of worse winter drought; Tables 2.2 and 2.4). Fledging occurred from late June to early August with 90 to 100% of nests fledging young during July each year. Successful nests produced 1 to 4 fledglings, with an average of 1.4 to 2.0 fledglings/nest (Tables 2.1 and 2.3). Breeding adults wearing leg bands, and some additionally wearing satellite transmitters, from related studies (Walker 2013, Groen 2015, Watson et al. 2017, Chapters 3, 4, and 6), returned to the same nesting territory every year; our only exceptions were four instances of three non-breeding birds (13% of those monitored with transmitters) making exploratory movements or only holding loose home ranges throughout summers.

Discussion

Swainson's hawks were a common breeding raptor in the study area, occupying at least 70% of the large stick nests we located throughout the study. Nests were typically located in solitary trees or in the largest tree in a patch or row, with the immediate landscape surrounding the tree/stand being open grasslands and/or agricultural fields. This was consistent with previous reports for breeding-season habitat use by Swainson's hawks in the region (Giovanni et al. 2007, Behney et al. 2010) and other arid southwestern landscapes (e.g., Bechard et al. 2010, Nishida et al. 2013). Several territories contained multiple nest locations and (presumably) pairs would switch between nest sites from year to year in those territories. Nests often survived the nonbreeding season to be reused or refurbished when hawks returned the following year, similar to that reported in the northwestern breeding range (Fitzner 1980). When nests were destroyed after storms and extreme wind events, hawks would often build a new nest in the same tree or nearby (mostly occurred in subsequent seasons, though we observed a few early destructions that led to a second nest attempt in the same season, but second nests always failed during our observations), though some territories would be abandoned after nest destruction.

We frequently found nests in dead trees; such nests were often unoccupied, and pairs that used those nests usually failed. We suspect nests were occupied before nearby trees grew leaves; the pair may have been reoccupying a nest from a previous year, not recognizing the tree as dead. Typically, nests in dead trees were abandoned in subsequent years and eventually fell apart.

Trees as primary nesting substrates which are being lost to drought brings up a potential long-term issue for nesting Swainson's hawks. Climate change is predicted to make the High Plains, and many other arid landscapes inhabited by Swainson's hawks, dryer and more drought-prone, potentially threatening tree persistence (Modala et al. 2017, Nielsen-Gammon et al. 2020). Most trees on the study-area landscape today are not native species; this region was historically largely a grassland with occasional mesquites (*Prosopis glandulosa*) and cottonwoods (*Populus deltoides*) in drainages, and junipers (*Juniperus virginiana*) lining cliff and canyon edges. Homesteading settlers planted non-native species, such as Siberian elm (*Ulmus pumila*), Russian olive (*Elaeagnus angustifolia*), and eastern red cedar (*Juniperus virginiana*), for shade and wind breaks. This increase in nesting habitat over the last century may have facilitated a shift in the breeding population away from more-northwestern areas, such as Oregon (Littlefield et al. 1984) and western Canada (Houston and Schmutz 1995*a*), towards a breeding range near the start of southward migration (Bechard et al. 2010, Kochert et al. 2011) with abundant prey, a longer growing season, and increasing trees suitable for nesting. However, today many homesteads have been abandoned and the trees are no longer cared for and new trees are not being planted. Increasing drought frequency, therefore, poses a risk of slowly losing these nest substrates that currently sustain the population. However, while we did not observe this in our study, Swainson's hawks use powerline poles as nest substrates, which can replace lost trees where available, though these poles also represent collision and electrocution hazards (Bechard et al. 2010). Additionally, urban sprawl near cities may bring a new wave of homesteaders and tree planting, to support at least a small population of hawks.

Adult Swainson's hawks with alpha-numeric coded bands and/or GPS transmitters (Walker 2013, Groen 2015, Chapter 3) appeared to return to the same territory each year. Our only exceptions were occasional hawks that did not appeared to breed, perhaps because they failed to find a mate or suffered such an early failure that the data showed too little pattern to establish a breeding attempt, or perhaps because we tagged some subadults in adult plumage (i.e., Swainson's hawks often molt into adult plumage in their third year but may not breed until their fifth year; Wheeler and Clark 1995, Vennum 2017, Chapter 5). For breeding hawks, site fidelity appeared high; one banded male had been located in the same territory from 2013 to 2020, oftentimes switching nest sites; given that he was in adult plumage at capture, the latest observation in 2020 (Rod Goodwin, personal communication) made him at least 9 years old. Our evidence of high territory re-use is consistent with reports of at least 71 to 90% breeding-territory fidelity (Fitzner 1980, Woodbridge 1991, Schmutz et al. 2006).

Nesting success and fledging numbers in this study were lower than other reports from across the breeding range. However, we found high variability across years, similar to other multi-year studies (e.g., Gilmer and Stewart 1984, England et al. 1995, Hansen and Flake 1995, Houston and Schmutz 1995*b*, Woodbridge et al. 1995*a*, Rodríguez-Estrella 2000, Schmutz et al. 2001, Houston and Zazelenchuk 2004, Wiggins et al. 2014). Most publications we examined did not estimate nest survival. Our overall nest survival estimate (DSR^{75}) of 58% was higher than the reported 34% by Inselman et al. (2015), higher than or equal to the 44% and 58% reported by Nishida et al. (2013) and lower than the 62% reported by Kolar and Bechard (2016). Nest survival in this study was higher than all previous reports in 2014 and 2015 and lower than all previous reports in 2018.

Swainson’s hawks were the dominant diurnal raptor species across this High Plains of Texas landscape during summer season. They were abundant, but also often the only large raptor observed within the study area and across nearby counties during the breeding season (Apr – Aug). This contrasts with other studies reporting Swainson’s hawk populations sharing the breeding landscape with a variety of raptor species (e.g., Schmutz et al. 1980, Bednarz 1988, Bechard et al. 1990, Bosakowski et al. 1996, Sibley 2003, Giovanni et al. 2007). This may be explained, at least in part, by the current land use and climate of the region.

The High Plains of Texas is an arid landscape that experiences hot summers and frequent drought, with years 2014, 2016, and 2018 being noted as drought years for the study area by the National Weather Service (https://www.weather.gov; Table 2.2). The SPEI suggested winters prior to breeding seasons of 2014 and 2016 through 2018 having drought conditions (with 2018 being the most significant; Table 2.2). This factor best represented annual differences in our DSR estimates; meaning, winter drought may have led to poor clutch and nestling survival the following breeding season. For the year of lowest DSR (2018), the breeding season additionally had the most severe drought conditions of all years.

Frequent droughts and extreme heat may render food resources unpredictable for raptors, with prey population sizes and their spatial dynamics varying widely from year to year (Dickman et al. 1999, 2011, Bradley et al. 2006, Prugh et al. 2018). This may cause species of raptors that rely heavily on mammal prey to perceive the landscape as poor quality or non-habitat for breeding due to inconsistent prey availability. However, the dietary plasticity of Swainson’s hawks may be an evolutionary advantage, enabling them to use this landscape for breeding habitat (Woffinden 1986, Johnson et al. 1987, Rodríguez-Estrella 2000, Giovanni et al. 2007, Bechard et al. 2010). Observations from the wintering grounds suggest their primary food sources are grasshoppers, dragonflies, and other large invertebrate prey (Jaramillo 1993, Tiranti 1996, Canavelli et al. 2003, Bechard et al. 2010). Additionally, large gatherings of Swainson's hawks have been observed feeding on outbreaks of grasshoppers and other invertebrates at pre-migratory staging areas on the breeding range (Woffinden 1986, Johnson et al. 1987, Littlefield and Johnson 2013). Swainson's hawks appear to only take larger prey, such as rodents and reptiles, during breeding seasons, when the adults and young probably need additional calories (Rodríguez-Estrella 2000, Giovanni et al. 2007, Bechard et al. 2010, Behney et al. 2010). This breadth of dietary options may allow Swainson's hawks to succeed in a landscape that is unfavorable to other larger raptors that typically feed higher on the food chain. Additionally, in contrast to many raptors (Schmutz 1987, Leptich 1994, Sánchez-Zapata et al. 2003), Swainson's hawks appear to do well in agricultural areas, again perhaps because they take advantage of insect prey, such as crop pests (Gilmer and Stewart 1984, Schmutz 1987, Wiggins et al. 2014). While adult Swainson's hawks on the High Plains are known to feed nestlings with vertebrate prey, they also deliver invertebrates (Giovanni et al. 2007, Behney et al. 2010), and we frequently observed fledglings catching grasshoppers on the ground. Grasshoppers and other insects are an important prey source that helps fledglings gain hunting experience and independence from adults.

The worst year for nesting Swainson's hawks in this study was 2018, where a severe drought likely caused a decrease in prey availability, which resulted in low occupancy and high nest abandonment and nestling mortality. That was also the only year where we handled fledglings for a related study in poor and starving condition; several fledglings were in too poor of condition to attach transmitters for inclusion in that study and those that received transmitters suffered high mortality (Chapter 5). As stated above, droughts are likely to reduce prey availability, resulting in lower reproductive success, and may result in killing trees which was also highly correlated with nest failure in our data. However, Swainson's hawks are long lived; we have records of minimum 8- and 9-year-old birds (Chapter 3) and records exist for 18-, 19-, 21-, and 24-year-old birds (Houston and Schmutz 1995*b*, Woodbridge et al. 1995*b*, Bechard et al. 2010). In addition to a generalist diet, being long-lived means hawks do not have to breed successfully every year to maintain a population, and instead have potentially a decade or more to minimally replace themselves. Even in years of poor reproduction, adult Swainson's hawks were commonly encountered throughout the region. Our overall impression was that the High Plains population appeared stable over time, with most territories consistently being filled by Swainson's hawk pairs year after year.

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Tables

Table 2.1. Summary of Swainson’s hawk nesting success and number of fledglings produced across the breeding range. Nest success means proportion of monitored pairs that fledged ≥ 1 young. Numbers were estimated from available information when not directly stated within the source. Numbers represent averages when source reported data across multiple years. ‘Overall averages’ were estimated from numbers in this table but were not weighted to sample sizes or adjusted for varying methodologies in the publications, so may be biased. Lines represent data that was not reported and could not be estimated.

Location	% Nest Success	Fledglings per nesting attempt	Fledglings per successful nest	Maximum fledglings	Source
Great Basin, Utah	80.0	1.40	1.75	2	Smith and Murphy 1973
Northeastern Colorado	54.6	1.19	2.18	4	Olendorff 1973
Kane County, Illinois	60.0	1.00	1.67	2	Keir 1976
Laramie Plains, Wyoming	60.0	1.24	2.06	-	Dunkle 1977
Sonoita, Arizona	54.5	1.18	2.17	3	Porton 1977
Southeastern Alberta	71.2	1.41	1.98	3	Schmutz et al. 1980
Southeastern Washington	72.3	1.41	1.85	4	Fitzner 1980
Zumwalt Prairie, Oregon	56.3	1.27	2.38	3	Cottrell 1981
Southeastern Washington	-	1.11	-	-	Bechard 1983
South-central North Dakota	64.0	1.55	2.42	4	Gilmer and Stewart 1984
Southeastern New Mexico	81.0	1.67	1.94	-	Bednarz 1988
Hanford Site, Washington	81.3	1.62	2.00	4	Poole et al. 1988
Northwestern North Dakota	60.7	1.14	1.88	3	Murphy 1993
Southeastern Idaho	80.2	1.31	1.62	-	Hansen and Flake 1995
Yolo County, California	82.1	1.35	1.64	-	England et al. 1995
San Joaquin County, California	80.0	1.38	1.73	-	England et al. 1995
Davis, California	70.9	1.16	1.64	-	England et al. 1995
Stockton, California	64.7	1.06	1.64	-	England et al. 1995
Butte Valley, California	65.5	1.53	2.50	-	Woodbridge et al. 1995*a*
Kindersley, Saskatchewan	78.1	1.49	1.91	4	Houston and Schmutz 1995*b*
Western and southeastern Minnesota	76.0	1.12	1.47	-	Martell et al. 1998
Mapimí desert, Durango, Mexico	82.9	1.57	1.90	-	Rodríguez-Estrella 2000
Hanna, Alberta	86.8	1.01	1.91	-	Schmutz et al. 2001
West-central Saskatchewan	76.3	1.44	1.88	5	Houston and Zazelenchuk 2004

Table 2.1. Continued.

Location	% Nest Success	Fledglings per nesting attempt	Fledglings per successful nest	Maximum fledglings	Source
Butte Valley, California	60.9	1.23	2.01	4	Briggs 2007
Southwest Idaho	80.2	1.80	2.30	-	Alsup 2012
Southeastern Arizona	63.8	1.04	1.63	-	Nishida et al. 2013
Cimarron County, Oklahoma	75.0	-	-	-	Wiggins et al. 2014
North Dakota and South Dakota	48.6	0.80	1.62	-	Inselman et al. 2015
Gilliam/Morrow Counties, Oregon	65.7	-	-	-	Kolar and Bechard 2016
Overall average or maximum	70.1	1.30	1.91	5	
Northern Texas	57.1	0.97	1.70	4	This study

Table 2.2. Environmental variables used to model daily survival rate in Program MARK. Classification of the study area region being in a drought year and annual precipitation were obtained from the National Weather Service, and Standardized Precipitation Evapotranspiration Index (SPEI) provides a measure of drought severity by month for landscapes across the globe. Winter refers to SPEI averaged across Nov to Mar prior to the breeding season that year, and breeding season refers to average SPEI across Apr to July each year.

Year	Drought Year	Annual Precipitation (cm)	Annual SPEI	Winter SPEI	Breeding Season SPEI
2014	Yes	49	-0.16104	-0.18077	0.03105
2015	No	88	0.42279	0.30727	0.78062
2016	Yes	44	-0.42853	-0.51430	0.03045
2017	No	67	-0.14066	-0.52704	0.10372
2018	Yes	35	-0.37392	-1.23595	-0.86090

Source: National Weather Service, <https://www.weather.gov>, Global SPEI database <https://spei.csic.es>.

Table 2.3. Summary of breeding activity for Swainson's hawks nesting east of Amarillo, Texas, across Lubbock County, Texas, and along the I-27 highway corridor. Number of nests we confirmed to exist varied with survey effort due to logistical constraints (i.e., more nests may have existed in the study area at any given time), and thus impacted the number of nests we monitored each year. Daily survival rate represents probability of a nest surviving each day of monitoring (DSR) or probability of a nest surviving the entire nesting period (about 75 days long; DSR^{75}); we reported standard error (SE) to show variability in DSR estimates.

Type of Information	2014	2015	2016	2017	2018
Number nests known to exist	39	52	81	219	38
Number nests monitored	39	52	81	104	36
Number occupied	24	37	53	79	17
Number successful	18	27	35	35	5
Number failed	6	7	14	27	12
Number with unknown fate	0	3	0	17	0
% Occupied	61.5	71.2	65.4	76.0	47.2
% Success (out of occupied)	75.0	73.0	66.0	44.3	29.4
Total fledglings observed	25	42	71	56	10
Max fledglings per nest	3	3	4	3	3
Fledglings per occupied nests	1.0	1.1	1.3	0.7	0.6
Fledglings per successful nests	1.4	1.6	2.0	1.6	2.0
DSR	0.997	0.996	0.993	0.991	0.980
SE	0.002	0.002	0.002	0.002	0.008
DSR^{75}	0.791	0.769	0.586	0.511	0.220
SE	0.045	0.038	0.025	0.018	0.014

Table 2.4. Regression models comparing annual daily survival rate (DSR) to various environmental variables, compared using Akaiki's information criterion (AICc); k represents the number of parameters in each model, ΔAICc represents the difference in each AIC from the top model, W represents the model's weight (the probability this model best represents the data). Classification of the study area region being in a drought year and annual precipitation were obtained from the National Weather Service, and Standardized Precipitation Evapotranspiration Index (SPEI) provides a measure of drought severity by month for landscapes across the globe. Winter refers to SPEI averaged across Nov to Mar prior to the breeding season that year, and breeding season refers to average SPEI across Apr to July each year.

Model Variable	k	AICc	ΔAICc	W
Winter SPEI	2	314.29	0.00	0.70
Breeding Season SPEI	2	316.99	2.70	0.18
Annual SPEI	2	320.60	6.31	0.03
Precipitation	2	321.80	7.51	0.02
Drought Year	2	323.96	9.67	0.01

Source: National Weather Service, <https://www.weather.gov>, Standardized Precipitation Evapotranspiration Index <https://spei.csic.es>.

Figures

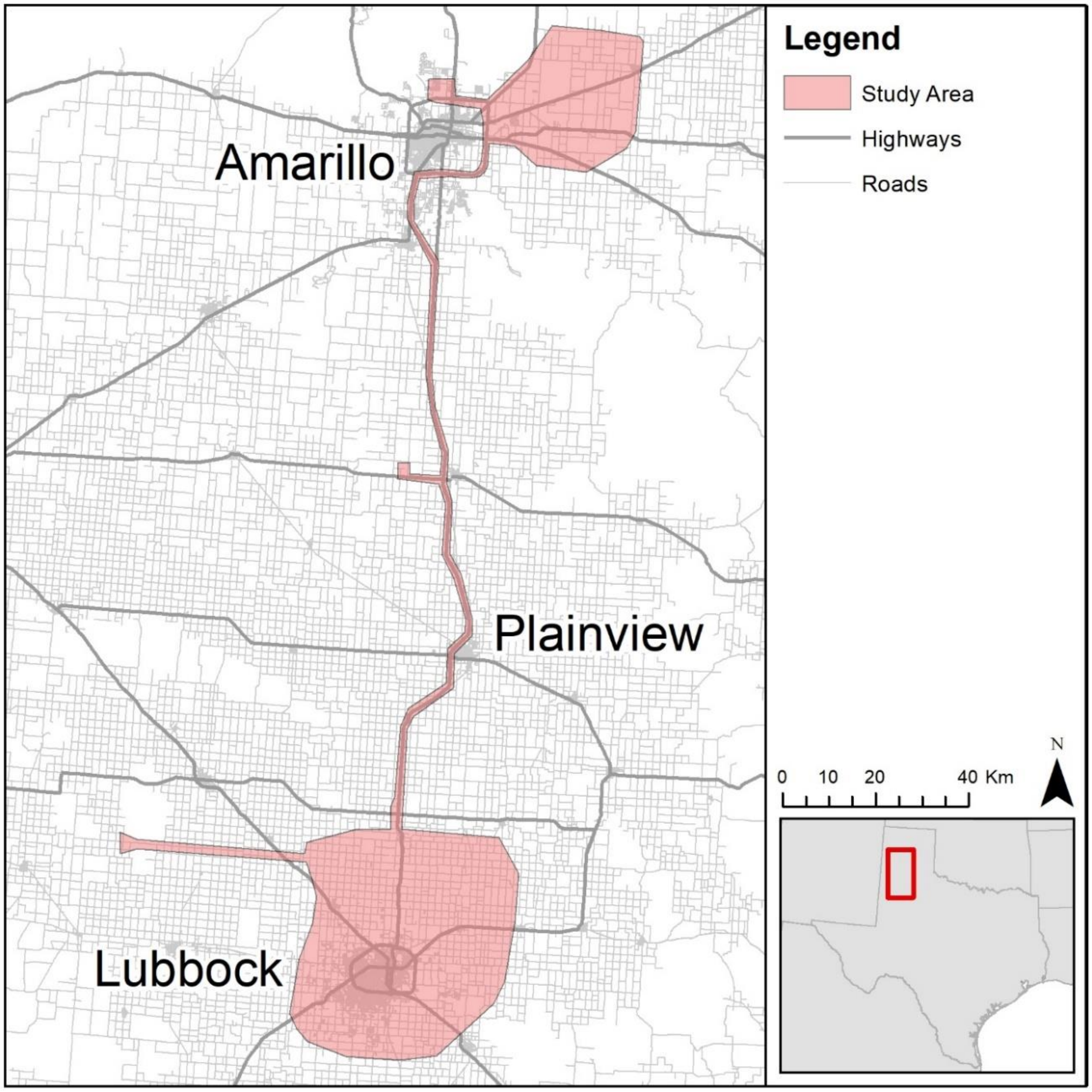

Figure 2.1. Total study area for monitoring Swainson's hawk nests from 2012 to 2018. Inset map shows location within Texas.
Source: Texas Natural Resources Information System, <https://tnris.org>.

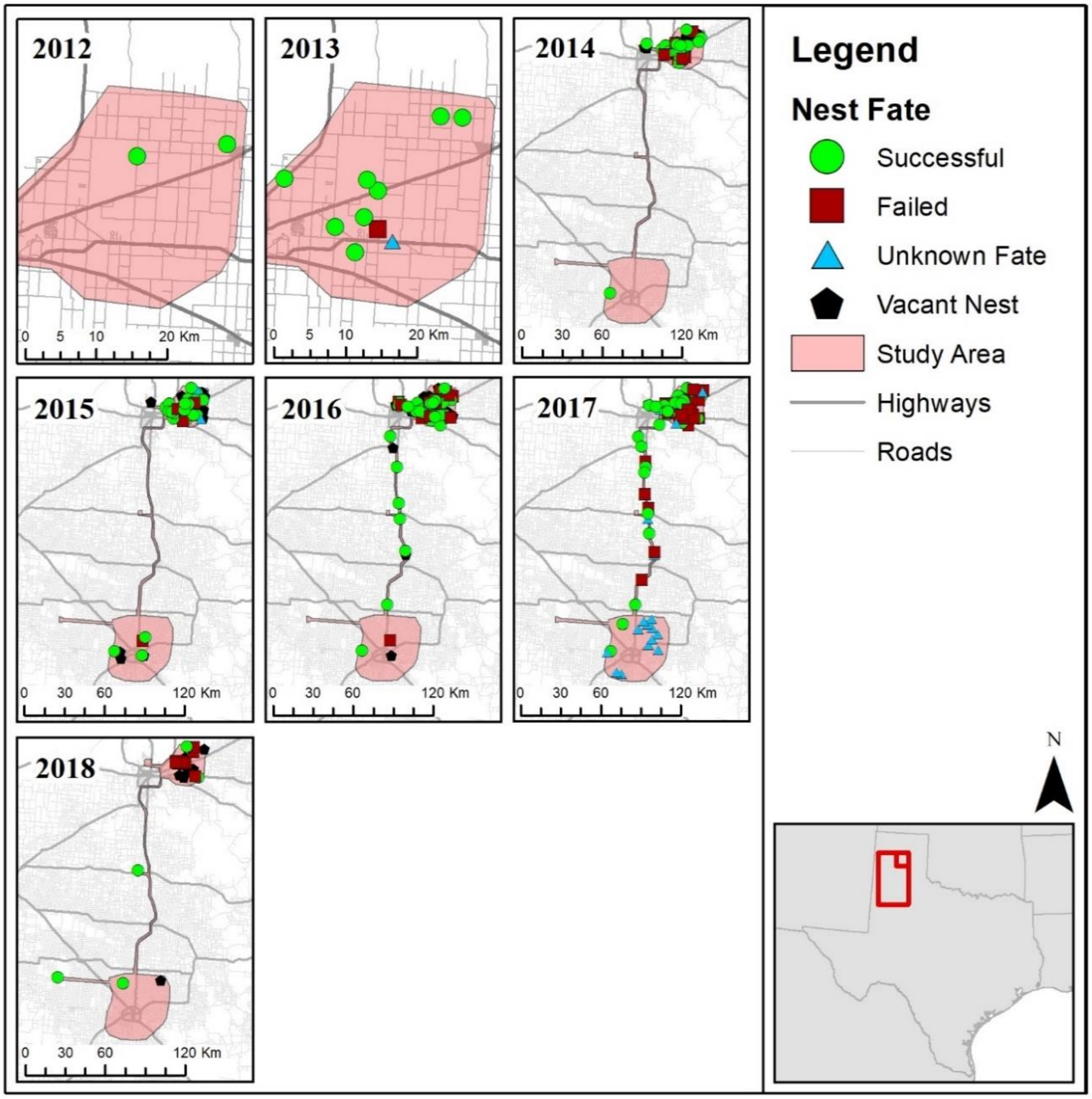

Figure 2.2. Swainson’s hawk nest locations and fate over seven years of nest monitoring. Monitoring effort varied over time, and some occupancy/fate information was obtained from adult Swainson’s hawks wearing satellite transmitters in a related study. Known, but unmonitored nests were not included. Inset map shows locations within Texas. *Source*: Texas Natural Resources Information System, <https://tnris.org>.

CHAPTER III

MIGRATION CHARACTERISTICS OF ADULT SWAINSON'S HAWKS

Abstract

Migration is an important period of many species natural history that is often poorly understood and understudied. Migration can be a risky endeavor, with species moving across unfavorable landscapes, but is necessary for many species that breed in climatically variable regions unsuitable for year-round occupancy. Swainson's hawks (*Buteo swainsoni*) migrate between breeding grounds across western North American grasslands and wintering grounds in similar grassland habitats in Argentina. We attached satellite transmitters to 24 adult Swainson's hawks to reveal migration characteristics and to compare migration from the southeastern edge of the breeding range to those hawks tracked by transmitters from other breeding areas. Swainson's hawks in our study followed the route described in previous research, with more variability than previous reports. Hawks made short over-water crossings but mostly avoided lakes and oceans. Hawks crossed mountains, but also avoided them where possible. Differences in migration timing mostly stemmed from breeding locations of hawks, with hawks traveling longer distances starting migration earlier and ending it later. Hawks traveled diurnally at 25 kmh^{-1} and covering 183 to 196 km/day (211 km/day when stops were excluded). Patterns of faster travel lined up with areas of extreme wind conditions and 10 to 20° N and S latitudes. We found some minor differences with breeding activities but no differences in sex. Migration strategies, such as soaring flight, mass migration flocks, and staging and stopover behaviors explain most patterns we uncovered in transmitter

data. Bottlenecks through Central America represent regions of conservation importance for this, and other, migratory species.

Swainson's hawks (*Buteo swainsoni*) are migratory raptors that breed in grasslands, shrublands, and croplands across western North America and spend their nonbreeding season in similar habitats in Argentina and Uruguay (Bechard et al. 2010). Long-distance migration complicates conservation efforts, as populations can be limited by factors at either ends of their global range, as well as along the entire migration pathway. For example, investigating the decline of breeding Swainson's hawks in California (Bloom 1980), Oregon (Littlefield et al. 1984), Nevada (Herron et al. 1985), and western Canada (Houston and Schmutz 1995*a*) led to the discovery of pesticide use causing mass mortality in Argentina (Woodbridge et al. 1995, 1996, Goldstein et al. 1999*a*, *b*). Migration itself is a risky behavior, with birds moving across unfamiliar and potentially dangerous landscapes for days to weeks at a time, using all available energy to the point of breaking down muscle to survive, and encountering hazards, such as predators, the ocean, power lines, and human persecution (Kerlinger 1989, Yosef 1996, Bildstein 2006). Conservation efforts require understanding the entire breadth of the ecological needs of a species, and migration remains an area that is poorly understood and under-examined. Here, we provide novel descriptions of Swainson's hawk migration and re-examine previously suggested patterns, to further our understanding of trans-continental migration ecology for this, and other, migratory species.

The first descriptions of Swainson's hawk migration patterns came from observations of passing flocks (e.g., Fox 1956, Thiollay 1980, Tilly 1992, Juhant 2010) and leg band recovery efforts (Houston 1990, Houston and Schmutz 1995*b*, Schmutz 1996). The onset of use of of satellite telemetry provided the opportunity to follow individuals across the Earth, which greatly expanded what we can learn about migration (Bittner 1988). From 1994 to 1997, researchers attached satellite transmitters to 46 adult Swainson’s hawks breeding in Arizona, California, Colorado, Idaho, Minnesota, Oregon, Utah, Alberta, and Saskatchewan (Fig. 3.1), which provided novel details such as timing, travel rates, and stopover locations (Woodbridge et al. 1995, Schmutz 1996, Fuller et al. 1998, Martell et al. 1998, Bechard et al. 2006, Kochert et al. 2011). Airola et al. (2019) used satellite transmitters to track 23 adult Swainson’s hawks from central California, providing the most recent descriptions of migration characteristics to date. In addition, migration research from more-heavily studied species, such as broad-winged hawks (*Buteo platypterus*; e.g., Haines et al. 2003), ospreys (*Pandion haliaetus*; e.g., Alerstam et al. 2006), and peregrine falcons (*Falco peregrinus*; e.g., Fuller et al. 1998), allows us to put location data into a behavioral context, so we may obtain a more-holistic understanding of Swainson’s hawk migration ecology.

To accomplish a migration across two continents (Bechard et al. 2010), Swainson’s hawks evolved behaviors and strategies that we are only beginning to explore and understand. Swainson’s hawks are an obligate-soaring species, primarily achieving lift during migration by circling in thermals (i.e., rising air currents created when patches of ground heat up faster than the surrounding landscape), then gliding until the next thermal is located (Smith 1985, Smith et al. 1986, Kerlinger 1989, Bildstein 2006, Bechard et al. 2010). Additional weather phenomena that may assist soaring migration include winds produced by storm fronts, deflection updrafts created by horizontal wind hitting vertical structures (i.e., orographic lift), ‘thermal streets’ which form when a line of thermals mix with a horizontal wind stream, and ‘cloud streets’ that form as thermal streets condense and provide a continuous linear pathway of constant lift (Pennycuick 1972, Smith 1985, Kerlinger 1989, Bildstein 2006, Bechard et al. 2010). Seeking out thermals, and other external sources of lift, allows large-bodied birds such as hawks, vultures, and eagles (Accipiteriformes), to soar long distances using minimal energy (Pennycuick 1972, Kerlinger 1989, Hedenström 1993, Bildstein 2006, Duriez et al. 2014). One effect of being an obligate-soaring species is route selection based (at least partly) on the availability of rising air currents, which may explain why many soaring species generally avoid crossing open water (where thermals are infrequent and landing means death), and instead detour across meandering land masses (Kerlinger 1989, Fuller et al. 1998, Bildstein 2006, Vansteelant et al. 2015). In addition, a migration strategy that relies on the availability of thermals typically results in diurnal migration activity (i.e., solar radiation is the primary mechanism for thermal formation), with birds resting at night and waiting for thermals to form again, thereby limiting the amount of time a bird can spend travelling each day and creating a start-and-stop pattern of migratory travel (Kerlinger 1989, Hedenström 1993, Bildstein 2006, Duriez et al. 2014). Descriptions from Panama support diurnal migration activity, with flights of many soaring species primarily occurring between 0745 and 1800 hours and hawks observed roosting in trees at night (Smith 1985). Diurnal migrants likely use the sun, and possibly magnetic fields, to orient, and experienced birds probably use visual landmarks to maintain consistent pathways (Kerlinger 1989, Bildstein 2006). Swainson’s hawks additionally migrate en masse (i.e., tens to thousands of birds in each flock) and with other soaring raptors, such as broad-winged hawks, Mississippi kites (*Ictinia mississippiensis*), and turkey vultures (*Cathartes aura*) that follow similar Central American pathways to their wintering grounds (Smith 1985, Parker 1999, Haines et al. 2003, Bechard et al. 2010, Dodge et al. 2014). The collective information within flocks likely allows for higher survival and migration success compared to solitary travel; advantages include easier location of thermals, keeping large numbers of birds on the same pathway, avoiding significant areas of wind drift, storms, and other poor conditions, and allowing inexperienced birds to find safe roosting areas and possibly food en route (Smith 1985, Kerlinger 1989, Bildstein 2006).

Fuller et al. (1998), Bechard et al. (2006), and Kochert et al. (2011) collectively demonstrated that Swainson's hawks breeding in different areas across their range funnel into a single, relatively narrow, migration route, with birds appearing to travel entirely over land, consistent with an obligate-soaring migration strategy. There is also evidence that Swainson's hawks may cross water, with hawks identified in Cuba and other islands in the Caribbean during migration and winter (Hayes 1999, Rodríguez-Santana 2010), but to date no hawk tracked with a transmitter from published literature has traveled such a route (Fuller et al. 1998, Bechard et al. 2006, Kochert et al. 2011, Airola et al. 2019), and therefore whether or not Swainson's hawks regularly travel over water remains a question. Swainson's hawks are known to cross other ecological barriers, such as the Andes Mountains in Colombia, but no one has described or speculated on the degree to which mountains act as ecological barriers or how much Swainson's hawks use these landscapes. For example, observations from Nicaragua suggest hawks cross this mountainous country without stopping (Bechard et al. 2010).

Reported evidence suggests Swainson's hawks from across the breeding range start fall (southward or outbound) migration from late August to early October and arrive on the wintering (nonbreeding) grounds from November to December (42 – 98 days of travel), and they start spring (northward or return) migration from mid-February to mid-March and arrive on the breeding grounds from April to early May (51 – 82 days of travel; Bechard et al. 2010, Kochert et al. 2011); possible exceptions exist with the population of Swainson's hawks breeding in the Central Valley of California, which migrate at different times, travel different routes, and over-winter in different locations (Hull et al. 2008, Bechard et al. 2010, Airola et al. 2019). Airola et al. (2019) provided evidence from the California population that breeding status may influence migratory timing; hawks that suffered failed nesting attempts left for fall migration earlier and those that returned to the breeding grounds earlier were more likely to breed successfully that summer. The straight-line distance traveled by hawks fitted with transmitters averaged 10,200 km from starting to ending locations (Fuller et al. 1998, Kochert et al. 2011). However, the cumulative distance birds actually traveled was 12,000 to 13,500 km, probably due to the circuitous overland route avoiding overwater crossings (Fuller et al. 1998, Kochert et al. 2011). Swainson's hawks have been observed flying an average of 188 km/day during fall migration and 150 km/day during spring migration (Fuller et al. 1998, Kochert et al. 2011), though hawks originating from California reportedly traveled slower during fall migration (72 km/day) and faster during spring migration (202 km/day; Airola et al. 2019). Fuller and colleagues (1998) broke the migration into three temporal segments and found that daily travel rate was fastest during the middle portion (upwards of 272 km/day; Kochert et al. 2011), which they attributed to greater and more-consistent solar radiation and thermal lift in the equatorial region.

Flight speed (km traveled/hour) was not elaborated on in the 1990's transmitter studies, presumably because transmitters reported data every 1 to 6 days and had an error of 250 to > 1,000 m associated with each location; researchers therefore selected one representative point per day, as available, for most analyses (Fuller et al. 1998, Kochert et al. 2011). Due to limited data, Kochert et al. (2011) reported speed as the distance between first and last points in a duty cycle (i.e., an 8-hour period of data collection) divided by elapsed time (M. Kochert, personal communication), which ranged from 9 to 86 kmh^{-1}. While this range is informative, it has limited use in interpretation; the lower limit excludes periods of rest, and the upper limit was truncated by data filtering (i.e., points indicating > 90 kmh^{-1} movements were considered errors and removed; Kochert et al. 2011). Flight speeds are influenced by wind, so it is important to consider environmental conditions when exploring ground-speed data (Safi et al. 2013); for example, Smith (1985) observed migrating Swainson's hawks, and other raptors, in Panama, and estimated soaring raptors typically fly at 25 to 40 kmh^{-1}, can fly 65 to 75 kmh^{-1} in a downward glide, and may be propelled > 80 kmh^{-1} in certain wind conditions.

Within a species or population, migration behaviors may differ by sex and age class. For example, female American kestrels (*Falco sparverius*) leave breeding and wintering ranges before males (Stotz and Goodrich 1989), male bald eagles (*Haliaeetus leucocephalus*) reach breeding territories before females (Harmata 1984), adult ospreys migrate before juveniles (Kjellén 1992), and juvenile Cooper's hawks (*Accipiter cooperii*) migrate before adults (Mueller et al. 2000). Differential timing may arise due to differential costs incurred during the breeding period, and thus one sex may need longer to accumulate fat reserves prior to beginning travel or may need more time to complete molt, or because of differential priorities, such as one sex being driven by territory competition at the destination (Bildstein 2006). Age differences may also be related to molting (e.g., molting adults taking longer to migrate), physiological condition (e.g., juveniles [or adults] may need more time to build fat stores), and inexperience (e.g., juveniles may wait to find adults to follow; Bildstein 2006). Kochert et al. (2011) and Airola et al. (2019) compared Swainson's hawk migration characteristics by sex and found either no difference in behaviors or differences were found insignificant in statistical testing. Campbell and Inzunza (2017) found that migrating Swainson's hawks passing through Veracruz, Mexico, showed no pattern of differential timing between juvenile and adult hawks, but their study was limited to a 3-day period of peak migration and photographing hawks that were flying within range of camera capture (i.e., their sample represented < 1% of Swainson's hawks counted that season). Due to the small sample sizes of observations so far, we additionally explored the questions of migration similarity or differences between the sexes in this study and between age classes in Chapter 5.

Additional adaptations that may play an important role in migration survival is staging and temporarily stopping while en route. Many species show a pattern of pre-migratory staging, where birds move from their breeding or wintering areas to specific, or variable, locations to build up fat stores on seasonally abundant food resources (Kerlinger 1989, Bildstein 2006, Warnock 2010). All migratory birds accumulate fat to some extent, but pre-migratory fattening is particularly important for long-distance migrants that cross ecological barriers (such as oceans or deserts) where resting and/or continued foraging are unlikely or impossible (Kerlinger 1989, Bildstein 2006, Warnock 2010). Swainson's hawks travel long distances, but entirely over land where nightly resting is possible, so it is unclear if they exclusively require fat stores, or if they are able to opportunistically forage en route (see Smith et al. 1986, Kirkley 1991, and Bechard et al. 2006 for discussion of this question). Woffinden (1986), McGrath (1988), Houston (1990), and Littlefield and Johnson (2013) described flocks of Swainson's hawks foraging on grasshoppers and other insects in agricultural fields prior to migrating southward, a behavior which both provides an opportunity to build fuel stores and the opportunity to aggregate into flocks prior to leaving the breeding range (Kerlinger 1989, Bildstein 2006). It is unknown if staging occurs prior to spring migration; descriptions indicate Swainson's hawks are likely gregarious, nomadic, and able to find abundant insect prey during the entire austral summer period (Jaramillo 1993, Canavelli 2000, Goldstein et al. 2000). In addition to possible staging behaviors, Kochert et al. (2011) described 3 to 9 day stops throughout the entire migration route (especially common during southward travel); these stops did not appear to concentrate on specific locations and were made by many birds, indicating that stopping en route may be opportunistic, rather than obligatory. Explanations for en-route stopovers may include requiring rest, the opportunity to forage on locally abundant prey, and getting delayed by unfavorable weather conditions (Smith 1985, Kerlinger 1989, Bildstein 2006).

We used satellite telemetry to examine migration characteristics of adult Swainson's hawks occupying the High Plains of Texas (Fig. 3.1). Our study area was in the southeastern extent of the species breeding range and was distributionally disparate from previously studied individuals (i.e., around 450 km from the nearest previous capture location; Kochert et al. 2011). We explored migration pathways for evidence of overwater crossings, mountain-range crossings, and other geographic patterns. We identified timing of migration, estimated distance traveled, and examined hourly location data to discern roosting periods and speed of travel. We additionally inspected data for evidence of stopping behaviors and differences by season, sex, and breeding status prior to or after migration. Our ultimate goals were to better understand Swainson's hawk migratory behavior by adding a layer of novel details to existing information, as well as explore aspects of migration where this population may differ from birds breeding farther west and north.

Methods

We trapped adult Swainson's hawks in Potter, Carson, and Armstrong counties, Texas (Fig. 3.1), using either a bal-chatri trap with a gerbil (*Meriones unguiculatus*), mouse (*Mus musculus*), or house sparrow (*Passer domesticus*) or a dho-gaza trap with a live great horned owl (*Bubo virginianus*) lure set near an occupied nest (Bloom et al. 2007). We determined sex of bird by mass at capture and behavior in breeding territories (i.e., female Swainson's hawks are larger and perform most incubating, brooding, and nest-attendance duties; Bechard et al. 2010). Each captured hawk weighing > 550 g was equipped with a solar-powered Global Positioning System (GPS) platform transmitter terminal (hereafter PTT; Solar PTT-100, Microwave Telemetry, Inc., Columbia, Maryland) on a backpack-style harness secured with Teflon® ribbon, as well as an aluminum leg band issued by the United States Geological Survey (USGS) Bird Banding

Laboratory (Meyburg and Fuller 2007); the weight restriction ensured transmitters added no more than 4% of a hawk's bodyweight (the transmitter weighed 22 g). PTTs were programmed to report daily GPS locations at 0000, 0500, 0700, 0900, 1100, 1200, 1300, 1500, 1700, 1800, 1900, and 2100, local time, until transmissions ended due to battery failure, malfunction, or hawk mortality.

We used three methods to filter data prior to analysis: automatic error removal, visual evaluation of implausible points, and post-mortality removal. We removed all data that contained an error message, a 2-D fix, or no location information. To identify implausible locations, we calculated orthodromes (i.e., great-circle distance, or distance that considers the curvature of the earth) between consecutive pairs of points, labeling each point with the distance traveled to the next location. We first examined all points with distance > 100 km, then all points with velocity (distance to next point / elapsed time) > 80 kmh^{-1}. Every selected point was visually evaluated in context of previous and subsequent location data to identify obvious breach of patterns, such as a single point far from a tight clustering of points or a single point at a right angle to a linear migration pattern. We were conservative in only removing points that were clear deviations; for example, it is unlikely for a migrating hawk to move 500 km perpendicular to their migration pathway and then to return to the exact same pathway one hour later. Finally, we removed redundant post-mortality points (or points from a dropped transmitter) when detected, retaining one point as the presumed last location. We analyzed all retained points as if they contained true location information (± 18 m error; Microwave Telemetry, Inc., Columbia, Maryland). We then visualized and analyzed data using ArcMap 10.7, Excel, and Program R 3.6.2 (packages 'stats', 'car', 'ggplot2', and ‘ggpubr’; R Core Team 2019, Fox et al. 2020, Kassambara 2020, Wickham et al. 2020), and the bulk of analyses were chosen to make direct comparisons to results from previous transmitter research, primarily summarized by Fuller et al. (1998), Kochert et al. (2011), and Airola et al. (2019).

We classified the beginning and ending of migration by modifying the methods laid out by Kochert et al. (2011) to help classify situations where birds made late migratory stopovers in Argentina but also continued overall southward progress. Fall migration started at the first point > 150 km away from and south of (bearing = 91° – 269°) the hawk’s capture location that began a pattern of points moving southward that showed no return to the buffer. Fall migration ended when the bird reached Argentina and stopped making progress in a southward direction for ≥ 10 days. Spring migration started at the first point in a series of consistently northward movements (preceded by ≥ 10 days of omnidirectional movement with no northward trend) and ended when the bird came within 150 km of its capture location. In the case of one hawk (A5; Table 3.1) that shifted from its 2012 trap location in the Amarillo area (it was unknown if the hawk nested in Amarillo or not, because it was trapped in July when most nests fledge young) to a nesting location 200 km south in 2013, we subsequently used a 150 km buffer around the nest location to identify migration start and end dates.

We visually examined vectors (lines connecting points) to understand pathways and variability across and within birds and for evidence of over-water and mountain crossings (using a shaded relief map created by Natural Earth, https://www.naturalearthdata.com). We used Julian migration start and end dates to calculate travel duration (number of days). We examined three different measures of speed: 1) PTTs reported an estimation of ground speed (kmh^{-1}) at the moment of connecting with satellites, which we used both as a representation of behaviors (i.e., 0 kmh^{-1} = stationary and ≥ 1 kmh^{-1} = movement) and as estimations of instantaneous flight speed (henceforth referred to as 'PTT speed'; we only examined data ≥ 1 kmh^{-1} unless otherwise stated), 2) we divided between-point orthodromes by elapsed time to estimate the minimum speed (kmh^{-1}) a bird would have to move to get from one point to the next (henceforth referred to as 'between-point velocity'; we, again, only examined data ≥ 1 kmh^{-1}), and 3) we estimated daily travel rate (km per day) by selecting one roosting location per day (i.e., we selected points at hour 0000 when possible; 2100, 0500, 0700, 1900 or 1800, in that order, when 0000 was not available; any point ≥ 12 hours difference from previous and subsequent points was selected when no nighttime points were available), then calculating additional pairwise orthodromes (including data < 1 km/day, because we wanted to additionally examine days of no significant movement). We examined hourly behavior (moving or not) and speed for indication of diurnal travel during migration, and classified points as "roosting" hours when > 75% of data indicated inactivity. We summed distances between daily roost points to determine minimum cumulative distance traveled (km) and we estimated straight-line distance (km) with an orthodrome between starting and ending locations. We used the duration of travel to separate each migration into three segments (number of days / 3) to examine estimates of speed per temporal segment, similar to methods of Fuller et al. (1998), and we divided the data into 10-degree latitudinal chunks to examine speed per geographic segment, similar to methods of Kochert et al. (2011).

We visually examined migration data (all points, daily roost points, and lines connecting roost locations) for possible evidence of ‘stops’ (i.e., a lack of forward migration progress, though birds may have wandered in omnidirectional patterns during such events). We identified stops as when a bird spent two or more roosting periods at the same relative location (< 1 km between roost locations) or when a bird moved in a direction contrary to the pattern of migration for > 24 hours and including two or more roosting periods. Stops started at the first point going in the opposite direction of migration or the first point in a series of non-moving points, and stops ended when the bird resumed consistent movement in the direction of migration. When birds made short duration (< 24 hours) movements in the direction of migration followed by more stopping behaviors, we grouped those points as part of the same stop; we recorded multiple stop events when movements in the direction of migration > 24 hours separated them. We added a 1,000-km buffer to trapping locations and evaluated stops within this buffer for evidence of pre-migratory staging at the start of fall migration. Rather than short-duration stops at a single location, evidence of staging included longer-duration stops with omnidirectional movements, suggestive of hawks that were spending time aggregating and foraging to accumulate fat reserves (Bechard et al. 2010, Kochert et al. 2011, Littlefield and Johnson 2013). We were not sure if pre-migratory staging behaviors occur during spring migration (Kochert et al. [2011] suggested only one stop near starting locations in spring), so we additionally examined data for any evidence of staging (i.e., similar behaviors as expected for fall staging periods) by placing a 1,000-km buffer around the northernmost winter location (northeastern Chaco province, Argentina) and analyzing patterns of early spring stops within or south of the buffer. We estimated duration, centroid, and area (km^2; using minimum convex polygons [MCP]) to describe and compare stop locations. In addition to speed, we examined number of stops and cumulative stop duration by temporal and geographic migration segments to further discern patterns.

We included all available data in our analyses, only censoring data when necessary information was missing; when a migration dataset was missing a start and/or end date (i.e., gaps in data made start or end unclear or [presumed] mortality occurred during migration), we excluded that data from relevant date descriptions, duration calculations, cumulative and direct distance calculations, and estimations of temporal segment patterns. We additionally left out one migration with a 5,000-km data gap from cumulative distance estimation, because the result implied the bird flew a shorter distance than the distance between starting and ending locations. After collecting and summarizing data, we ran exploratory analyses of variance models (ANOVA, alpha = 0.05) to detect seasonal patterns, patterns involving sex of bird, and patterns in speed by segments, and we used Hedge's *g* to determine effect size with groups of varying sample sizes (package "effsize" in program R, code 'cohen.d' modified with 'hedges.correction'; Hedges 1981, Torchiano 2020) when models indicated differences among groups (for simplicity, we compared largest and smallest means when model variable included > 2 groups). We used Pearson's Correlation Coefficient (r) to examine correlations among variables and identify patterns for further exploration when $r \geq 0.7$ or ≤ -0.7. We used results from a related nest-monitoring study (Chapter 2) combined with collected transmitter data to determine nesting status before fall migration and after spring migration to see if there were any patterns in timing of migration or stopping behaviors, similar to Airola et al. (2019), again using exploratory ANOVAs. Standard deviations (SD) were provided with means to describe variability, and sample size (n) was reported as number of migrations (when $n < 100$) or number of points ($n > 100$) included in analyses.

Results

We tagged 24 hawks with PTTs and collected data from 2012 to 2017, with an average of 698 ± 474 days of data per hawk (Table 3.1). Two hawks (A5 and A16) survived beyond our logistic ability to collect data (at least 4-5 years) and two additional hawks (A9 and A14) survived at least three months beyond the life of their transmitters (Chapter 2). We found two carcasses on breeding territories (hawk A15 was shot and hawk A21 collided with a wind turbine blade), and we assumed mortality for six additional hawks that each had repeated points in final locations (which may also indicate attachment failure). Eight transmitters showed a pattern of degrading data quality as transmissions ended (including the two birds later confirmed to be alive). Additionally, we had five situations where data transmissions suddenly ended for no apparent reason, and thus we assumed mortality, though transmitter failure could not be ruled out (Table 3.1, Fig. 3.2). Assuming mortalities were the cause of unknown data cessation, ten hawks (42%) died during the breeding season, three hawks (13%) died during the nonbreeding season, and seven hawks (29%) died during or just after ending migration; four (17%) migrating northward and three (13%) migrating southward (Table 3.1, Fig. 3.2).

We filtered out 9.3% of data received from transmitters, of which 93% were points with error messages or that contained no location data, 6% were assumed post-mortality points, and 1% were points we manually identified as implausible locations and removed as likely errors. Our final dataset consisted of 152,227 points, of which 46,467 points were classified as migration data. We logged 93 migrations for 23 birds (Table 3.1, Fig. 3.3); eight migrations (9%) had insufficient data for some analyses. We selected 4,587 points to represent nightly roosting locations; due to limited data reporting or filtering, 2% of points were outside of the preferred nighttime hours, and therefore may not have been representative of actual roosting locations.

The route hawks traveled

Swainson's hawks in this study transited 15 countries during migration: the United States, Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Brazil, Bolivia, Paraguay, and Argentina (Fig. 3.3). Routes in both directions were concentrated from 20 to 25˚ N in Mexico through Central America. The smallest distance across all points measured 54 km in the Oaxaca region of Mexico, 67 km along the pacific coastline of El Salvador, Honduras, and Nicaragua, and 37 km along the Isthmus of Panama (Fig. 3.3 and 3.4). Hawks traveled almost entirely over land, occasionally appearing to cross open water for distances ≤ 25 km and rarely up to 75 km (Fig. 3.5). Hawks switched coastlines multiple times when crossing Central America, and all birds avoided the open waters of Managua Lake and Lake Nicaragua, two large lakes in Nicaragua (Fig. 3.4). Hawks also appeared to avoid mountain ranges; they flew adjacent to, but rarely within mountain ranges at the beginning and end of migration trips but had no alternative to traversing mountainous landscapes through Central America (Fig. 3.6). In the Oaxaca region of Mexico, hawks crossed the Sierra

Madre Mountains through a low-elevation passageway to then follow the Pacific coastline until Nicaragua (Fig. 3.6). Over-mountain flight appeared necessary through El Salvador, Honduras, and eastern Nicaragua, because there was no other path without crossing water (Fig. 3.6). Two routes appeared to be common through Panama; along the Atlantic coastline, which avoided mountains, and along the Pacific coastline, which caused hawks to cross mountains in western Panama and Costa Rica to get back on route. The Pacific-coastline route was undertaken 28 times by 70% of hawks; 93% of times this route was used occurred during spring migration (Fig. 3.4 and 3.6). Sixty percent of all spring migrations followed this route, and it was used in every year of data collection, though most frequently in 2014 (39%). Another region of unique routes across mountain ranges was through southern Mexico, Guatemala, and Honduras, which were traveled 11 times (55% spring migration, 45% fall migration) by eight birds (Fig. 3.4 and 3.6). Last, all hawks crossed the Andes in Colombia in both directions, with hawks often detouring through valleys where available (Fig. 3.6).

While the overall pattern of migration was similar, there was considerable variability in routes traveled across and within seasons, years, and individuals. There was greater variability in spring migration routes; 68% of spring migration routes might be considered unique due to some birds traveling different routes through Bolivia or Colombia, taking the Pacific route in Panama, or flying a straight line from Nicaragua to southern Mexico (Fig. 3.3 and 3.4). In contrast, route variations made up only 10% of fall migrations.

Migration timing

Swainson's hawks in this study started fall migration from 28 Aug to 13 Oct (mean = 2 Oct ± 9 days, n = 46) and arrived on the wintering grounds from 8 Nov to 23 Dec (mean = 27 Nov ± 10 days, n = 49; Fig. 3.7). Birds departed for spring migration from 7 Feb to 15 Mar (mean = 23 Feb ± 10 days, n = 42) and arrived on the breeding grounds from 21 Mar to 7 May (mean = 13 Apr ± 12 days, n = 40; Fig. 3.7). Spring migration start and end dates were correlated (r = 0.81), while fall dates were not (r = -0.04; Table 3.2, Fig. 3.8).

Fall migration lasted 36 to 104 days (mean = 56 ± 14 days, n = 46) and spring migration lasted 40 to 73 days (mean = 48 ± 7 days, n = 40); fall migration was an average of 8 days longer than spring (Table 3.3, Fig. 3.9). Fall migration end date correlated with duration of travel (r = 0.78; Table 3.2, Fig. 3.10). In addition, migration duration (of both seasons) was correlated with daily travel rate (r = -0.90), between-point velocity (r = -0.80), number of stops birds made during migration (r = 0.75), and cumulative number of days birds spent at stop locations (r = 0.90; Table 3.4, Fig. 3.10).

Distance and rate of travel

Hawks traveled cumulative distances of 8,637 to 11,453 km (mean = 9,920 ± 589 km, n = 46) during fall migration and 8,312 to 10,643 km (mean = 9,338 ± 482 km, n = 39) during spring migration (Table 3.3, Fig. 3.9). Distance between starting and ending locations ranged from 7,891 to 9,149 km (mean = 8,646 ± 251 km, n = 85) but did not differ by season (Table 3.3). Cumulative distances flown ranged from 400 to 2,846 km longer (fall mean = 1,442 ± 461 km, spring mean = 997 ± 338 km) than direct-line distance (Fig. 3.11); in other words, the migration route was 5 to 32% (mean = 14 ± 5%) longer than a straight-line path.

Swainson's hawks in this study traveled 0 to 871 km/day (overall mean = 189 ± 134 km/day, n = 4,587); 99% of data were < 590 km/day and 95% of data were < 430 km/day. Daily travel rate data indicated birds, on average, traveled 13 km farther per day during spring migration (effect size [0.10] indicated a negligible difference), but mean travel rate per migration did not differ by season (Table 3.3, Fig. 3.12). In addition to duration, mean daily travel rate correlated with mean between-point velocity (r = 0.86), number of stops (r = -0.70), and cumulative stop duration (r = -0.76; Table 3.4, Fig. 3.13). Vectors where distance traveled per day exceeded 500 km (113 vectors or 3%) were clustered at the Texas-Mexico border, in southern Mexico and Central America (during spring migration only), and from Bolivia to central Argentina (Fig. 3.14). When days classified as stops were removed from analysis, both fall and spring migration travel rates increased to 211 km traveled/day (fall mean = 211 ± 130 km/day, spring mean = 211 ± 123 km/day).

Speed reported by PTTs at the moment of data transmission indicated movements from 1 to 127 kmh^{-1} (mean = 23 ± 12 kmh^{-1}, n = 21,816). PTTs indicated no movement (0 kmh^{-1}) 53% of the time. PTT speed data differed by season, but the difference was not biologically significant (difference = 1 kmh^{-1}, effect size = 0.07 and 0.31; Table 3.3, Fig. 3.12). While maximum speed implies travel up to and possibly beyond the transmitter's capacity to estimate speed (maximum recordable = 127 kmh^{-1}, Microwave Telemetry, Inc., Columbia, Maryland), 99% of data were ≤ 52 kmh^{-1} and 95% of data were ≤ 42 kmh^{-1}. Examining PTT speeds (including speed = 0) reported by hour indicated a strong pattern of diurnal migration activity, with > 45% of data suggesting movement between 0900 to 1700, and > 80% of data suggesting stationary hawks from 1800 to 0700; velocity and daily travel rate data agreed with this pattern, we therefore only presented PTT speed results here (Fig. 3.15). Seventeen reported PTT speeds (0.04%) were ≥ 90 kmh^{-1}, and five transmitters reported the maximum possible transmitter speed of 127 kmh^{-1} (Microwave Telemetry, Inc., Columbia, Maryland) six times (Fig. 3.16). High PTT speeds (> 50 kmh^{-1}) were distributed across the migration pathway, with clustering in the same areas where daily travel rates > 500 km/day occurred (Fig. 3.14 and 3.17).

Between-point velocity indicated movements between 1 to 123 kmh^{-1} (mean = 24 ± 18 kmh^{-1}, n = 25,561) and did not differ by season; 99% of data were ≤ 75 kmh^{-1} and 95% were ≤ 55 kmh^{-1}. Data indicated little to no movement (< 1 kmh^{-1}) 45% of the time. We recorded 56 velocities (0.12%) that were ≥ 90 kmh^{-1} (Fig. 3.16). Vectors with high velocities (> 50 kmh^{-1}) were distributed across the migration pathway, with clustering in similar areas as daily travel rates > 500 km/day, especially with the highest velocities (> 90 kmh^{-1}) clustering at the Bolivia-Argentina border (Fig. 3.14 and 3.18).

Neither data from raw PTT speed and between-point velocities nor the migration means of these data correlated (r = 0.46 and 0.43), and extreme values were often linked with low values of the opposite measure (i.e., high speed at low velocity and vice versa). Especially concerning were 7 points where PTT speed > 50 kmh^{-1}, but velocity indicated the bird did not substantially move locations over time (< 5 kmh^{-1}; Fig. 3.16).

To further understand the relationship between daily travel rate and speed (i.e., did daily travel increase because of faster speed?), we compared average and maximum flight speed each day to that day's daily travel rate for six migrations that included extreme daily travel 3 times (all others had ≤ 2 daily vectors > 500 km); we looked at 310 days across 5 birds and both seasons. Daily travel rate correlated with mean daily velocity (r = 0.93) and maximum daily velocity (r = 0.87), but not mean or maximum PTT speed (r = 0.58 and 0.64; Fig. 3.19).

Migration travel stops

We recorded 172 ‘stop’ events (i.e., periods when hawks were not making forward migration progress, but may or may not have been stationary): 99 during fall migration and 73 during spring migration (Fig. 3.20). All birds made stops during at least one migration and eleven birds (48%) stopped during every migration. We also recorded 15 migration tracks (16% of migration tracks, 8 in fall, 7 in spring) with no stop events among 12 birds (52%). Hawks averaged 2 ± 2 stops (0 – 8 stops) per migration. Overall, stops were made across the entire migration route; 68% had centroids within borders of the United States or Argentina and no stops were found within the migration stretch from Guatemala to Nicaragua (Fig. 3.20). Eight birds made eleven stops during spring migration (15% of spring stops) within 150 km of Mar Chiquita Lake, Argentina (mostly northeast of the lake area); otherwise, it was uncommon for more than a few tracked birds to have overlapping stop locations (Fig. 3.20 and 3.21).

Stop duration ranged from 1 to 31 days (mean = 4 ± 4 days). In addition to migration duration and mean daily travel rate, number of stops was correlated with cumulative stop duration (r = 0.77; Table 3.4, Fig. 3.10 and 3.13). Cumulative stop duration was 0 to 43 days per migration and was longer during fall migration (fall mean = 8 ± 10 days, spring mean = 4 ± 4 days; Fig. 3.9). Birds made short-duration (< 3 days) stops 67% of the time, moderate-duration stops (3 – 9 days) 28% of the time, and long-duration stops (> 9 days) 4% of the time (Fig. 3.20). MCP area of stops ranged from < 1 to 39,074 km^2 (mean = 2,203 ± 5,771 km^2; Fig. 3.21), with the majority of 'stop' events consisting of omnidirectional movements (thus resulting in large MCP), rather than stationary periods. Short-duration stops ranged from 0 to 4,800 km^2 (mean = 424 ± 977 km^2), moderate-duration stops ranged from 6 to 39,074 km^2 (mean = 4,841 ± 8,471 km^2), and long-duration stops ranged from 607 to 31,958 km^2 (mean = 11,886 ± 9,983 km^2; Fig. 3.21).

Stops during early fall migration made within 1,000 km of trap locations (i.e., possible staging locations) were 1 to 31 days (mean = 7 ± 6 days, n = 30; Fig. 3.20) long with a MCP area of 2 to 31,958 km^2 (mean = 3,567 ± 6,787 km^2; Fig. 3.21). Stops during the remainder of fall migration were 1 to 9 days (mean = 3 ± 2 days, n = 69; Fig. 3.20) long with MCP area of 0 to 28,709 km^2 (mean = 1,775 ± 4,276 km^2; Fig. 3.21). Stops during early spring migration made no further than 1,000 km north of the northernmost wintering location were 1 to 5 days (mean = 2 ± 1 days, n = 32; Fig. 3.20) long with MCP area of 0 to 12,838 km^2 (mean = 1,267 ± 2,805 km^2; Fig. 3.21). Stops during the remainder of spring migration were 1 to 9 days (mean = 3 ± 2 days, n = 41; Fig. 3.20) long with MCP area of 0 to 39,074 km^2 (mean = 2,615 ± 8116 km^2; Fig. 3.21). All stops > 9 days long (n = 7) were located within Texas and Oklahoma during fall migration, and 90% of stops within the migration stretch from Mexico to Bolivia were < 3 days long (n = 51; Fig. 3.20 and 3.21).

Dividing data by temporal and geographic segments

When we divided each migration into three temporal segments based on travel duration, the last leg of travel was most often the fastest segment in all measures of speed, with the strongest trend in daily travel rate during spring migration (Fig. 3.22). However, excessive variation among raw data and migration summaries prevented interpretation beyond general trends (Fig. 3.22). When we divided the migration data by geographic segment (10° latitudinal bins), stronger patterns were revealed (although error bars still overlapped substantially); all measures of speed showed identical trends, so for simplicity we presented only daily travel rate results as the clearest pattern (Fig. 3.23). Fall migration started out relatively slow, increased to around 200 km/day from Mexico to Brazil, increased to 280 km/day as hawks passed through Bolivia, and slowed down as hawks settled into wintering areas in Argentina (Fig. 3.23). Spring migration showed a similar pattern, with hawks travelling between 150 and 200 km/day through South America, then travel rate increased to 330 km/day through Central America and southern Mexico, then slowed down as hawks settled into breeding areas (Fig 3.23). Spikes in raw travel rate data during fall migration occurred around 30°N (Texas) and from 15 to 30°S (Bolivia and Argentina), spikes during spring migration occurred from 10 to 30°N (Central America to Texas) and 15 to 40°S (Bolivia and Argentina), and there was a distinct lull in all data from 10°N to 10°S (where hawks pass over the Andes Mountains and the Amazon rainforest; Fig. 3.23). These geographic patterns in travel rate matched up well with locations of high speeds and exceptional distances traveled, principally the overlap of high values from Texas to Mexico, Bolivia to Argentina, and through Central America and Mexico during spring migration (Fig. 3.14, 3.17, 3.18, and 3.23). Because taking out stopped days altered mean daily travel rates so significantly, we additionally compared datasets (all data and no stops) by latitude segment; we found negligible differences that generally followed the pattern of the original data (Fig. 3.24). The largest difference occurred at > 30°N during fall migration, where data excluding stops was more similar to the following two thirds of migration and to spring migration trends (Fig. 3.24).

Examining stop data by three temporal segments had a similar problem of overlapping error bars as examining different types of speed data, but general trends indicated that birds spent the most time stopped at the beginning and end of travel (Fig. 3.22). Examining data by latitude segments showed a clearer pattern that agreed with rate descriptions above (Fig. 3.25). During fall migration, birds stopped for the longest duration at the beginning of travel and stopped the most frequently towards the end of travel (Fig. 3.22 and 3.25). During spring migration, birds stopped most often at the beginning of travel and for the longest duration towards the end of travel (Fig. 3.22 and 3.25). All migrations showed a lack of stopping behaviors from 10 - 20°N (Fig. 3.25).

Migration compared by sex of bird and breeding status

In general, male and female Swainson’s hawks behaved the same way across all migration measures, including routes and stopping behaviors (Table 3.3). The only signal detected in exploratory models indicated that females may fly faster than males, but the effect sizes (difference = 1 kmh^{-1}, effect size = 0.07 and 0.05) were negligible (Table 3.3, Fig. 3.26).

Hawks that bred successfully the previous summer took longer to migrate southward (mean = 58 ± 13 days, n = 26), than hawks with unsuccessful attempts (mean = 45 ± 4 days, n = 4) or hawks that did not breed (mean = 44 ± 8 days, n = 4; Table 3.3, Fig. 3.27); successful breeders also accounted for 100% of fall migrations > 53 days long (n = 18). Hawks that bred successfully also traveled southward at a slower pace (grand mean = 185 ± 34 km/day, n = 28) than unsuccessful (grand mean = 222 ± 9 km/day, n = 4) and nonbreeding hawks (grand mean = 221 ± 26 km/day, n = 4; Table 3.3, Fig. 3.27). Mean fall start dates were very similar across groups, and while considered statistically insignificant by the model, successful hawks ended fall migration an average of 10 days later than unsuccessful and nonbreeding hawks (Table 3.3). Successful breeders stopped more (mean = 2 ± 2 stops, n = 28) than unsuccessful (mean = 1 ± 1 stops, n = 4) and nonbreeding hawks (mean = 0 ± 1 stops, n = 4) during fall migration; successful breeders also tended to stop for longer durations (mean = 9 ± 10 days, n = 28) than unsuccessful (mean = 1 ± 1 days, n = 4) and nonbreeding hawks (mean = 1 ± 3 days, n = 4), though the model suggested that, too, was not statistically significant (Table 3.3, Fig. 3.27).

Spring start and end dates were not different by hawk breeding status the following season, but hawks that did not end up breeding (n = 5) tended to leave 6 days later than hawks that attempted to breed (n = 32), and nonbreeders arrived on the breeding range on average 12 days later than breeders (dates were similar between successful and failed breeders; Table 3.3, Fig. 3.28). Spring migration was on average 5 days shorter for hawks that attempted to breed (Table 3.3, Fig. 3.28), and breeders traveled at a faster pace (grand mean = 208 ± 20 km/day) than non-breeders (grand mean 192 ± 31 km/day); hawks with failed breeding attempts the following summer traveled at the fastest pace during their previous spring migration (failed grand mean = 224 ± 18 km/day [n = 8], successful grand mean = 203 ± 18 km/day [n = 24]; Fig. 3.28). Stopping behaviors during spring migration did not differ for hawks of various breeding status the following season, though there was a tendency for breeders to stop for 3 fewer days than non-breeders, which was consistent with faster travel (Table 3.3).

Discussion

Using satellite telemetry in migration research

Satellite transmitters are an important tool for studying animal behavior, especially for highly mobile and migratory species (Bittner 1988, Meyburg and Fuller 2007, Hebblewhite and Haydon 2010, Alarcón and Lambertucci 2018). PTTs in this and other studies allowed the possibility to describe details of Swainson’s hawk migratory behavior that were previously unknown or were hypothesized, but unverified, based on ground observations, band recoveries, and data from other species. These behaviors include a strong pattern of diurnal travel, avoidance of open water and mountains, use of staging periods prior to fall migration, and evidence of facultative stopover events throughout the migration pathway (Houston and Schmutz 1995*b*, Fuller et al. 1998, Bechard et al. 2006, Kochert et al. 2011, Airola et al. 2019). The drawbacks for using satellite telemetry to date have primarily been cost (i.e., PTTs cost thousands of US dollars per unit plus fees for using the satellite systems), length of data collection (e.g., battery limits, attachment failures), accuracy on free-living animals in varying environmental conditions, and unit weight (primarily driven by battery weight). These issues limit the types of animals that can be studied, the types of questions that telemetry can be used to answer, and sample sizes within studies (Steenhof et al. 2006, Lindberg and Walker 2007, Hebblewhite and Haydon 2010, Byrne et al. 2017). Solar power recharging reduces battery size and weight, and can extend transmitter life to allow year-round study of raptors, which is essential for studies of long-distance migratory behaviors (Patton et al. 1973).

However, PTTs, and other automated location-recording devices, alone cannot answer all questions in behavioral and ecological research. For example, we described locations of stopovers and speculate on possible explanations (below), but we did not have the appropriate data to verify what Swainson's hawks were doing during these periods (e.g., the debate over fasting versus foraging; Smith et al. 1986, Kirkley 1991, Bechard et al. 2006). Additionally, transmitter data from free-living animals is inherently error-prone and accuracy can be influenced by satellite position, atmospheric conditions, topography, canopy cover, time of day, position of the antenna, battery voltage, animal behavior, etc.; we must therefore recognize errors exist and attempt to filter data in any telemetry dataset being analyzed (Cain et al. 2005, D'Eon and Delparte 2005, Ganskopp and Johnson 2007, Belant 2009, Byrne et al. 2017). We addressed obvious errors in this study by filtering data prior to analyses, but we had no reasonable way to evaluate how much of the final dataset still contained errors. Britten et al. (1999) explained that using a theoretical maximum speed (kmh^{-1}) to filter transmitter data worked well when data were temporally close together (minutes to an hour apart) but could only point out egregious errors when data were hours or days apart; gaps of several hours to several days were common in our dataset, giving us a similar difficulty in visually detecting errors and restricting us to only removing the most implausible locations. We tested one PTT from this study (recovered after mortality) for location accuracy by placing it in five known locations with level terrain, little to no canopy cover, and variable weather for 36 days, and we found that reported points ranged from 6 to 473 m (mean = 25 ± 47 m) from true locations; however, the transmitter we tested was 4 years old and reported numerous ‘battery drain’ and other errors throughout testing, so we weren’t sure how representative this was of our deployed PTTs, and thus we relied on the manufacturer’s estimate of location error (± 18 m) in all analyses. Additionally, deployed PTTs were subjected to varying terrain, canopy cover, bird movement and behaviors, and a wide range of weather conditions, all of which make errors in GPS estimation more likely (and more egregious) than the conditions under which our one PTT was tested (Cain III et al. 2005, D’Eon and Delparte 2005, Ganskopp and Johnson 2007, Belant 2009, Byrne et al. 2017). Moreover, we did not know how much error and bias existed in PTT speed data (Microwave Telemetry declined to provide us with testing information). Our tested PTT erroneously showed movement of either 1 or 4 kmh^{-1} five times, indicating an error rate of 1.4%, but we did not test a moving transmitter to understand the range of speed errors. Measuring speed as distance between successive points by elapsed time may be a more reliable estimation than PTT-reported speed for descriptions and analyses, but location errors play a role in those estimations as well, which is why we chose to report data from both kinds of speed estimations here.

We recognize that errors likely persisted in our data post-filtering. The presence of errors may be insignificant for broad-scale conclusions, such as identifying migratory pathways across continents, but may have impacted our ability to accurately estimate and interpret fine-scale space use, cumulative distance traveled, daily travel rate, speed, and stopping behaviors (Hays et al. 2001). Additionally, transmitters may affect bird behavior, flight efficiency, and survival, which we had no way to tease apart from 'normal' migratory behavior (Pennycuick et al. 2012). We did not test for effects of wearing a transmitter or monitor a control set of hawks, and we assume there may be some biases in our data that might differ from untagged Swainson's hawks. Perkins (2019) found that Swainson's hawks pairs where one adult was equipped with a transmitter delivered prey with lower mass to nestlings than pairs that had not been tagged with a transmitter, indicating that transmitters may affect hunting and prey capture. Steenhof et al. (2006) found that PTTs had no effect on nesting success of female prairie falcons (*Falco mexicanus*), but females that removed their transmitters significantly increased their probability of survival. Britten et al. (1999) suggested that the survival and return rate of PTT-tagged peregrine falcons was similar enough to untagged falcons to declare no significant effects of wearing the device. Sergio et al. (2015) found that PTTs had no effect on black kite (*Milvus migrans*) survival, productivity, or the behaviors they examined. However, it is difficult to track migrating raptors by any method other than an attached device, and we therefore have no way to determine if and how transmitters affect migratory behavior at this time (Britten et al. 1999). Hawks in this study were given ample time (2 – 5 months) to habituate to transmitters prior to migration, so we believe any negative influence of PTTs on our study animals and our results was likely negligible. Finally, we recognize that our data are obtained from a sample of birds captured within a small portion of the breeding range. Although many of our conclusions are likely relevant for the species across its breeding range, our results are most relevant to adult Swainson's hawks breeding in the southern Great Plains (Lindberg and Walker 2007).

Survival of tagged hawks

We collected data on hawk movements for 1 month to > 5 years; two hawks (hawks A5 and A16) were known to be alive when we stopped data collection, and two additional hawks (A9 and A14) outlived their transmitters during the study. We considered last known transmitter-derived locations of hawks as locations of presumed mortalities, but an indeterminate amount of data cessation could also have been due to transmitter or attachment failure. Steenhof et al. (2006) found that prairie falcons were capable of tearing Teflon ribbon and dropping their transmitters, which affected 15% of their sample. Transmitter drop is indistinguishable from hawk mortality without locating the transmitter or obtaining visual or physical recapture of individual birds; in both situations, the received data shows a pattern of many points in one location until the transmitter stops attempting fixes. Transmitter failure may appear as data suddenly cutting off (which also may occur due to mortality if the transmitter was damaged) or as poor and infrequent data transmissions, with increasing error reports, until data stop coming in. We confirmed two instances of transmitter failure; hawks A9 and A14 were confirmed still alive on their breeding grounds three months after we stopped receiving data (Chapter 2). However, other hawks wearing PTTs were no longer spotted on breeding territories after data transmissions ended, supporting our assumption of mortality. Because we failed to locate most transmitters after data cessation, we interpreted these occurrences as hawk mortalities (except the four hawks we knew to have survived), but we limited our interpretations to general patterns, rather than a detailed survival analysis.

More than half of (presumed) hawk mortalities (58%) occurred on the breeding range (in Texas and Oklahoma, U.S.A., and Tamaulipas, Mexico), 21% occurred on the wintering range in Argentina, and while seven mortalities were associated with migration movements, only one occurred outside of breeding/wintering areas (Panama). We recovered two carcasses, indicating hawk A15 was shot 18 days after capture and hawk A21 collided with a wind turbine blade during the breeding season; all other causes of presumed mortality remained unknown. On the breeding range near Amarillo, Texas, hazards to raptors include wind turbine collision, persecution, vehicular collision, electrocution, accidental poisoning, disease, and predators (Houston and Schmutz 1995*b*, Stone et al. 1999, Saito et al. 2007, Loss et al. 2014). The most-concerning hazard for Swainson's hawks in Argentina was once the widespread use of organophosphate pesticides on grasshoppers (Acrididae), which was significantly reduced due to efforts of researchers and activists in the 1990's (Woodbridge et al. 1995, 1996, Goldstein et al. 1999*a*, *b*). Today, we expect hazards on the nonbreeding range are generally similar to those on the breeding range, because hawks prefer similar open habitats where ranchers raise livestock, conversion to row-crop agriculture is widespread, and roadways and power lines transect the landscape (Gavier-Pizarro et al. 2012, González-Calderón 2017, Sarasola et al. 2020). One difference that may have led to higher mortality risk on the High Plains breeding range was the presence and density of wind energy facilities, a known hazard for soaring raptor species (Kuvlesky et al. 2007, Chapter 6). Within 20 km of our study area, USGS reported 163 wind turbines in 2012, the year we began this study, which had increased 235% to 546 turbines when our study ended in August 2017; functionally, wind turbine hazards near known nesting territories tripled in five years (Hoen et al. 2018, Chapter 6). Across the region of the United States that hawks in this study occurred (i.e., Texas, eastern Oklahoma, and a small portion of southern Kansas), USGS reported more than 15,000 turbines in operation by August 2017 (Hoen et al. 2018). Similar data were not available for South America, so we used satellite imagery to estimate that fewer than 100 wind turbines may have existed across the entire wintering region of Argentina during our study (Chapter 6). However, no last location of any hawk occurred in areas where we found possible wind farms in Argentina (Chapter 6). Hawks from this study also may have encountered as many as 213 turbines in Uruguay, though most (87%) Uruguayan locations were not near suspected wind energy facilities (Chapter 6). We additionally found 2,500 turbines along the migration route (between Mexico and Panama), none of which were near last known hawk locations (Chapter 6).

We concluded that Swainson’s hawks in this population may be at highest risk of mortality during the breeding season. These hawks spend the largest proportion of the year (5 – 6 months) in a landscape that has many hazards, including the growing wind energy industry and associated power lines and vehicular traffic (Houston and Schmutz 1995*b*, Kuvlesky et al. 2007). Additionally, breeding activities may amplify vulnerability to local hazards. For example, females sitting on nests for weeks of incubation and brooding may be more vulnerable to depredation and persecution, whereas hunting males may be more vulnerable to turbine blades, electrocution, and vehicular collisions (Bechard et al. 2010). Nonbreeding hawks may also be more vulnerable to landscape-wide hazards, such as wind turbines, because instead of holding a territory, hawks are free to range nomadically if they so choose. Swainson's hawks face hazards on the nonbreeding range, but the chance of mortality may be lower due to spending less time there (2 – 4 months) and their nomadic behavior (Jaramillo 1993, Kochert et al. 2011).

One third of our tagged hawks may have perished in association with migratory activities; two during fall migration, one just after reaching the wintering range, three during spring migration, and one just after reaching the breeding range. Considering that Swainson's hawks spend half, or more, of the year making migratory movements, we suggest that the 29% assumed mortality rate of hawks perishing during this period is a relatively low proportion. Our data are in contrast to Klaassen et al. (2014), who found that migration had six times the mortality rate than stationary periods for three old-world raptor species. The benefits provided by evolving migratory strategies, such as migrating en masse, using energy-efficient soaring flight, spending little time in any one location, and possibly opportunistic foraging en route, may aide in producing relatively high survival during this period of Swainson's hawk life history (Kerlinger 1989, Bildstein 2006).

The migration route

Swainson's hawks migrated across 15 countries and generally used the same pathway for outbound and return migration, as was reported in previous transmitter research (e.g., Fuller et al. 1998, Kochert et al. 2011, Airola et al. 2019), observational studies (e.g., Fox 1956, Thiollay 1980, Smith 1985, Tilly 1992, Juhant 2010), and leg band recovery efforts (e.g., Houston 1990, Houston and Schmutz 1995*b*, Schmutz 1996). While the vast majority of Swainson's hawks likely use the route we described through

Central and South America, major exceptions exist throughout North America for hawks originating from, and aiming for, more-western breeding ranges than hawks from our sampled population (Fuller et al. 1998, Kochert et al. 2011, Airola et al. 2019).

We found three minor route differences from previous telemetry research. Bechard et al. (2006) explained why their reported migration distances may have been shorter during spring migration as hawks taking different coastal routes through Central America, specifically a Pacific route while travelling southward and a Caribbean route while travelling northward. In contrast, most hawks in our study followed nearly identical routes through Central America during both seasons, specifically travelling the Pacific coastline from Mexico to Nicaragua, then crossing to the Caribbean coastline through Costa Rica and Panama; during spring migration, some hawks in this study often traveled a Pacific-coastline route through Panama and Costa Rica, which might be a longer pathway than the one most traveled. Instead, the routes we described were more consistent with the transmitter tracks reported by Airola et al. (2019). In addition, a quarter of birds in this study had inland, rather than coastal, pathways through southern Mexico, Guatemala, and Honduras, a pattern that was not found in previous studies (Fuller et al. 1998, Kochert et al. 2011, Airola et al. 2019). Differences may lie in the different technology used (i.e., older studies had lower-resolution data with which to draw conclusions), individual variation (e.g., varying energy levels, body condition, and choices made), hawks encountering inclement weather or difficult wind patterns (and thus stopping, bypassing hazards, or getting blown off course), and hawks following soaring birds of different species. For example, Mississippi kites, turkey vultures, and broad-winged hawks are all observed traveling en masse through the same Central

American route during migration (Kerlinger 1989, Parker 1999, Haines et al. 2003, Bildstein 2006, Dodge et al. 2014). Last, the wintering destination of hawks in this study agreed with those hawks tracked by Fuller et al. (1998) and Kochert et al. (2011), but Airola et al. (2019) tracked hawks to unique overwintering grounds north of Argentina and along the migration route, resulting in shorter distances traveled and longer stopover periods for the California population.

Distance from migration start to end for hawks in this study ranged from 8,000 to 9,000 km, which was shorter than the 10,000 or more km described for hawks tracked by Fuller et al. (1998) and Kochert et al. (2011). Our study area, approximately 450 to 1,800 km southeast of previous capture locations (Fig. 3.1), is along the migration pathway, and is used as a common staging location, for many other studied Swainson’s hawks (Fuller et al. 1998, Kochert et al. 2011). The cumulative distance traveled by Swainson’s in this study was 5 to 32% longer than a straight-line path, similar to results presented by Fuller et al. (1998). This can be explained by 1) hawks avoiding water and mountain crossings, which forces the path to bend and stretch, 2) obligate soaring, which requires hawks to fly from thermal to thermal (a potentially crooked pathway) to maintain lift, 3) staging and stopover behaviors, where hawks sometimes wandered hundreds of km without making progress in the direction of migration, and 4) some hawks deviating off course or taking longer routes than the bulk of studied birds. Also unsurprising, the cumulative distances traveled by hawks in this study (8,312 – 11,453 km) were generally shorter than hawks nesting at more-northern latitudes (8,449 – 13,209 km; Fuller et al. 1998, Kochert et al. 2011). In contrast, Swainson’s hawks from California traveled 2,500 to 10,000 km, a wide range of distances due to the variable wintering locations among that sample of individuals (Airola et al. 2019).

Among raptors, avoidance of water crossings > 25 km are common behaviors (Kerlinger 1989, Bildstein 2006). Kerlinger (1985) suggested the tendency to cross water may be linked with wing shape and aspect ratio, with longer- and pointed-winged (similar to seabird wing shapes) species, such as falcons and ospreys, being more likely to undertake over-water passages than raptors with shorter and wider wings that are built for soaring. Our data indicated that Swainson's hawks generally avoided water, including the complete avoidance of Managua Lake and Lake Nicaragua during Central American passage, as expected of an obligate-soaring species (Kerlinger 1989, Bildstein 2006, Chapter 4). And, while trajectories indicated the possibility of over-water crossings, we received very few locations over open water (Fig. 3.5). Thus, some individuals may have actually traveled routes over land, but we could not confirm this due to the temporal resolution of our data. However, some locations were obtained over water, at peninsulas, and on islands, which suggest that Swainson's hawks, at least occasionally, travel across coastal inlets, perhaps to take advantage of some ideal wind condition or to save time with a more-direct route (Kerlinger 1989, Bildstein 2006). There is observational evidence elsewhere that some Swainson's hawks end up in Florida and on Caribbean islands via routes we do not understand to date (Hayes 1999, Rodríguez-Santana 2010). Osprey, peregrine falcons, and merlins (*Falco columbarius*) often migrate through the Caribbean islands (Clark 1985, Fuller et al. 1998, Martell et al. 2001), which may influence Swainson's hawks found along those routes due to their mass-migratory and mixed-flocking behaviors. Interestingly, in a related study where we tracked juvenile

Swainson's hawks with transmitters, we found one first-year bird crossing to Coiba Island, Panama (a 19-km trip over water), then returning to the migration route during southward travel, a behavior that to our knowledge has never been described for this species (Chapter 5). Our evidence combined with that of previous transmitter research (Fuller et al. 1998, Bechard et al. 2006, Kochert et al. 2011, Airola et al. 2019) suggests that Gulf observations (e.g., Hayes 1999, Rodríguez-Santana 2010) were likely vagrants, rather than an indication of an unknown migratory pathway. Furthermore, the closest relatives of Hawaiian hawks (*Buteo solitarius*) and Galapagos hawks (*Buteo galapagoensis*) are thought to be Swainson's hawks, implying that occasional vagrancy across vast oceanic distances may be possible for this species (Hull et al. 2008, Bechard et al. 2010).

Hawks appeared to avoid crossing mountains at the beginning and end of travel, bending the otherwise-straight pathways, but passage through Central America and Colombia required over-mountain flight. Crossing the Andes Mountains in Colombia was particularly unavoidable, but hawks appearded to travel through valleys where possible and probably detoured to the easiest path across (i.e., most hawks crossed in the same general locations; Fig. 3.6); one hawk migrating northward appeard to try to avoid crossing a second time, producing an extended migration track that went to the Caribbean coastline in Colombia before the hawk turned southward to relocate the route through Panama. Most routes through Central America were circuitous to, presumably, avoid major mountain and water body crossings. The Pacific-coastline route through Panama that led to crossing mountains in Costa Rica (Fig. 3.6), which specifically affected some hawks migrating northward, may have been linked to seasonal wind conditions. Data from Panama City indicated that when hawks passed this region in March and early April, they faced stronger (average speed = 6 – 7 mps) headwinds, while during fall passage from mid-October through mid-November, hawks encountered weaker (average speed = 3 – 4 mps) winds from variable directions, often with a trend of southerly winds that may help maintain the Caribbean-coastline route (Weather Spark, https://weatherspark.com). These variable pathways suggest hawks are adaptable to localized changing conditions; some hawks in this study deviated from the regular route but found their way back and survived the journey. However, departing from the apparent normal route may consume additional energy that incurs a survival or fitness cost to the bird. In a related study, we monitored breeding Swainson’s hawks (Chapter 2), and out of the datasets containing failed breeding attempts or seasons where we found no indication the tagged hawk attempted to breed (41% of known outcomes), 77% were associated with hawks travelling the Pacific-coastline route during the previous spring migration. However, 58% of successful breeding attempts were also associated with departures from the apparent normal route; our small sample size therefore limits our ability to detect a clear breeding cost, if there is any.

We believe the migration pathway is primarily selected to reduce energy costs by keeping birds in range of thermals and other sources of environmental lift (Kerlinger 1989, Bildstein 2006). An entirely land-based pathway also allows for rest at night and the possibility of opportunistic foraging en route (Kerlinger 1989, Kirkley 1991, Bildstein 2006). For example, migrating Swainson’s hawks were filmed apparently gleaning insects from the leaves of roost trees as they landed in the evening and leaving roosts to forage in fields before taking off in the morning in southern Mexico (Kirkley 2017).

Importantly, Swainson’s hawks, and other species with similar migration routes (e.g., Smith 1985, Haines et al. 2003, Dodge et al. 2014), appear to bottleneck in the Oaxaca region of Mexico, along the Pacific coastline of El Salvador, Honduras, and Nicaragua, and throughout the Isthmus of Panama, which may represent regions of potential conservation concern for these migratory species (Fuller et al. 1998, Kochert et al. 2011; Fig. 3.3 and 3.4).

Fall migration characteristics

Fall migration for hawks in this study was longer, in both timing and distance, than spring migration. Average initiation (2 Oct) was slightly later than the 12 Aug to 9 Oct reported by Kochert et al. (2011), because birds captured at higher latitudes migrate earlier; hawks they captured in Arizona, Colorado and Utah began migration at dates similar to those in this study. Average end date of fall migration (27 Nov) was similar to the 8 Nov to 23 Dec reported by Kochert et al. (2011), which was no surprise as all hawks between the two studies ended migration at roughly the same latitudes in Argentina, and the mass-migratory behavior implies that most hawks travel together at roughly the same time (Bechard et al. 2010). Swainson’s hawks in this study on average spent less time migrating southward due to the shorter distance required compared to the more northern-breeding birds (Fuller et al. 1998, Kochert et al. 2011). We additionally found a broader range of fall migrations (36 – 104 days) than the 42 to 98 days found for hawks originating in more northern latitudes (Kochert et al. 2011), adding to our understanding of the variability of migration behaviors for this species.

In a recent study of Swainson's hawks in California, Airola et al. (2019) suggested a significantly earlier initiation of fall migration (15 June – 12 Oct), and some of the California-breeding hawks settled into their unique wintering areas later with a wider range of arrival dates (5 Nov – 15 Jan), though the mean arrival date (25 Nov) was similar to our results. Hawks in their study also traveled for a longer period (99 days), even though they had the shortest distances to travel (Airola et al. 2019).

Airola et al. (2019) explained some of their results by noting that hawks that suffered failed nesting attempts left California and arrived on wintering grounds three weeks earlier than hawks that successfully raised a brood. We did not find a difference in fall migration start dates, but hawks that bred successfully took longer to migrate southward, traveled at a slower pace, and stopped more often and for longer periods compared to hawks that did not breed or that had suffered failed nesting attempts.

Staging and stopovers are common behaviors of migrating birds, such as cranes (e.g., Végvári 2002), shorebirds (e.g., Myers 1983), passerines (e.g., Németh and Moore 2007), and waterfowl (e.g., Ebbinge and Spaans 1995). Stops are thought to be opportunities for birds to accumulate needed fat stores before travel, opportunities for flocks to aggregate, opportunities for rest and recovery before continuing travel, opportunities to molt flight feathers during migration, and situations where birds must wait for suitable weather conditions before progressing forward (Kerlinger 1989, Kirkley 1991, Leu and Thompson 2002, Bildstein 2006, Warnock 2010). Many species show distinct geographic locations where many, if not all, migrating individuals gather, and thus a clear pattern of staging behaviors or mid-migration stopovers may be identified (Myers 1983, Ebbinge and Spaans 1995, Warnock 2010).

Tracking data suggests Swainson's hawks have both a pre-migratory staging period and make stopovers en route, but unlike other species, Swainson's hawks stop at seemingly random locations throughout the entire migration pathway, with few geographic patterns emerging from data collected so far (Kochert et al. 2011, Airola et al. 2019, this study). For example, eleven early stopovers in this study during spring migration were located near Mar Chiquita Lake, in Córdoba, Argentina (one of the few geographic patterns we could discern; Fig. 3.20 and 3.21), but MCP areas and date ranges varied, and few trajectories indicated significant time spent on lakeshores or crossing the water, so we weren't sure if that was a pattern or a coincidence. We additionally found no evidence of stopovers along the pathway from Guatemala to Nicaragua in either season (Fig. 3.20), however, Kochert et al. (2011) identified at least 9 stopovers across the same region. Swainson's hawks have been observed in agricultural fields during and just after harvest activities that expose prey such as grasshoppers (Bechard 1982, Smallwood 1995, Canavelli et al. 2003, Bechard et al. 2010, Littlefield and Johnson 2013). Perhaps variation across landscapes and years represents the patchy availability of these foraging opportunities. Additionally, if hawks are stalled by poor weather conditions (Smith 1985), it makes sense to expect those stops to occur at variable locations and times throughout migration.

In this study, we use the word 'stop' loosely, for lack of a better term, to group staging and stopover behaviors together. During 'stop' events in this study, birds often moved omnidirectionally, rather than staying in one location, and thus we found high variability in MCP areas (from < 1 – 39,074 km^2) and shapes of polygons. We suspect stopping behaviors for hawks in this study were generally facultative and associated with local conditions (e.g., abundant food, poor weather) and condition of the individual (e.g., needing rest). Therefore, movement during staging periods and stopovers may indicate foraging on locally abundant food sources, as suggested by Kirkley (1991, 2017), or attempting to find a route around a significant weather system, whereas stopovers with little to no movement are more likely connected with being stalled by poor weather or an individual needing rest.

Typically, hawks in this study stopped twice during fall migration (range = 0 – 8 stops), usually a longer staging period and a short-duration stopover somewhere en route, but 16% of migration tracks were continuous (i.e., no evidence of stops). Hawks in this study appeared to make different choices (e.g., to stop or not, to stage prior to beginning full migration or not, location and duration of stop[s], whether to wander during a stop event or to stay in one location, etc.) every migration in both seasons. Migrating ospreys tracked with satellite telemetry similarly showed variable stopping behaviors, with 15% migrating continuously and cumulative stop durations of 4 to 44 days for others (Kjellén et al. 2001). We found fall stopping behaviors occurred most frequently towards the beginning and end of migratory travel; about 80% of fall migration stops were within the borders of the United States or Argentina. When birds stopped, it was for an average of 4 days, with shorter-duration (mean = 2 days) stops typically occurring across the stretch from Mexico to Bolivia.

Staging is an opportune time for accumulating fat reserves and aggregating in preparation for migration (Warnock 2010), and Swainson’s hawks are known to gather in groups of tens to hundreds of birds between breeding season and migration, oftentimes being found gorging on locally abundant insects (McGrath 1988, Houston 1990, Bechard et al. 2010, Littlefield and Johnson 2013). Because the High Plains region where we trapped hawks is a frequently used staging area (Kochert et al. 2011, Littlefield and Johnson 2013), we were not sure how much staging behaviors we would observe, as it is possible that regionally nesting hawks were already ‘in’ a staging habitat. We identified stops made by 16 hawks (70%) that were within 1,000 km of their general breeding territories, which we might classify as ‘staging’ behaviors. One third of the hawks we studied did not show obvious staging behaviors at the beginning of fall migration, but may have instead staged (i.e., accumulated fat and located flocks) close to or within their breeding territories, and thus may not have needed additional stopping time when they ‘began’ migration. Additionally, evidence of staging was not constant within birds; 80% of sampled hawks for which we recorded multiple fall migrations did not make early stops every migration. Stops within 1,000 km of breeding territories were most common during fall of 2012 (92% of birds), and occurred less often in 2013 (40%), 2014 (11%), 2015 (0%), and 2016 (33%), which may be indicative of annual environmental conditions. For example, 2012 was a severe drought year for northern Texas (National Weather Service, https://www.weather.gov/) with improved, but still drought conditions, in 2013, 2014, and 2016; whereas 2015 had abundant rain (National Weather Service, https://www.weather.gov/).

Stops made within 1,000 km of trapping locations were longer (mean = 7 days) than those made throughout the remainder of the migration route (mean = 3 days), and the longest-duration stops recorded in this study (10 – 31 days) only occurred within Texas and Oklahoma, which is consistent with our expectation of a pre-migratory staging period. Additionally, staging locations had larger MCP area (mean = 3,500 km^2) than en route stopovers (mean = 1,800 km^2), suggesting more wandering occurred, which is consistent with hawks foraging and locating flocks to join. Kochert et al. (2011) reported hawks from across the breeding range showing similar stopping behaviors (longer-duration staging periods in North America, mostly short stopovers through the rest of fall migration), and locations and durations of stop events were similarly variable. Airola et al. (2019) also reported hawks from the Central Valley of California population making stops, but in different locations from hawks in this or previous studies (Kochert et al. 2011), primarily along the western coast of Mexico, and hawks stopped for much longer durations (11 – 112 days during fall migration), which likely contributed to other areas where we found discordant migration results, such as their longer fall migration duration and slower daily travel rates (described below).

Spring migration characteristics

Average initiation of spring migration (23 Feb) was similar to the 13 Feb to 26 Mar reported by Kochert et al. (2011) and the 1 Feb to 8 Mar reported by Airola et al. (2019). Unlike fall migration, spring migration initiation was strongly correlated with dates of arrival on the breeding range. Spring migration may have stronger selection for less variability in timing, due to the drive adults may have to compete for territories and mates and to begin the breeding process upon arrival (Kerlinger 1989, Bildstein 2006). Average spring migration end date (13 Apr) was substantially earlier than the 20 Apr to 1 June reported by Kochert et al. (2011), but somewhat later than the average 30 Mar reported by Airola et al. (2019). Similar to fall migration, hawks in this study spent less time migrating northward (mean = 48 days, range = 40 – 73 days) compared to birds heading farther north (mean = 62 days, range = 51 – 82 days; Kochert et al. 2011). Variable results likely stem from breeding destinations and total distances required to travel.

Northern Texas vegetation begins growing earlier (average period of last spring freeze 16 – 30 Apr) than more-northerly breeding locations (last freezes range from 1 May – 30 June) (National Oceanic and Atmospheric Administration [NOAA], https://www.ncdc.noaa.gov). Hawks aiming for other destinations may be at a disadvantage if they arrive too early, before food sources (small vertebrates and large insects) become readily available. However, hawks breeding in our study region find growing vegetation and prey becoming active by the time they arrive in March and April (NOAA, https://www.ncdc.noaa.gov). Therefore, hawks breeding in northern Texas may have the advantages of a longer breeding season, earlier nesting phenology, and more time for individuals to molt and improve body condition prior to migration. Additionally, if a nest fails early in the season, the hawk pair may have enough time to attempt a second nest (Bechard et al. 2010, Chapter 2). The California population, and all southern breeders, may have similar early-growing-season advantages, as signaled by their even-earlier arrival dates (Airola et al. 2019).

Spring migration in our study was 8 days shorter than fall migration, similar to the 5-day difference reported by Kochert et at. (2011). The cumulative distance traveled was also 580 km shorter during spring migration. One potential explanation for these results was that some hawks initiated spring migrations at a more northerly latitude than where hawks ended fall migrations in Argentina (Fig. 3.29), however the statistical test indicated no difference in the direct distance between starting and ending locations among seasons, so we didn't consider this explanation sufficient. Another possible explanation was that hawks traveled a more-direct route during spring migration. However, spring migration had more variability in routes traveled. An additional explanation may be the propensity for staging (i.e., wandering without making forward progress) during fall migration. In addition, towards the end of fall migration hawks made stopovers, again moving tens to hundreds of km, as they slowly settled into nonbreeding areas. Hawks made stops during spring migration, but spent fewer days stopped, and stopping behaviors were more likely to occur in a single location rather than the bird moving about the landscape (explained further below). Last, if hawks genuinely travel a more-direct route when returning to the breeding range, it may be because they are driven to travel more quickly, because of the need to reach the breeding range to compete for territories and mates (but see comments on this theory below); hawks also may need to preserve body condition with shorter, more-direct travel, to maximize success in the next breeding attempt (Bildstein 2006).

Airola et al. (2019) examined how breeding may have been impacted by spring migration activities and found that hawks which arrived on the breeding grounds earlier tended to be more successful the following summer. For spring migration, we found that hawks that bred the following summer migrated faster and started and ended migration earlier (though models suggested dates were not significantly different); however, we were not sure if this meant that hawks deliberately migrated sooner and faster when they were planning to breed, or if a quick spring migration led to a hawk being more likely to breed. While patterns existed in this study and somewhat supported previous conclusions (Airola et al, 2019), more research is needed to understand causal relationships between migration performance and breeding success. Additionally, the confounding factor of breeding behaviors likely contributes to the variability we found in many migration measurements reported in this study; migration is a complex combination of many interacting factors, which makes it difficult to explain patterns and outliers in a simplified behavioral-environmental context, as we have attempted to do here.

Stop duration and area data from this study suggested that Swainson's hawks do not stage prior to spring migration, with early spring stops appearing to have similar patterns (i.e., 1 – 5 days stopped, smaller MCP area) as the stopovers made throughout the migration route. Both previous studies also reported few stops during spring migration (mostly clustered on the breeding range), which may also have contributed to their reports of shorter migration durations and faster travel speeds (Kochert et al. 2011, Airola et al. 2019).

Hawks in this and previous studies showed a pattern of late-season stopovers as they approached breeding regions (Kochert et al. 2011). If hawks sped up during spring migration because of impending competition for mates and territories on the breeding grounds, we would expect them to mostly fly non-stop as they approached old territories, but we found the opposite pattern. Airola et al. (2019) stated that California hawks were unlikely to be driven by intraspecific competition, as pairs often stayed together for > 4 years and showed high territory fidelity (also supported by Schmutz et al. 2006); they suggested that breeding competition may be more important for young and unmated hawks and possibly important against other species using similar breeding habitats (e.g., great horned owls, red-tailed hawks, and white-tailed kites [*Elanus leucurus*]). We therefore concluded that seasonal differences found in this study and previous studies were most likely caused by environmental factors (e.g., seasonal wind and thermal conditions, availability of harvested agricultural fields) and behavioral factors other than intraspecific competition. For example, earlier arrival on the breeding range allows for earlier nesting and, possibly, greater nesting success, and traveling a more-direct route with fewer stops, along with making late-season stopovers, may help preserve and improve body condition prior to breeding (Bildstein 2006, Airola et al. 2019).

Other behaviors

We estimated daily travel rates based on vectors connecting daily roost locations for comparability to previous analyses (Fuller et al. 1998, Kochert et al. 2011) and found immense variability, from 0 to 871 km traveled/day. We observed an average fall migration daily travel rate for Swainson’s hawks in this study of 183 km/day, which was consistent with the 188 km/day reported by Fuller et al. (1998) and 177 km/day reported by Kochert et al. (2011). These travel rates, however, were substantially faster than the 72 km/day (range = 40 – 102 km/day) reported for the California population (Airola et al. 2019). In contrast, we found a faster spring migration speed of 196 km/day than the 150 km/day reported by Fuller et al. (1998) and Kochert et al. (2011). However, our spring travel rate was similar to the average 202 km/day reported for the California population (Airola et al. 2019).

Minor differences among studies may have several causes. Variation in travel conditions among the periods of the difference studies are a likely contributing factor. There could also be a behavioral difference for hawks breeding in more-southerly regions; an earlier growing season may facilitate earlier breeding opportunities (NOAA, https://www.ncdc.noaa.gov). Additionally, there was a difference in technology used among studies, with GPS transmitters in this study and Airola et al. (2019) providing more locations per day and higher-quality location fixes compared to Doppler transmitters used in the 1990's (Fuller et al. 1998, Kochert et al. 2011). Some, or all, of these factors, combined with small sample sizes, may have confounded our ability to tease apart clear explanations.

Importantly, when we removed stop days from analyses, both fall and spring travel rates increased to 211 km/day. This indicates travel rates during active migration periods were not different between seasonal migrations and illustrates the importance of considering stopping behaviors in understanding the pace of migratory travel for Swainson's hawks. We assume previous researchers also included all possible migration data in their estimations of travel rate (Fuller et al. 1998, Kochert et al. 2011, Airola et al. 2019) and argue that a seasonal difference may not exist or may be less apparent if they examined only periods where hawks were making forward progress. We suggest the real seasonal difference between migration characteristics lies within the stopping behaviors, and they should always be considered when interpreting migration results for this species.

We found indications of significantly higher daily travel rates than previously reported, with 113 vectors exceeding 500 km/day and eight exceeding 800 km/day. Further, our results indicate these occasional extreme distances covered in a day were not exclusive to specific individuals. Periods of extreme travel occurred between Texas and Mexico, between Bolivia and Argentina, and (during spring travel only) through Central America. These travel rates not captured by previous telemetry studies may additionally contribute to some differences noted between seasons and among studies and provides new insights as to the flight capabilities of Swainson's hawks. The geographic clustering of these extreme vectors suggests the possibility of environmental causes, with the potential of ideal travel conditions (e.g., fast tailwinds and strong, readily available thermals) occurring at general (i.e., regions) or specific (e.g., high wind speeds coming off a mountain) locations along the migration pathway. Situations that may facilitate faster-than-average flight lends credence to the proposition that temporal differences in environmental conditions may be a major contributor to the discordant results across studies, though the variability in resolution of data, due to differing technologies, likely plays a role as well.

Other migrating raptor species have shown variable, and oftentimes similar, rates of travel. For example, peregrine falcons migrating between North and South America traveled 172 to 198 km/day (Fuller et al. 1998). A lesser spotted eagle (*Clanga pomarina*) migrating between Europe and Africa covered 144 to 214 km/day (up to 521 km; Meyburg et al. 2004*a*, *b*). A short-toed eagle (*Circaetus gallicus*) migrating across Africa averaged 234 km/day (up to 467 km; Meyburg et al. 1998). Migrating golden eagles (*Aquila chrysaetos*) navigating the Appalachian Mountains traveled 99 km/day (14 – 412 km; Rus et al. 2017) and those migrating from Alaska to the contiguous United States traveled up to 472 km/day (McIntyre et al. 2008). An Egyptian vulture (*Neophron percnopterus*) traveled 1,000 km across the Sahara Desert in two days. Ospreys from the U.S. traveled 111 to 380 km/day to variable North and South American wintering locations (Martell et al. 2001), and European ospreys traveled 108 to 431 km/day (up to 675 and 746 km; Kjellén et al. 2001). Swainson's hawks are therefore not unique in the daily distances they typically travel during migration, the variability, or the moments of extreme daily travel; large soaring avian species tend to travel in similar ways due to the convergent evolution of taking advantage of similar environmental conditions for migration (Kerlinger 1989, Bildstein 2006).

Speed data indicated a strong pattern of diurnal activity from 0900 to 1700 during migration; because of the dramatic shift in data from 0700 to 0900 (a 59% increase in PTTs reporting movement), we suggest that Swainson's hawks generally began morning movements around 0700 to 0800, with variability likely involving local conditions. Some early-morning movements may involve hawks leaving roosts to forage nearby as they wait for thermals to form (Kirkley 2017). Swainson's hawks appeared to end daily activities between 1500 and 1900, with a less-stark contrast among hourly reports compared to morning movements. Timing of settling into a roost may depend on local weather conditions, availability of thermals into the evening, altitude a hawk was at late in the day, energy levels of the individual, and behavior of the flock. Observations suggest Swainson's hawks also communally roost outside of the breeding season (Smith et al. 1986, Goldstein et al. 1999*a*, Sarasola and Negro 2006), so hawks may follow others into a roost regardless of flight conditions. Migration data from Ospreys similarly indicated their likely active periods were 0800 to 1800 throughout migration (Kjellén et al. 2001).

We truncated both speed metrics at 1 kmh^{-1} to exclude stationary birds in mean estimates and correlations, and one could argue that migratory flight should only include even faster speeds; if we further truncated data to include only movements > 5 kmh^{-1}, $>$ 10 kmh^{-1}, etc., this resulted in an in an overall average flight speed estimate of ~ 25 kmh^{-1}. The measurements we reported (both PTT speed and estimated velocity) are 'ground speed' (or cross-country speed), which means distance the bird was linearly moving across the landscape over time (e.g., a bird circling in a thermal has low ground speed, while a bird gliding between thermals has relatively high ground speed), which includes the influence of wind (Pennycuick 1969). In contrast, some researchers report 'airspeeds', which is speed that does not include wind (i.e., wind is mathematically removed from observed data to obtain airspeed estimate, if wind was a factor at all during measurement). Airspeed does not directly translate to ground speed; for example, a hawk moving 10 kmh^{-1} airspeed might be hovering (< 1 kmh^{-1}) if facing into a headwind or might be propelled 20 kmh^{-1} across a landscape in a tailwind. While airspeed is important to understanding the biology and physiology of flight, we argue ground speed is more ecologically relevant to understanding migration behaviors, because it includes the influence of environmental conditions.

Smith (1985) reported average ground speeds of migrating hawks (including Swainson's hawks) passing Panama as ~ 25 kmh^{-1} and measured higher speeds of 35 to 75 kmh^{-1} in some gliding conditions. Kjellén et al. (2001) reported ground speeds of migrating ospreys as 19 to 48 kmh^{-1} and airspeeds in glides between thermals as 39 to 71 kmh^{-1}. Rus et al. (2017) reported average ground speed of migrating golden eagles as 22 kmh^{-1}, and McIntyre et al. (2008) reported speeds ranging from 16 to 73 kmh^{-1} for golden eagles. Duerr et al. (2012) demonstrated how eagle ground speed varied with flight strategy, with birds circling in thermals at ~ 7 kmh^{-1}, slope soaring at ~ 25 kmh^{-1}, and gliding at ~ 61 kmh^{-1}. Kerlinger (1989) described ground speeds for various raptors migrating in the eastern United States, with speeds during ridge-gliding ranging from 20 to 97 kmh^{-1} (most means ~ 45 kmh^{-1}) and inter-thermal glides ranging from 70 to 88 kmh^{-}

^{1}. Pennycuick et al. (2013) examined airspeeds of various birds across the taxonomic spectrum and reported average speeds of 40 to 75 kmh^{-1}, with three raptor species (kestrel [*Falco tinnunculus*], goshawk [*Accipiter gentilis*], and white-tailed eagle [*Haliaeetus albicilla*]) clocking in at 45 to 58 kmh^{-1}. Compared to estimates from other species, Swainson's hawks are on average slower flyers, and data from other species supports the higher end of speeds we reported as being biologically reasonable.

Maximum speeds we reported were 127 kmh^{-1} (the maximum our PTTs could report; Microwave Telemetry, Inc., Columbia, Maryland) and 123 kmh^{-1} (based on successive locations), but data ≥ 90 kmh^{-1} (the maximum flight speed considered reasonable by Fuller et al. 1998 and Kochert et al. 2011) were so rare (17 PTT speeds [0.04%] and 56 between-point velocities [0.1%]), it was difficult to tell if those speeds were biologically reasonable or were due to errors that survived our manual-filtering methods. Smith (1985) noted that various hawks migrating through Panama (including Swainson's hawks) could occasionally be propelled > 80 kmh^{-1} in the right wind conditions. Kerlinger (1989) did not discuss maximum flight speeds but reported average speeds upwards of 88 to 97 kmh^{-1} for various raptor species. Peregrine falcons can reach horizontal speeds upwards of 150 kmh^{-1} (Ponitz et al. 2014), and the maximum gliding airspeed recorded for a white-backed vulture (*Gyps africanus*) was 141 kmh^{-1} (Tucker 1988). Meinertzhagen (1955) listed maximum recorded speeds across taxa, which included several notes of speeds > 100 kmh^{-1}. We therefore believe moments of extremely fast speeds may be possible for Swainson's hawks in exceptional environmental conditions.

Locations of high speeds clustered towards the beginning and end of migration in both seasons. Vector data (velocities and daily travel rates) showed the strongest geographic patterns, with the highest speeds clustering on the bend in the migration route where hawks followed the eastern edge of the Andes through central Bolivia, then turned southward toward their Argentinian destination. Ground speed is highly influenced by wind speed (Pennycuick 1969, Safi et al. 2013), so we examined measures of wind speeds in the Bolivian region. Average weather data from Santa Cruz de la Sierra, Bolivia (located at the bend in the migration route), indicates winds during both migration seasons are typically northerly at 12 to 15 kmh^{-1}, and other cities along the Andes report similar or lower average wind speeds (Weather Spark, https://weatherspark.com). However, municipal weather stations used for modelling and predicting local conditions relevant to people are generally measured near ground level. Wind speeds increase with altitude (Justus and Mikhail 1976), and atmospheric interaction with that portion of the Andes may cause higher-altitude wind gusts that would not be reflected in municipal weather data.

Swainson's hawks frequently fly between 370 and 2,650 m above ground, occasionally achieve heights of 6,000 to 7,000 m, and some anecdotal reports exist of hawks flying > 9,000 m (Smith 1985). In a related study, we estimated altitude of migrating Swainson's hawks as up to 9,818 m above ground (mean = 135 m above ground and 16% of data were > 500 m above ground), though we had little way of accounting for altitude errors in our PTT data (Poessel et al. 2018, Chapter 6). Therefore, we must examine atmospheric conditions high above the landscape to understand how wind might affect migrating hawks.

We used the Ventusky application (InMeteo, https://www.ventusky.com) to get a better idea of wind conditions that hawks might have encountered as they passed through Bolivia, focusing on the edge of the Andes and the valley to the east during periods of passage (mid-Feb to mid-Mar and throughout Nov). Wind speeds at all heights examined (10 – 5,500 m above ground) generally ranged from 5 to 50 kmh^{-1}, with a pattern of higher wind speeds at the bend in the route and southward into Salta province, Argentina; wind gusts at speeds of 60 to 130 kmh^{-1} occurred frequently enough to support the idea that winds might occasionally propel hawks to incredible ground speeds in this region. Scaling outwards to the entire migration pathway, regions with generally higher wind speeds also included Texas and Argentina during fall migration and Central America, southern Mexico, and the gulf coast from Mexico to Texas during spring migration, and the route through Colombia and Brazil rarely produced winds > 30 kmh^{-1}, all of which lined up well with patterns in exceptional speed data of this study.

Hawks moving at high speeds can move long distances when propelled by tailwinds, but high airspeeds are not sustainable; the faster a hawk moves in a glide, the faster it sinks (Kerlinger 1989). Therefore, to achieve movements > 500 km in a day, high speeds might be combined with extreme starting altitudes (to allow hawks the longest possible glide), frequent opportunities to re-gain lift and return to high speeds (e.g., frequent thermals combined with higher-altitude tailwinds), or ideal atmospheric conditions that allow for constant lift (e.g., lenticular cloud streets, which can sustain level glides > 60 km; Smith 1985) without sacrificing speed. The clustering of all types of speed data suggests Bolivia, western Paraguay, and northern Argentina, and, to a lesser extent, Central America, Northern Mexico, and Texas, occasionally produce both ideal wind and thermal conditions that promote moments of high-speed and long-distance travel.

When we compared instantaneous PTT speed with the velocity the bird would have to move to get to the next point, we found a skewed relationship with no correlation. There were 5,457 instances (12% of data) where PTT speed = 0 kmh^{-1}, but velocity to get to the next point was ≥ 1 kmh^{-1}, which means while the PTT did not detect movement at the moment of connection with satellites, the bird had moved by the time another location was reported. There were also 1,756 cases (4% of data) where velocity to the next point was < 1 kmh^{-1}, but PTT speed was > 0 kmh^{-1}, which means the PTT detected movement at the moment of data transmission, but the next location implied the bird had not moved over time. PTTs may report no movement if 1) the bird is stationary (i.e., perched on a structure or on the ground), 2) the bird is hovering due to headwinds (i.e., the transmitter doesn't happen to detect movement), and 3) possibly when the bird is moving in tight circles within air thermals. Because PTTs might report no movement when the bird was actually flying, this may explain why PTT speed was more zero-inflated than velocity estimates. However, it is also possible that hawks perched for short periods more often during the daytime than between-point velocity can detect, due to our data-collection schedule (1 – 6 hours between points, depending on time of day). PTTs also may report movement if the bird is walking on the ground or along a perch. The conflict between datasets where PTTs reported no movement is easily reconciled, because a bird that was perched at one location could move to the next location between hourly data transmissions; if we had collected more locations per day, data would show less conflict in these types of cases. The opposite conflict, however, is more difficult to explain; how does a PTT report movement, but successive locations imply a stationary bird? Some proportion could have been moments where hawks were landing at a roost site (or some other perch), thus PTTs detected movement at the moment of connection with satellites, but locations did not change substantially by the next data transmission. A hawk might also leave a perch at the moment of data transmission, so the PTT detects movement, then return to the same perch or land on a new perch < 1 km away within the hour, thus resulting in no substantial change in distance between two reported locations. Additionally, while we do not know the error rate of PTT-reported speeds, location error influences velocity estimates, which may result in data conflicts that are not biologically relevant, such as a PTT reporting no movement, but velocity estimating small-distance movements from a stationary bird due to errors in trilateration or connection with satellites (e.g., signals bouncing off of nearby buildings and topography). We rounded distance and velocity data to the nearest km as an attempt to account for small-distance errors expected from the technology, but larger errors may have persisted.

The comparison between PTT speed and velocity also showed some interesting data conflicts at the higher ends of estimates; some of the highest speeds were reported where the velocity to the next point was low, and some higher velocities occurred after low and zero PTT-reported speeds. Again, PTT speed is an instantaneous measurement, and sink rate increases with airspeed (Kerlinger 1989), so it is possible for the transmitter to detect moments of high speed, such as the bird in a steep glide, even when the bird covers little distance over time. There is also the possibility that the bird returned to a previous location before the next point was recorded. High speeds at low vector velocities also support the possibility of undetected errors in PTT speed data. Importantly, trends in velocity data showed a more-consistent increase with higher PTT speeds than vice versa, suggesting vectors are the more-reliable measurement to describe bird travel speed with transmitter data. We therefore have more confidence in using vector data when describing flight behavior than the instantaneous speed reported by PTTs.

Following Fuller et al. (1998), we divided migration data into three temporal segments and found discordant results. Fuller et al. (1998) concluded that migration travel was fastest during the middle portion and explained that air thermals were likely stronger and more readily available throughout the equatorial region. Data we collected pointed towards the last segment being the portion of fastest travel for most measurements, but there was no apparent significant difference between segments. The differences between our results and those of Fuller et al. (1998) may be due to a temporal difference in environmental conditions, a difference in technology, a difference in hawks, with our sample coming from a portion of the breeding range not previously examined, and random chance combined with small sample sizes and high variability. Dividing migration by length of time placed the segments in varying geographic locations for our migration datasets, and we suggest geography and local conditions play a large role in speed of travel for obligate-soaring species. Therefore, we additionally examined migration speed by geographic segments (10° latitude bins, following the methods of Kochert et al. 2011), which revealed somewhat clearer patterns, though error bar overlap was still significant.

Swainson’s hawks in this study had a similar pattern of travel in both seasons, which appeared as inverse trends when data was plotted by latitude (Fig. 3.23). Hawks generally started out slow and moved to a fairly steady rate of travel through the first two thirds of the trip. Hawks sped up in Bolivia during fall travel (a pattern than correlated geographically with instances of extreme daily travel and high hourly speeds described above), then slowed down as they settled into nonbreeding areas in Argentina. During northward travel, hawks sped up through Central America and Mexico (which also correlated with days of extreme travel and high hourly speeds), and, again, slowed as they neared breeding territories. We did not find that rate of travel was faster through the equatorial region, again a departure from Fuller et al. (1998); if anything, that region was relatively equal with most of the migration pathway. If the pattern of faster travel was correlated with geographic position, principally Central America during spring migration (our most significant pattern), this may explain why the middle segment was considered fastest by Fuller et al. (1998); Swainson’s hawks migrating to locations such as western Canada may pass through that region during the ‘middle’ of their travel, whereas Swainson’s hawks aiming for Texas in this study passed that region during their last segment of travel, thus possibly reconciling our seemingly discordant results. However, we have no explanation for the middle segment being fastest during fall migration in the previous study (Fuller et al. 1998), as our data indicated that Bolivia may be the region of fastest travel, which should be traversed during the last portion for all migrating Swainson’s hawks that overwinter in Argentina. We also found higher average rates and a different trend from the results presented by Kochert et al. (2011), where previously studied hawks migrating southward appeared to travel fastest from Texas to Mexico (a region where we also found instances of high speeds), and the pattern indicated two peaks of travel rate towards the beginning (i.e., after leaving staging grounds in the southern breeding range) and end of migration. Additionally, Kochert et al. (2011) also did not find the fastest rates in the equatorial region, disagreeing with Fuller et al. (1998), and lending credence to our conclusions. As with the other study, differences between our study and the results presented by Kochert et al. (2011) were likely influenced by temporal variation, technology, capture location of hawks, low sample sizes, etc.

Stopping behaviors in this study showed almost the inverse pattern of travel rate, with high stop frequency and duration corresponding to regions of slower average travel, and vice versa, which agreed with the negative correlation we found between cumulative days stopped and travel rate. When we examined travel rate data with and without stop days included, the pattern was essentially the same, which means stopping behaviors were independent of whatever processes were driving seasonal latitude patterns.

If the entire migration pathway is selected for the availability of thermals for soaring flight, then minor differences in travel rate may be explained by random environmental factors (e.g., linear thermals and cloud streets may produce faster travel, while storm systems and crosswinds may slow birds down) that can affect a large number of birds at once, due to the mass migration behavior and annual differences in numbers of hawks tracked; those influences may also change seasonally and annually, thus producing different results among studies spread out across time. Although error bars overlapped enough to suggest no difference for most geographic segments of travel, there may be a trend of increasing travel rate towards the end of migration, specifically in Bolivia during fall migration and Central American during spring migration, that could have at least two causes: 1) hawks may behave differently (travel at a faster speed or for more hours per day) as they pass geographic markers that signal nearing the end of travel, a pattern that may have most significance during northward travel when birds are preparing to begin reproduction, or 2) hawks encountered wind conditions that permitted faster travel, such as increased thermal availability and tailwinds to propel hawks in the direction of travel (especially significant in Bolivia, as described above), and fewer barriers to travel, such as storms (Kerlinger 1989, Bildstein 2006). Additionally, the speed measurements we examined were influenced by individual behaviors and choices other than literal flight speed, which clouds our ability to determine clear patterns and explanations. For example, hawks may spend more time resting and stopping over during the first leg of the trip, because they are still building fat stores and looking for flocks to join, while they may choose to rest less frequently throughout the middle of travel; if flight speed and thermal availability were equivalent across the whole trip, the location data may still show patterns of slower and faster travel due to the confounding behaviors of staging and stopping over. It is therefore difficult to draw strong conclusions, as the data can easily be interpreted as showing no real trend during fall migration and only perhaps a trend of faster travel for spring migration, due to error bar overlap. Because of the variability of data and potential confounding factors in this study, as well as discrepancies with previous transmitter research, we finally concluded that 1) hawks likely travel at generally the same rate across the entire migration pathway (supported by error bar overlap and our inability to detect a seasonal difference if we removed stop days from analysis), 2) there is likely a real pattern of slower travel at the beginning and end of migration due to staging and stopover behaviors, and 3) hawks may encounter seasonally optimal travel conditions in the 10 - 20°N and S latitude ranges, but those conditions likely have annual variability that resulted in some studies finding faster travel and others failing to find that pattern due to the random years hawks were tracked.

Last, while many observations have indicated the possibility of migration behavioral differences between the sexes in raptors (e.g., Harmata 1984, Stotz and Goodrich 1989, Kjellén 1992, Mueller et al. 2000, Bildstein 2006), we found no such differences for Swainson’s hawks in migration timing, pathway, pace of travel, stopping behaviors, or final destinations. The only minor signal found in models showed that females might fly slightly faster than males, which may be related to the larger female body size or some minor differences in flight capabilities or behaviors, but the difference (1 kmh^{-1}) was too negligible to indicate any biological significance for explaining migratory patterns. It is possible that we did not correctly determine the sex of all captured hawks, as our best confirmation came from observing nesting behaviors, and some hawks were captured away from nests or may have been nonbreeding or transient birds (i.e., we relied on mass of the bird instead, but sexes are known to overlap; Kochert and Mckinley 2008). However, Kochert et al. (2011), Campbell and Inzunza (2017), and Airola et al. (2019) additionally looked for migration differences among sexes and age classes, and also found no significant patterns, thus our results support the conclusion that all Swainson’s hawks likely behave similarly during migration (but see Chapter 5 for possible differences among inexperienced hatch-year Swainson’s hawks). The lack of differences is most likely driven by the mass migration behavior, where hawks rely upon migrating in large flocks for travel efficiency and to stay on track, thus negating any selection that might drive sexes or ages to act differently during this important period (Kerlinger 1989, Bildstein 2006).

Conclusion

Our descriptions of migration characteristics build a more-complete picture of how Swainson's hawks survive and succeed at long-distance migration. Overall, this study supports the data and conclusions of previous researchers; discrepancies can mostly be explained by differences in where hawks were captured, differences in wintering locations, temporal differences in environmental conditions during migration, and differences in the technology used, and thus the quality and quantity of data analyzed (Fuller et al. 1998, Kochert et al. 2011, Airola et al. 2019). Importantly, discrepancies add to our understanding of the variability in behaviors and plasticity among migrating hawks. Terrestrial migration allows for thermal soaring, nightly resting, and possibly opportunistic foraging en route, which contribute to migration success (Kerlinger 1989, Bildstein 2006). Daily travel ranged from no movement to > 800 km traveled per day, with patterns that may signal topographic and weather influences in addition to decisions made by individuals. Flight speed ranged from stationary to > 100 kmh^{-1} and supported a strong pattern of diurnal travel; high speeds showed strong geographic patterns, such as hawks encountering high wind speeds when they skirt around the Andes Mountains in Bolivia (Safi et al. 2013). We found that spring migration was generally traveled faster than fall migration, which may indicate a sense of urgency to return to the breeding range (e.g., competition for mates and nesting territories), but also may have a random environmental cause, as previous research did not always find the same results (Fuller et al. 1998, Kochert et al. 2011); when we removed stopping behaviors from analysis, mean daily travel was identical across seasons, implying that stopping influences seasonal differences more than flight speed. Staging (i.e., stopping to put on fat and joining flocks) may be essential to fall survival and migration success, and facultative en-route stopovers may be explained by poor weather conditions and, possibly, opportunities for resting and foraging (Kerlinger 1989, Kirkley 1991, Bildstein 2006, Warnock 2010). Finally, our descriptions and explanations may be broadly applied to many species of soaring migratory raptors, especially those that share migration pathways and bottlenecks with Swainson’s hawks, such as Mississippi kites, broad-winged hawks, and turkey vultures (Parker 1999, Haines et al. 2003, Dodge et al. 2014). We additionally suggest that while plasticity in specific routes likely allows raptor survival during migration, bottlenecks, such as the Oaxaca region of Mexico and others identified in Central America, may be regions of conservation importance for these and many other migratory species.

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Tables

Table 3.1. PTT information for adult Swainson's hawks captured in the High Plains of Texas in 2012 and 2013. End dates represent date of last known locations, excluding redundant post-mortality data. Two PTTs (hawks A5 and A16) were still reporting data when we stopped tracking birds and we confirmed 2 hawks (A9 and A14) were alive after transmitters stopped reporting data. We confirmed the mortality of 2 hawks by locating carcasses. All other birds were presumed dead after the end date. Number of migrations indicates how much data from each bird was used in analyses.

Hawk number	PTT number	Sex	PTT deployment date	End date	Length of data collection (days)	Number fall migrations	Number spring migrations
A1	115937	Male	11 May 2012	27 Apr 2013	351	1	1
A2	115938	Female	11 May 2012	12 May 2014	731	2	2
A3	115939	Male	14 May 2012	12 Nov 2013	547	2	1
A4	115940	Male	14 May 2012	20 May 2014	736	2	2
A5	120328	Male	2 July 2012	1 Sept 2017 *	1,887	5	5
A6	120329	Female	3 July 2012	12 July 2015	1,104	3	3
A7	120330	Female	4 July 2012	9 Oct 2013	462	1	1
A8	120331	Female	9 July 2012	18 July 2015	1,104	3	3
A9	120332	Male	10 July 2012	25 Apr 2015 *	1,019	3	3
A10	120333	Male	11 July 2012	24 Apr 2013	287	1	1
A11	120334	Male	12 July 2012	14 June 2014	702	2	2
A12	120335	Male	20 July 2012	30 Jan 2014	559	2	1
A13	122081	Male	18 June 2013	10 Dec 2013	175	1	0
A14	122082	Female	27 June 2013	21 Apr 2015 *	663	2	2
A15	122083	Female	29 June 2013	17 July 2013 #	18	0	0
A16	122084	Female	1 July 2013	2 Sept 2017 *	1,524	4	4
A17	122085	Male	2 July 2013	19 Dec 2013	170	1	0
A18	122086	Male	3 July 2013	23 Jan 2014	204	1	0
A19	122087	Female	3 July 2013	29 June 2016	1,092	3	3
A20	122088	Female	10 July 2013	15 May 2014	309	1	1

Table 3.1. Continued.

Hawk number	PTT number	Sex	PTT deployment date	End date	Length of data collection (days)	Number fall migrations	Number spring migrations
A21	122089	Male	10 July 2013	9 July 2014 #	364	1	1
A22	122090	Female	10 July 2013	28 June 2017	1,449	4	4
A23	122091	Male	18 July 2013	14 May 2015	665	2	2
A24	122092	Male	29 July 2013	18 Apr 2015	628	2	2

* Bird was known to be alive when we stopped receiving data.

\# We confirmed bird mortality.

Table 3.2. Correlation matrix comparing fall (southward) or spring (northward) migration start and end dates with each other and with number of days birds spent migrating (duration). Boxes surround correlations we considered significant (r ≥ 0.7 or ≤ -0.7). Data obtained from 23 Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

	Fall start date	Fall end date	Spring start date	Spring end date	Fall/spring duration
Fall start date	1	-0.04	-	-	-0.67
Fall end date		1	-	-	0.78
Spring start date			1	0.81	-0.05
Spring end date				1	0.55
Fall/spring duration					1

Table 3.3. Results of exploratory analyses of variance, including degrees of freedom (df), F-statistic (F) and P-value (P). Mean difference is the difference between means (or grand means) when a variable was significant at alpha = 0.05; for variables that had more than two groups, we provided the difference between the highest and lowest group means. Effect size was estimated using Hedge's *g*, with larger effect sizes suggesting stronger differences between groups.

Response variable	Explanatory variables	df	F	P	Mean Difference	Effect Size
Duration	Season	1	9.301	0.003	8 days	0.71
	Sex	1	0.290	0.592	-	-
	Residual	83				
Cumulative Distance	Season	1	24.133	< 0.001	582 km	1.07
	Sex	1	0.132	0.718	-	-
	Residual	82				
Direct Distance	Season	1	3.860	0.053	-	-
	Sex	1	0.000	0.992	-	-
	Residual	82				
Daily Travel Rate	Season	1	24.518	< 0.001	13 km per day	0.10
	Sex	1	1.784	0.182	-	-
	Duration Segment	1	44.870	< 0.001	38 km per day	0.25
	Latitude Segment	1	11.860	< 0.001	219 km per day	1.48
	Residual	4,188				
Mean Daily Travel Rate	Season	1	1.376	0.244	-	-
	Sex	1	0.207	0.651	-	-
	Residual	90				

Source: Chapter 2.

Table 3.3. Continued.

Response variable	Explanatory variable	df	F	P	Mean Difference	Effect Size
PTT Speed	Season	1	23.097	< 0.001	1 kmh^{-1}	0.07
	Sex	1	29.326	< 0.001	1 kmh^{-1}	0.07
	Duration Segment	1	0.005	0.946	-	-
	Latitude Segment	1	7.684	0.006	4 kmh^{-1}	0.39
	Residual	20,050				
Mean PTT Speed	Season	1	10.552	0.002	1 kmh^{-1}	0.31
	Sex	1	3.049	0.084	-	-
	Residual	90				
Between-point Velocity	Season	1	0.093	0.761	-	-
	Sex	1	8.654	0.003	1 kmh^{-1}	0.05
	Duration Segment	1	23.867	< 0.001	4 kmh^{-1}	0.21
	Latitude Segment	1	0.062	0.803	-	-
	Residual	23,343				
Mean Between-point Velocity	Season	1	0.852	0.358	-	-
	Sex	1	2.999	0.087	-	-
	Residual	90				
Number of Stops	Season	1	1.162	0.284	-	-
	Sex	1	0.345	0.558	-	-
	Residual	90				
Cumulative Stop Duration	Season	1	6.684	0.011	4 days	0.55
	Sex	1	1.134	0.290	-	-
	Residual	90				

Table 3.3. Continued.

Response variable	Explanatory variable	df	F	P	Mean Difference	Effect Size
Fall Start Date	Sex	1	0.500	0.485	-	-
	Did hawk nest?	1	0.179	0.675	-	-
	Success?	1	0.436	0.514	-	-
	Residual	29				
Fall End Date	Sex	1	1.871	0.181	-	-
	Did hawk nest?	1	0.657	0.424	-	-
	Success?	1	3.937	0.056	-	-
	Residual	32				
Fall Duration	Did hawk nest?	1	0.840	0.367	-	-
	Success?	1	4.257	0.048	14 days	1.08
	Residual	30				
Fall Mean Daily Travel Rate	Did hawk nest?	1	1.092	0.304	-	-
	Success?	1	4.603	0.039	37 km per day	1.13
	Residual	33				
Fall Number Stops	Did hawk nest?	1	0.696	0.410	-	-
	Success?	1	4.262	0.047	2 stops	1.11
	Residual	33				
Fall Cumulative Stop Duration	Did hawk nest?	1	0.670	0.419	-	-
	Success?	1	2.803	0.104	-	-
	Residual	33				

Table 3.3. Continued.

Response variable	Explanatory variable	df	F	P	Mean Difference	Effect Size
Spring Start Date	Sex	1	1.272	0.268	-	-
	Did hawk nest?	1	0.462	0.501	-	-
	Success?	1	0.030	0.864	-	-
	Residual	33				
Spring End Date	Sex	1	0.303	0.586	-	-
	Did hawk nest?	1	3.658	0.065	-	-
	Success?	1	1.074	0.308	-	-
	Residual	33				
Spring Duration	Did hawk nest?	1	5.588	0.024	5 days	0.88
	Success?	1	2.472	0.125	-	-
	Residual	34				
Spring Mean Daily Travel Rate	Did hawk nest?	1	9.540	0.004	16 km per day	0.75
	Success?	1	6.702	0.014	32 km per day	0.54
	Residual	34				
Spring Number Stops	Did hawk nest?	1	0.673	0.418	-	-
	Success?	1	0.885	0.354	-	-
	Residual	34				
Spring Cumulative Stop Duration	Did hawk nest?	1	1.760	0.194	-	-
	Success?	1	0.222	0.641	-	-
	Residual	34				

Table 3.4. Correlation matrix comparing number days birds spent migrating (Dur), cumulative distance traveled (CD), direct distance between starting and ending locations (DD), mean daily travel rate (km per day, DTR), mean speed at moment of data transmission (kmh^{-1}, Spe), mean between-point velocity (kmh^{-1}, Vel), number of times bird stopped (Stop), cumulative stop duration (number days, CSD). Boxes surround correlations we considered significant ($r \geq 0.7$ or ≤ -0.7). Data obtained from 23 Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

	Dur	CD	DD	DTR	Spe	Vel	Stop	CSD
Dur	1	0.67	0.17	-0.90	-0.35	-0.80	0.75	0.90
CD		1	0.61	-0.41	-0.10	-0.37	0.51	0.60
DD			1	0.02	-0.07	-0.04	0.10	0.07
DTR				1	0.41	0.86	-0.70	-0.76
Spe					1	0.43	-0.35	-0.27
Vel						1	-0.63	-0.68
Stop							1	0.77
CSD								1

Figures

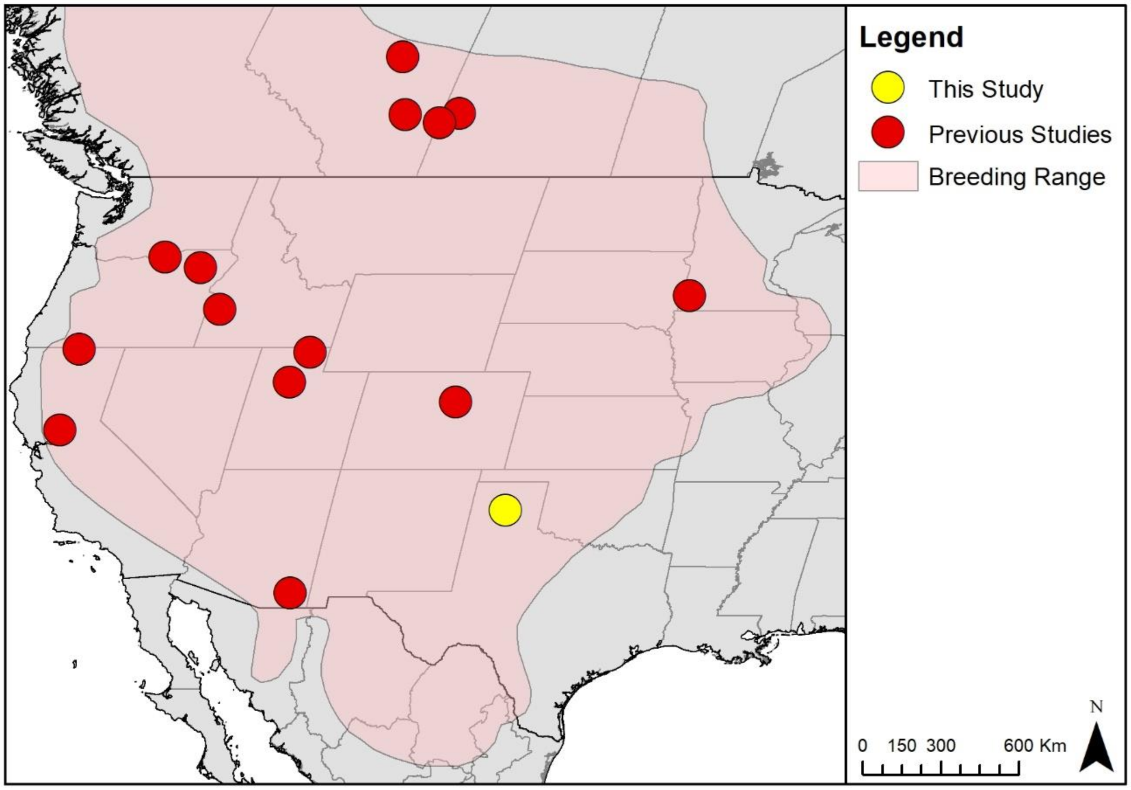

Figure 3.1. Capture locations of Swainson's hawks tagged with satellite transmitters in this study compared to previous studies.
Adapted from: Bechard et al. (2010), Kochert et al. (2011), Airola et al. (2019).

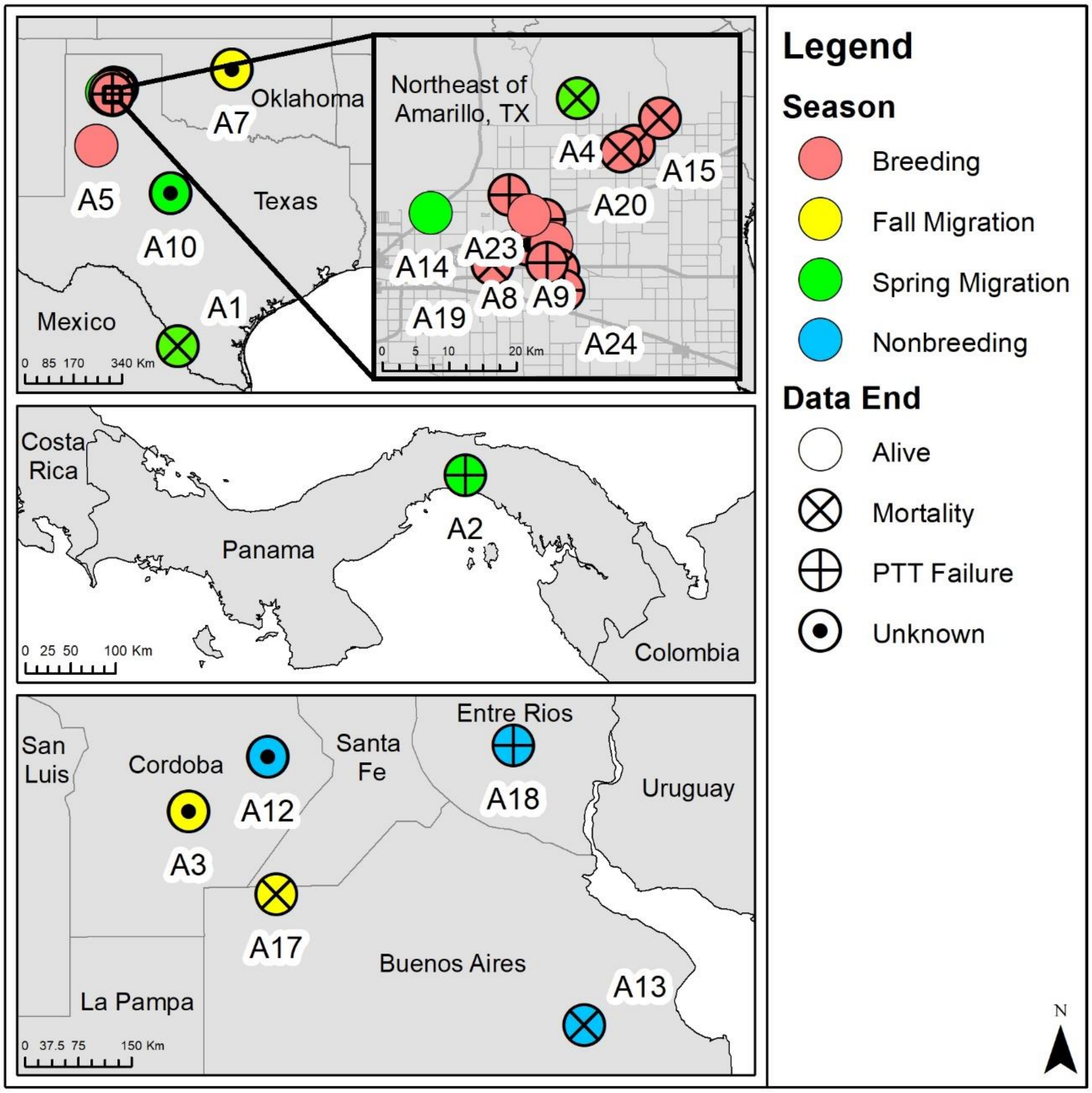

Figure 3.2. Last locations of adult Swainson's hawks wearing GPS transmitters from 2012 – 2017. Fall season is southward (outbound) migration and spring season is northward (return) migration. 'Alive' represents situations where birds were confirmed to still be alive after we stopped receiving data. 'Mortality' represents situations where we found carcasses or transmitters sent many points from the same location until batteries ran out (which also may indicate attachment failure rather than mortality). 'PTT failure' represents situations where transmitters were sending scarce data until data stopped coming in, but locations indicated bird may have been alive at data end. 'Unknown' fate represents situations where transmissions suddenly ended, presumably because of bird death and transmitter damage or destruction.
Source: Texas Natural Resources Information System, <https://tnris.org>.

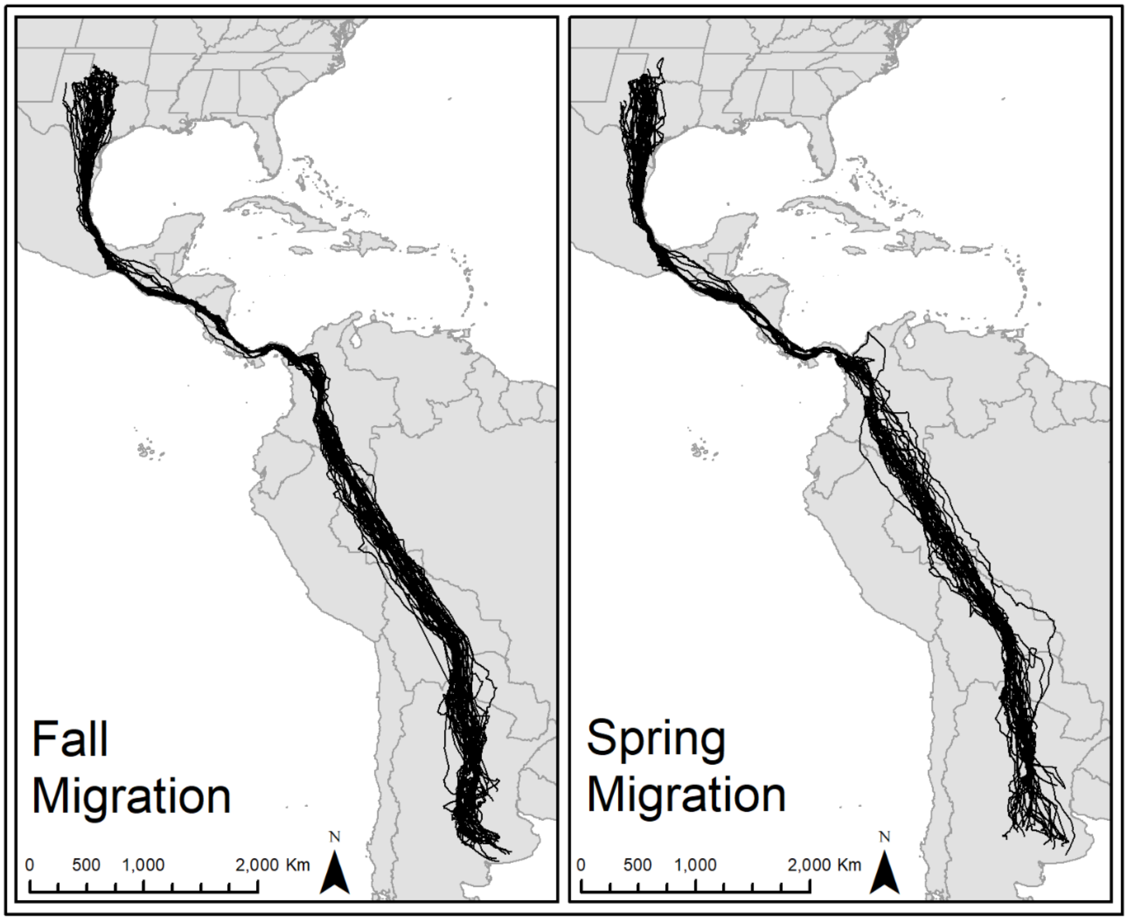

Figure 3.3. Fall (southward) and spring (northward) migration data recorded by satellite transmitters on adult Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

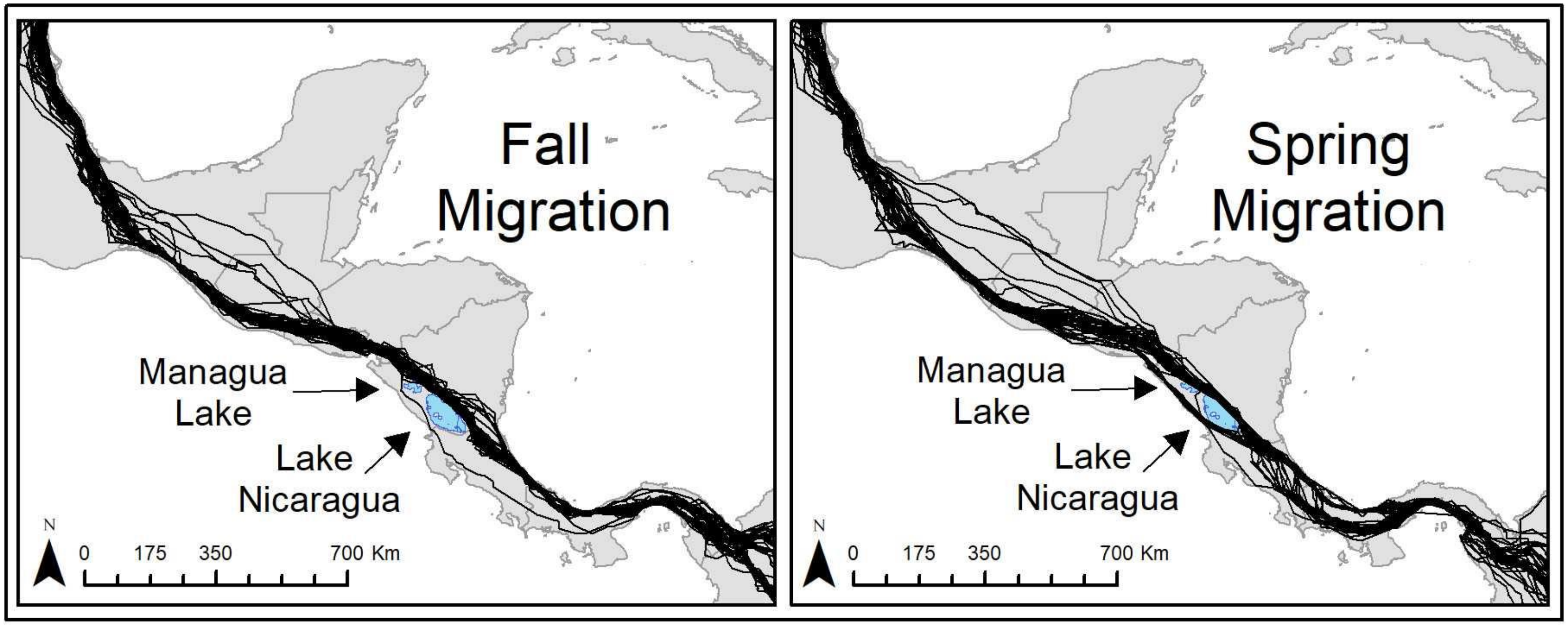

Figure 3.4. Migration routes through Central America for Swainson’s hawks wearing satellite transmitters from 2012 to 2017. Hawks avoided crossing two large lakes in Nicaragua and had variable routes throughout this region.
Source: Berkeley Library Geodata, University of California, <https://geodata.lib.berkeley.edu>.

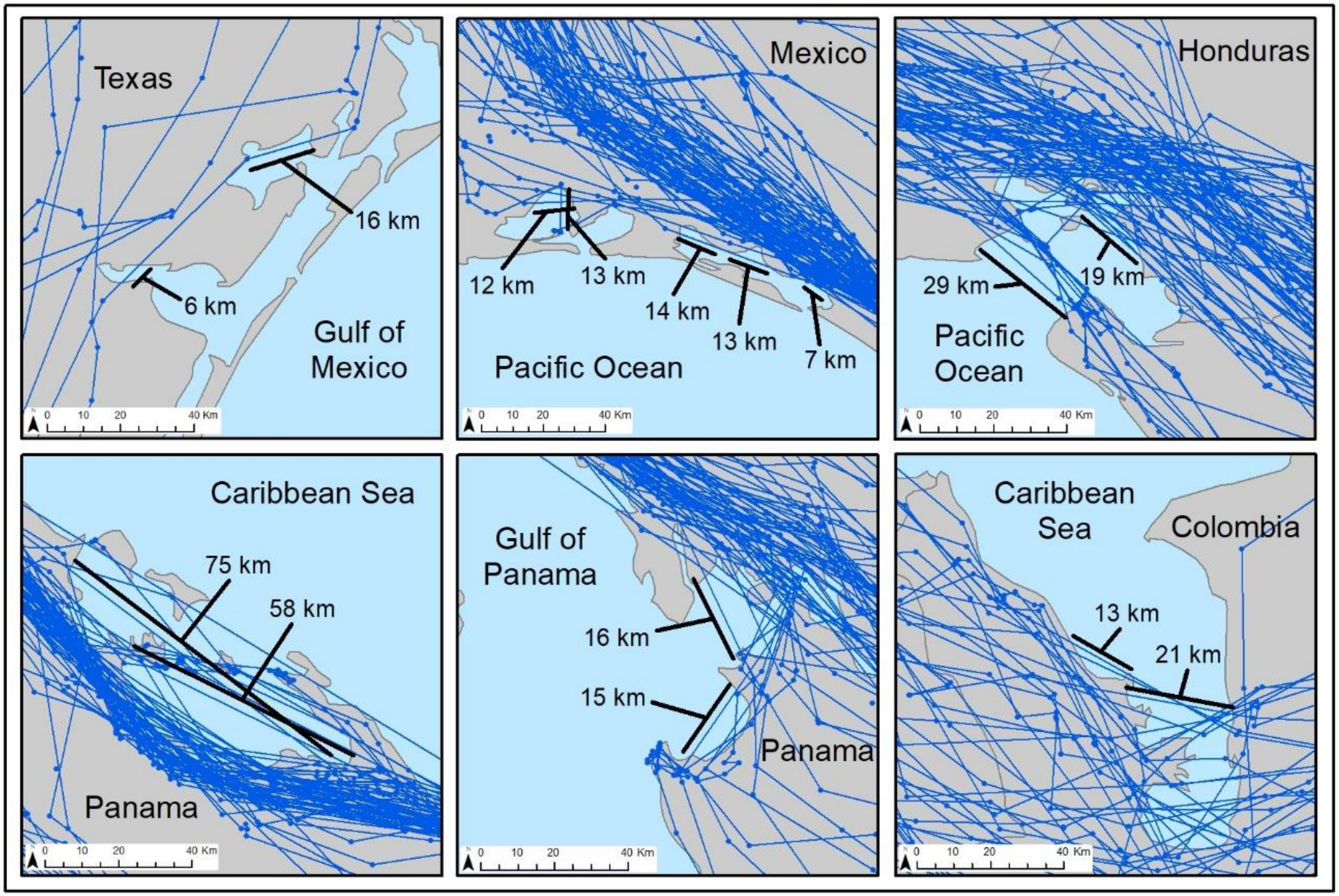

Figure 3.5. Swainson's hawk migration routes that indicated birds may have crossed over open water, with longest distances possibly traveled listed. Data obtained from adult Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

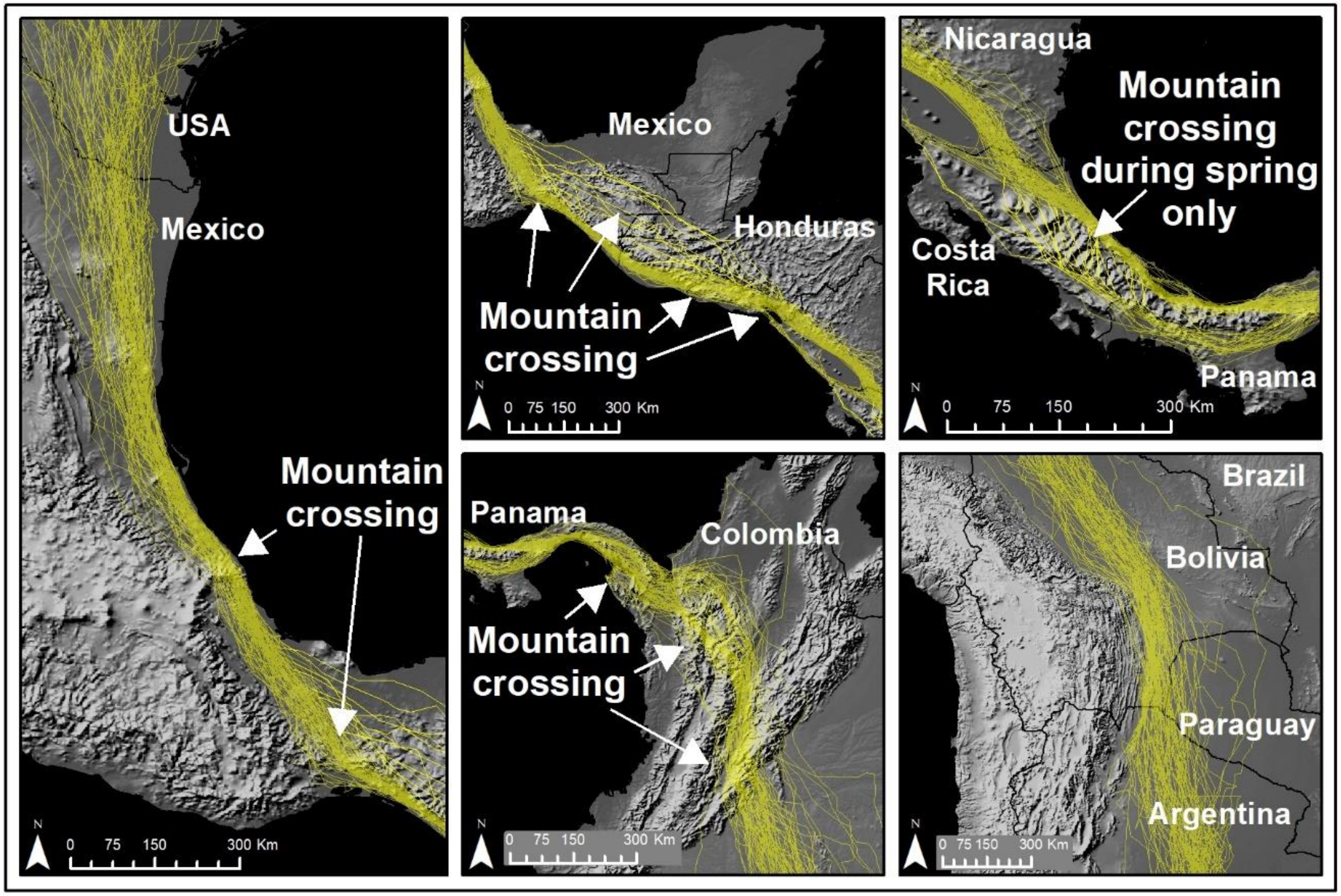

Figure 3.6. Swainson’s hawk migration routes against a shaded relief map to highlight where birds made mountain crossings and where mountains were avoided. ‘Spring’ refers to northward migration. Data obtained from adult Swainson’s hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.
Source: Natural Earth < https://www.naturalearthdata.com>.

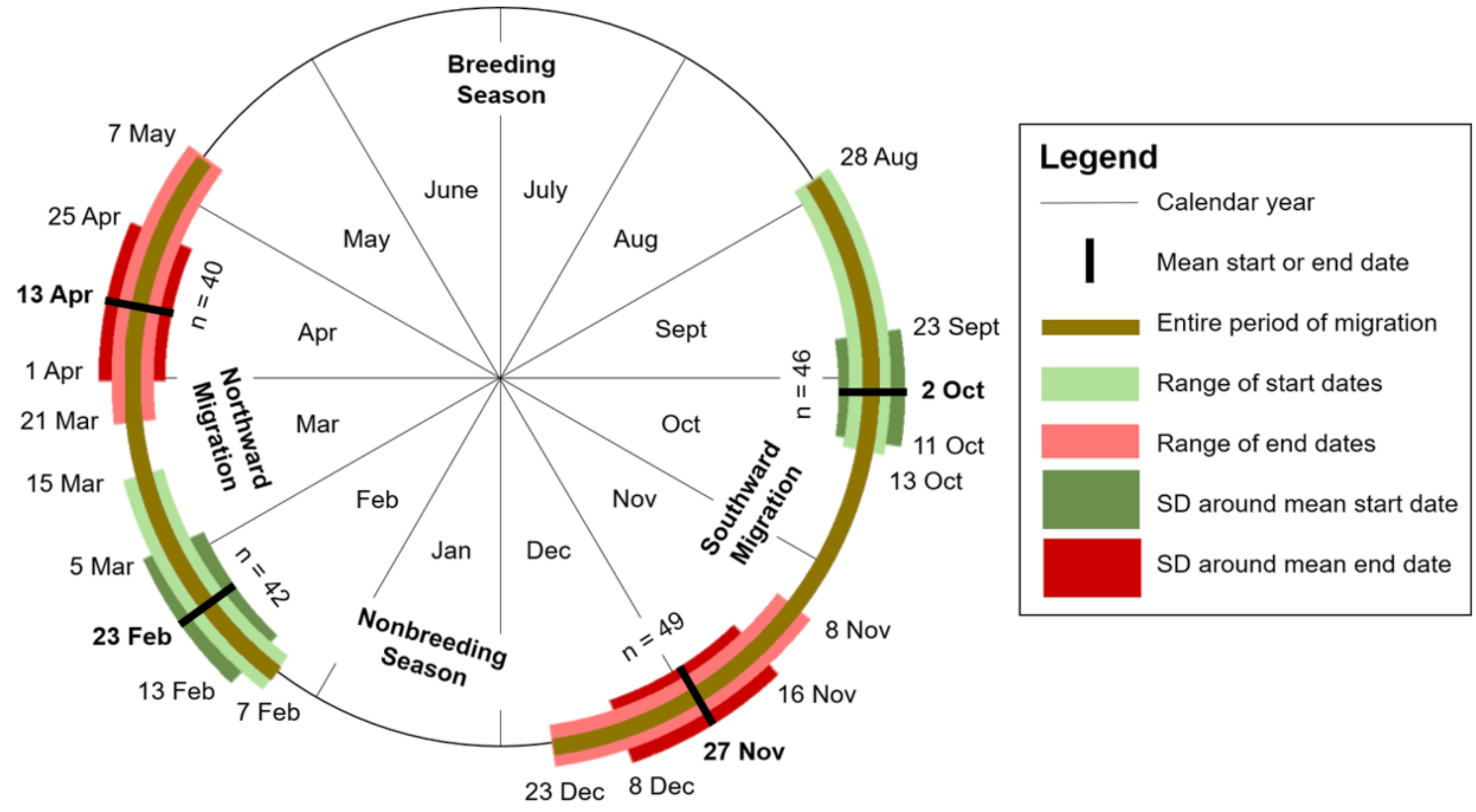

Figure 3.7. Summary of Swainson’s hawk migration dates, including mean (bold) start and end dates, standard deviation (SD), range, and sample size (n). Data obtained from adult Swainson’s hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

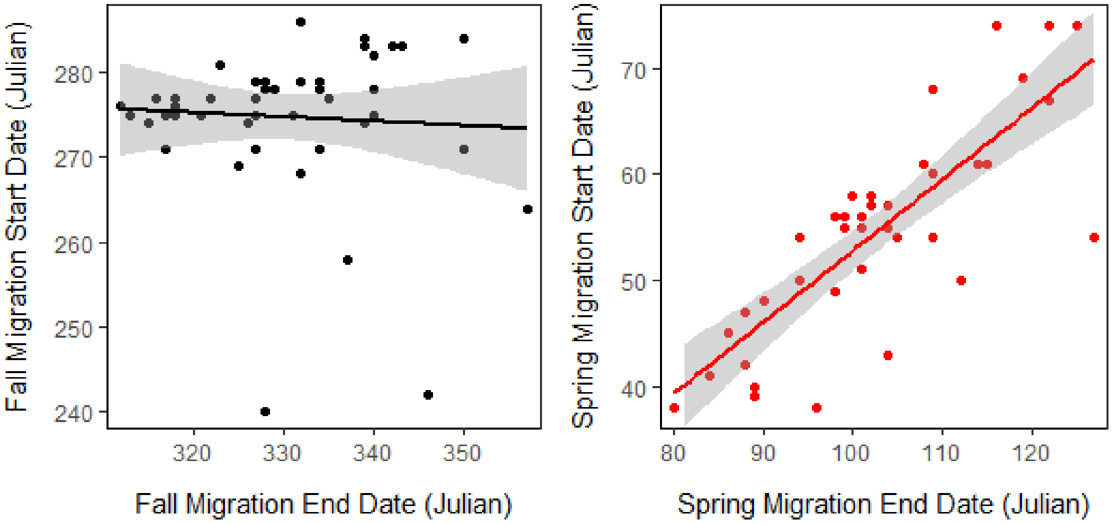

Figure 3.8. Comparison of start and end dates for fall (southward) and spring (northward) migration. Grey bars indicate 95% confidence intervals along regression lines. Data obtained from adult Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

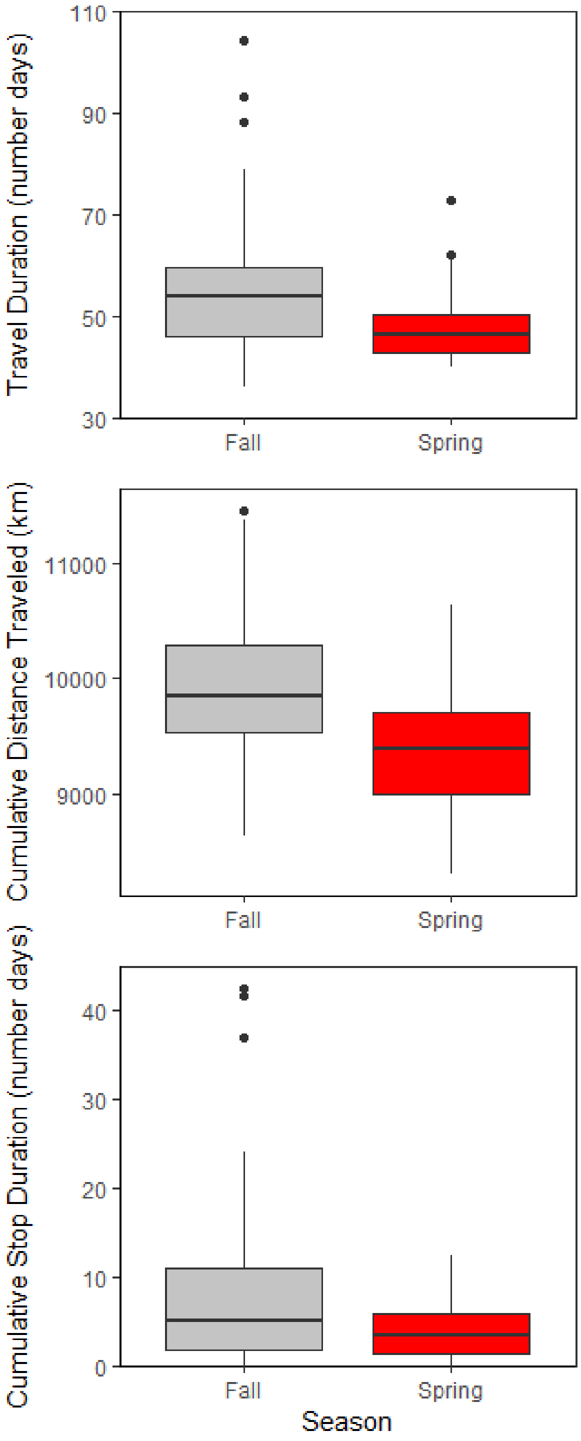

Figure 3.9. Travel duration (number days), cumulative distance traveled (km), and cumulative stop duration (total number days stopped) by season of migration (fall = southward and spring = northward migration). Data obtained from adult Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

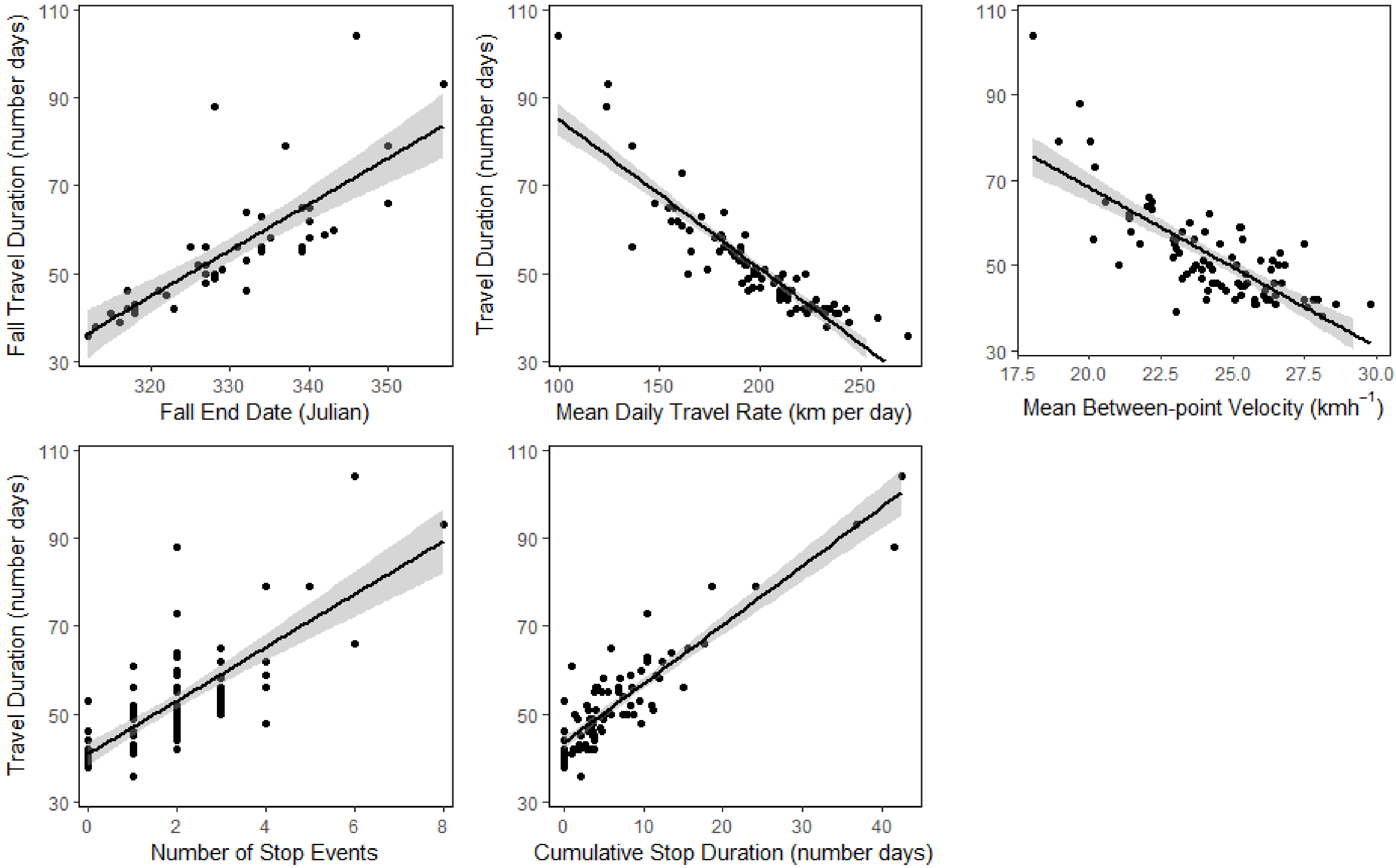

Figure 3.10. Five migration variables that correlated (r ≥ 0.7 or ≤ -0.7) with travel duration (number days birds were migrating). Grey bars indicate 95% confidence intervals along regression lines. Data obtained from adult Swainson’s hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

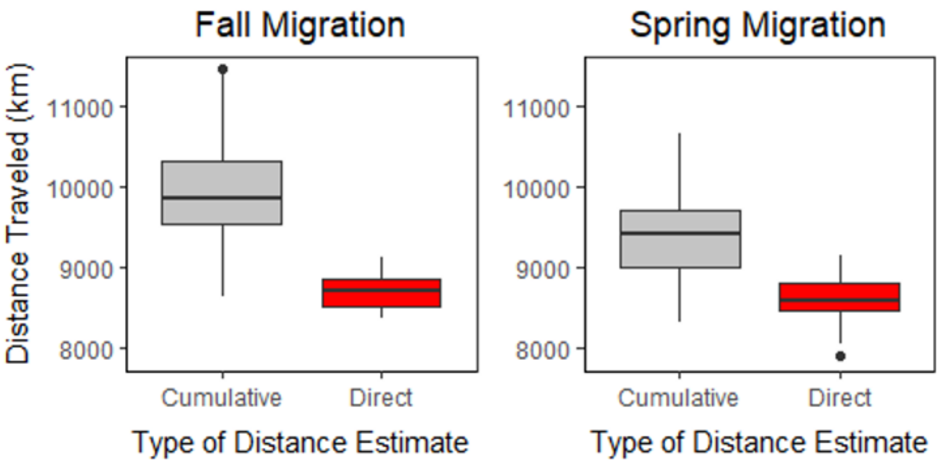

Figure 3.11. Comparison of cumulative distance traveled (sum of vectors between daily roosting locations) and direct distance (distance between starting and ending locations) for fall (southward) and spring (northward) migrations. Data obtained from adult Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

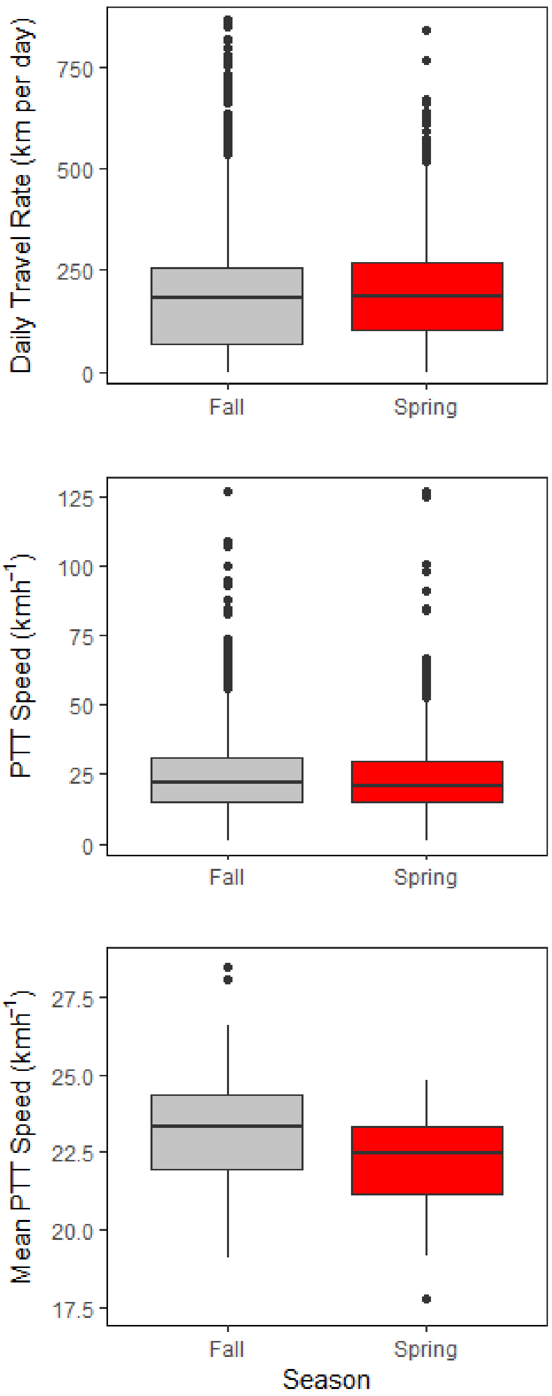

Figure 3.12. Daily travel rate (km per day), speed reported by transmitters (PTT speed, kmh^{-1}), and average PTT speed (kmh^{-1}) per migration compared by season (fall = southward migration and spring = northward migration). Data obtained from adult Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

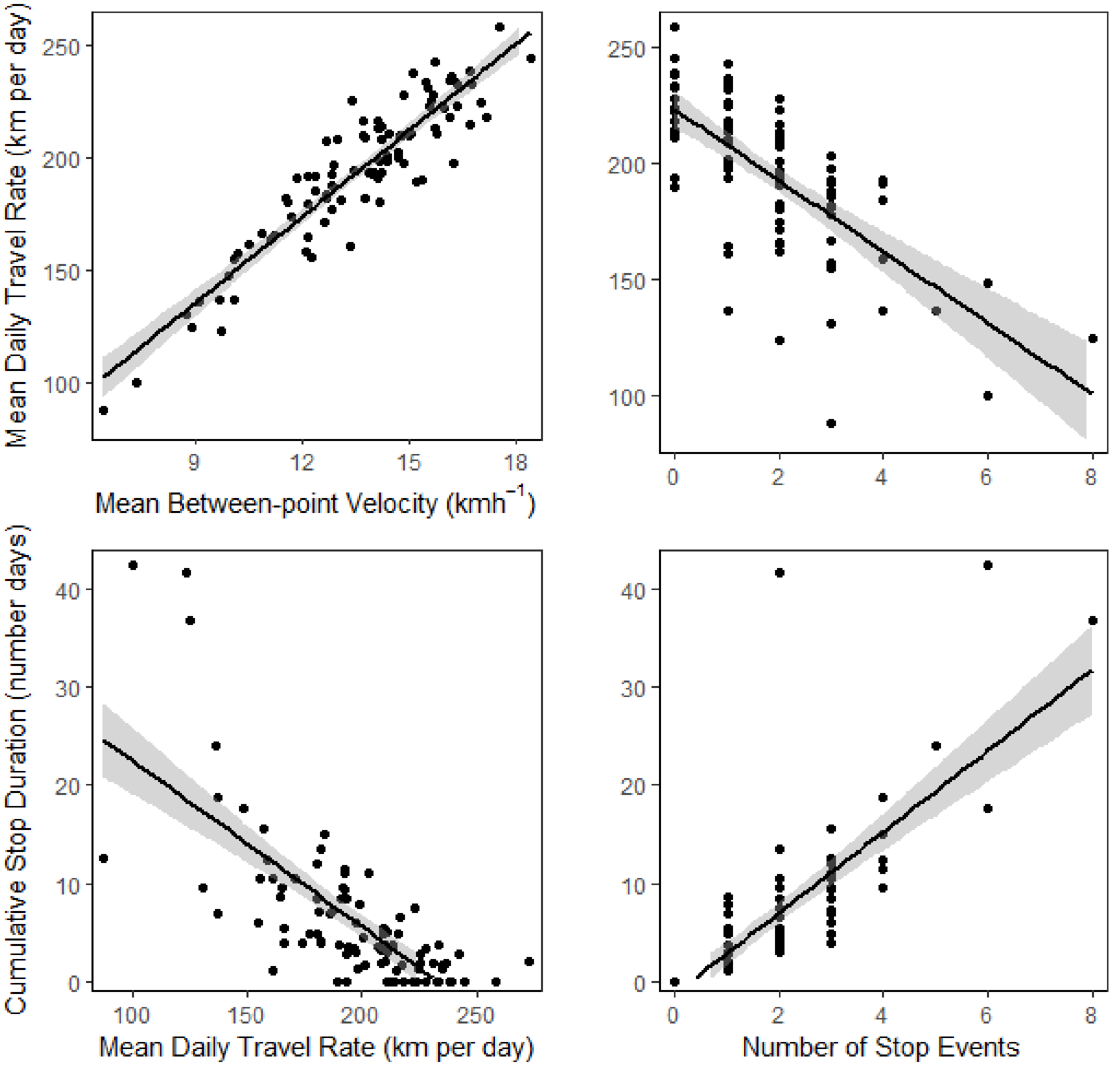

Figure 3.13. Four significant correlations (r ≥ 0.7 or ≤ -0.7) among migration variables. Grey bars indicate 95% confidence intervals along regression lines. Data obtained from adult Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

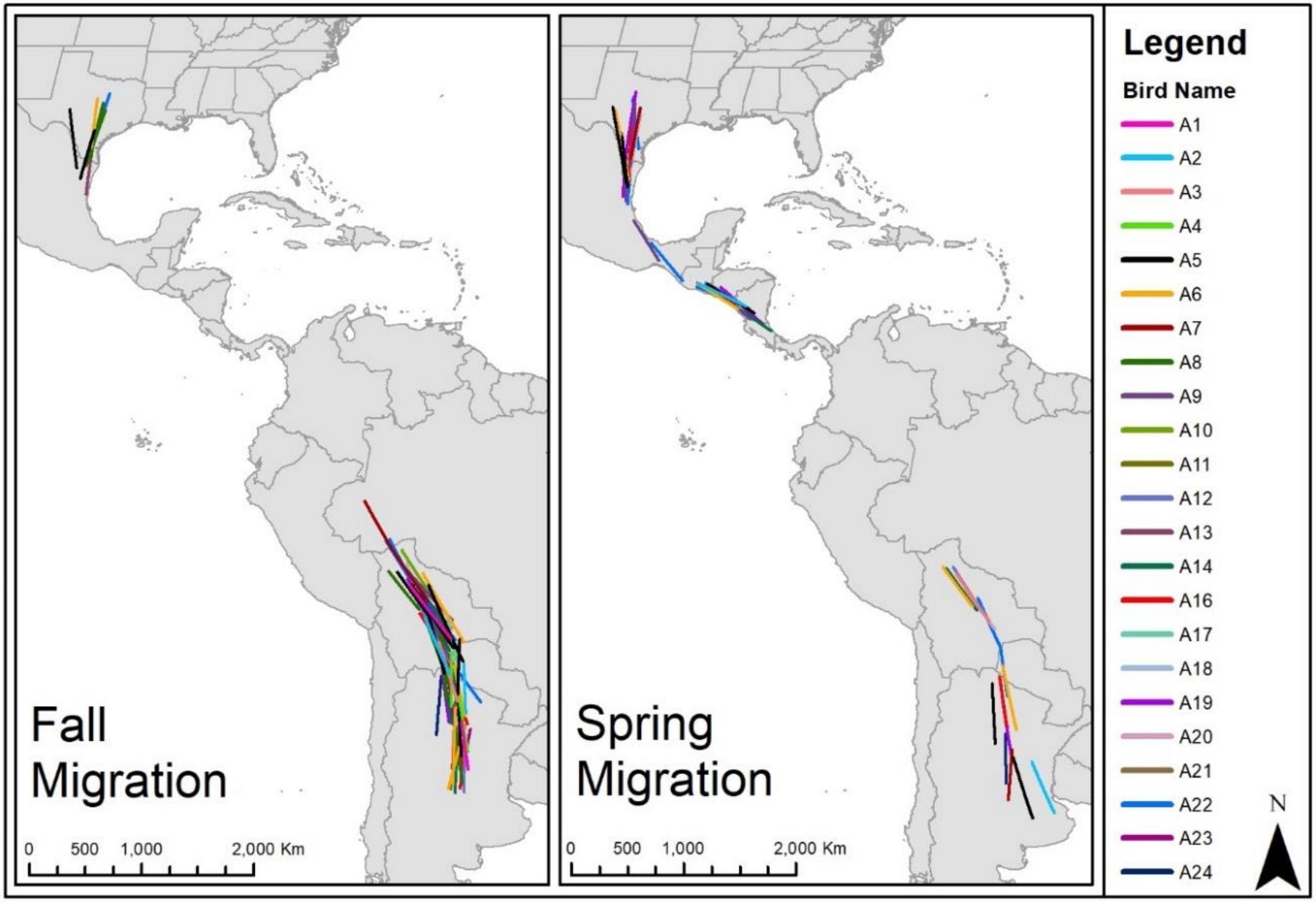

Figure 3.14. Locations where daily travel rate (distance the bird traveled per day) during fall (southward) and spring (northward) migration exceeded 500 km per day. Data obtained from adult Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

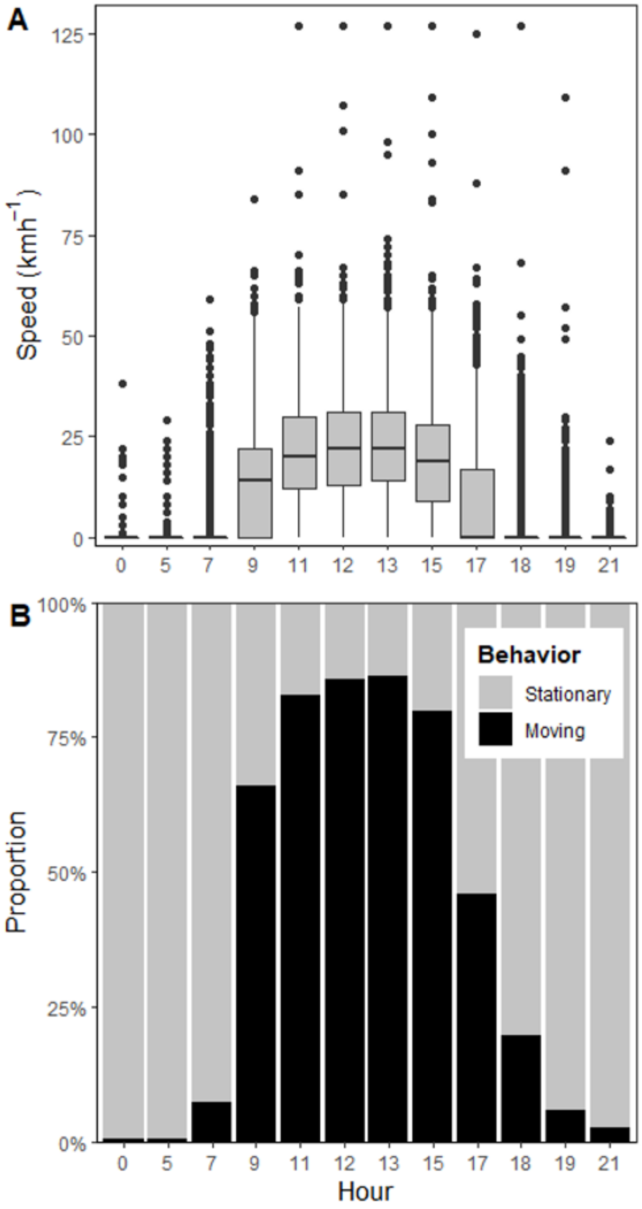

Figure 3.15. (A) All PTT speed data reported by transmitters worn by adult Swainson's hawks from 2012 to 2017 and (B) proportion of points that reported moving (speed > 0 kmh^{-1}) or stationary (speed = 0 kmh^{-1}) behaviors over time (hour of data transmission).

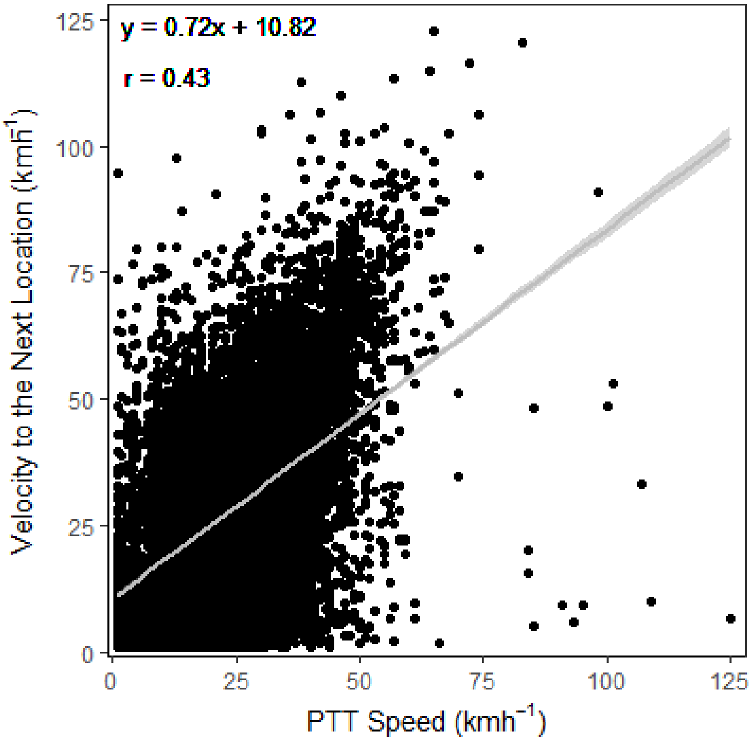

Figure 3.16. Transmitter (PTT) speed reported at the moment of satellite acquisition compared to velocity measured as the distance to the next location by elapsed time with a regression line (grey bar). Data obtained from adult Swainson’s hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

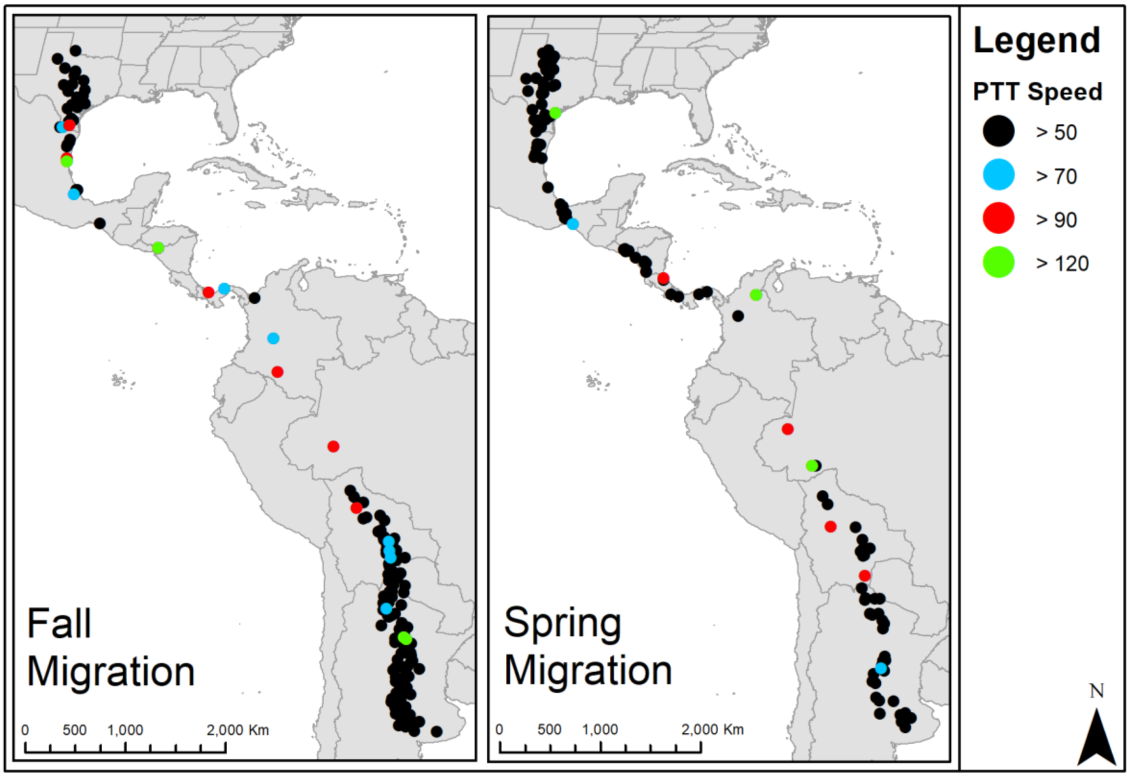

Figure 3.17. Locations of speeds reported by transmitters at the moment of data transmission that were > 50 kmh^{-1}, > 70 kmh^{-1}, >90 kmh^{-1}, and > 120 kmh^{-1} across fall (southward) and spring (northward) migration data. Data obtained from adult Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

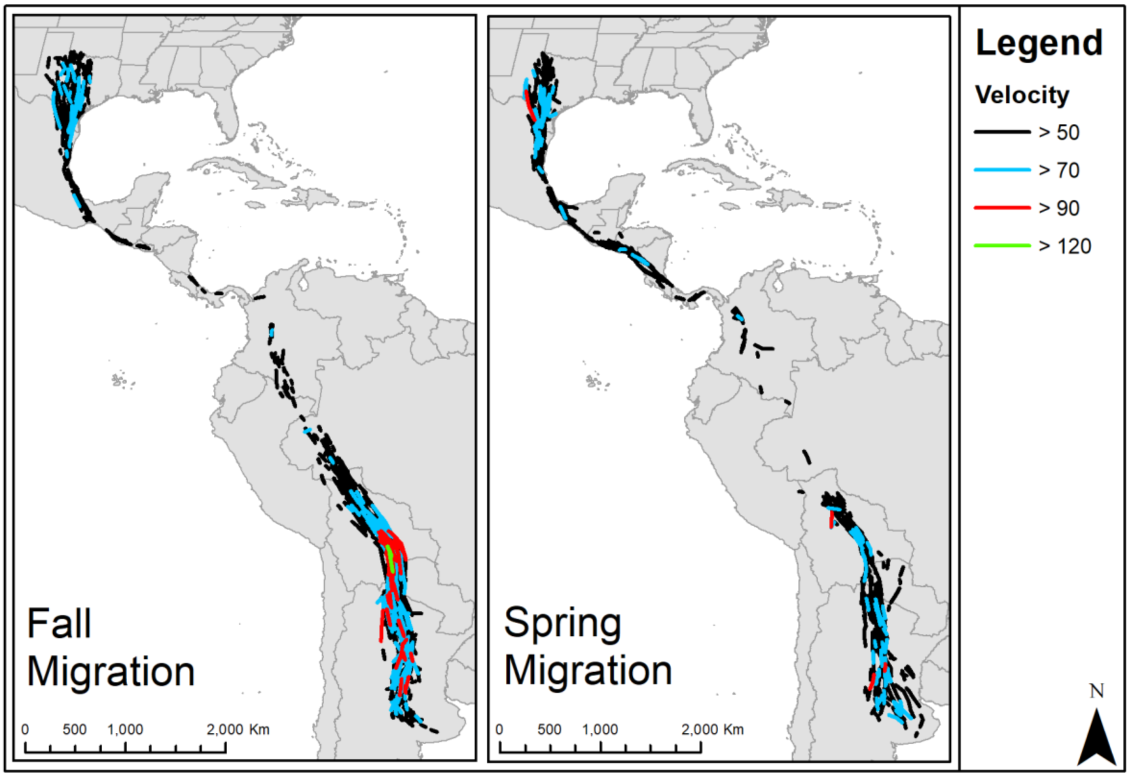

Figure 3.18. Locations of vectors with estimated velocities (distance between points / elapsed time) that were > 50 kmh^{-1}, > 70 kmh^{-1}, > 90 kmh^{-1}, and > 120 kmh^{-1} across fall (southward) and spring (northward) migration data. Data obtained from adult Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

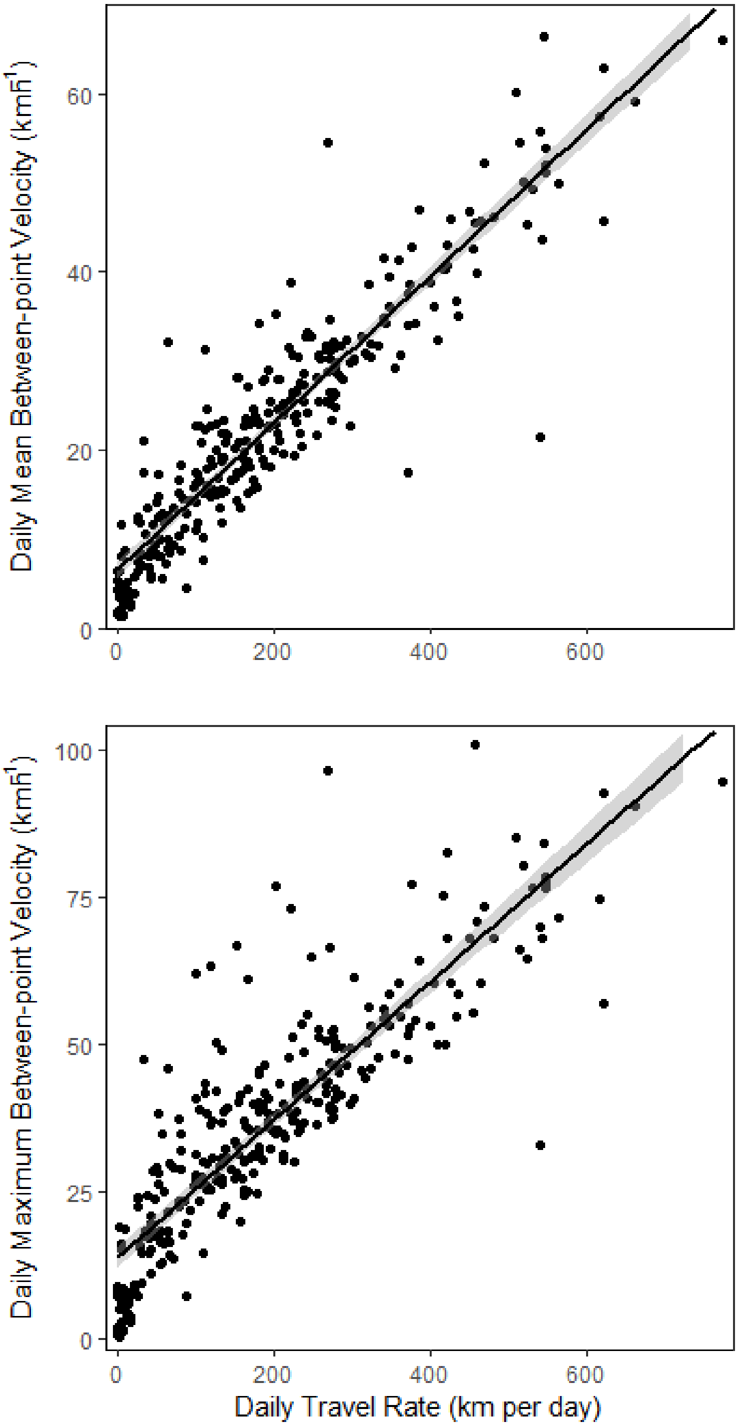

Figure 3.19. Daily average and maximum between-point velocities correlated with daily travel rate (distance bird moved per day during migration). Grey bars indicate 95% confidence intervals along regression lines. Data obtained from adult Swainson’s hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

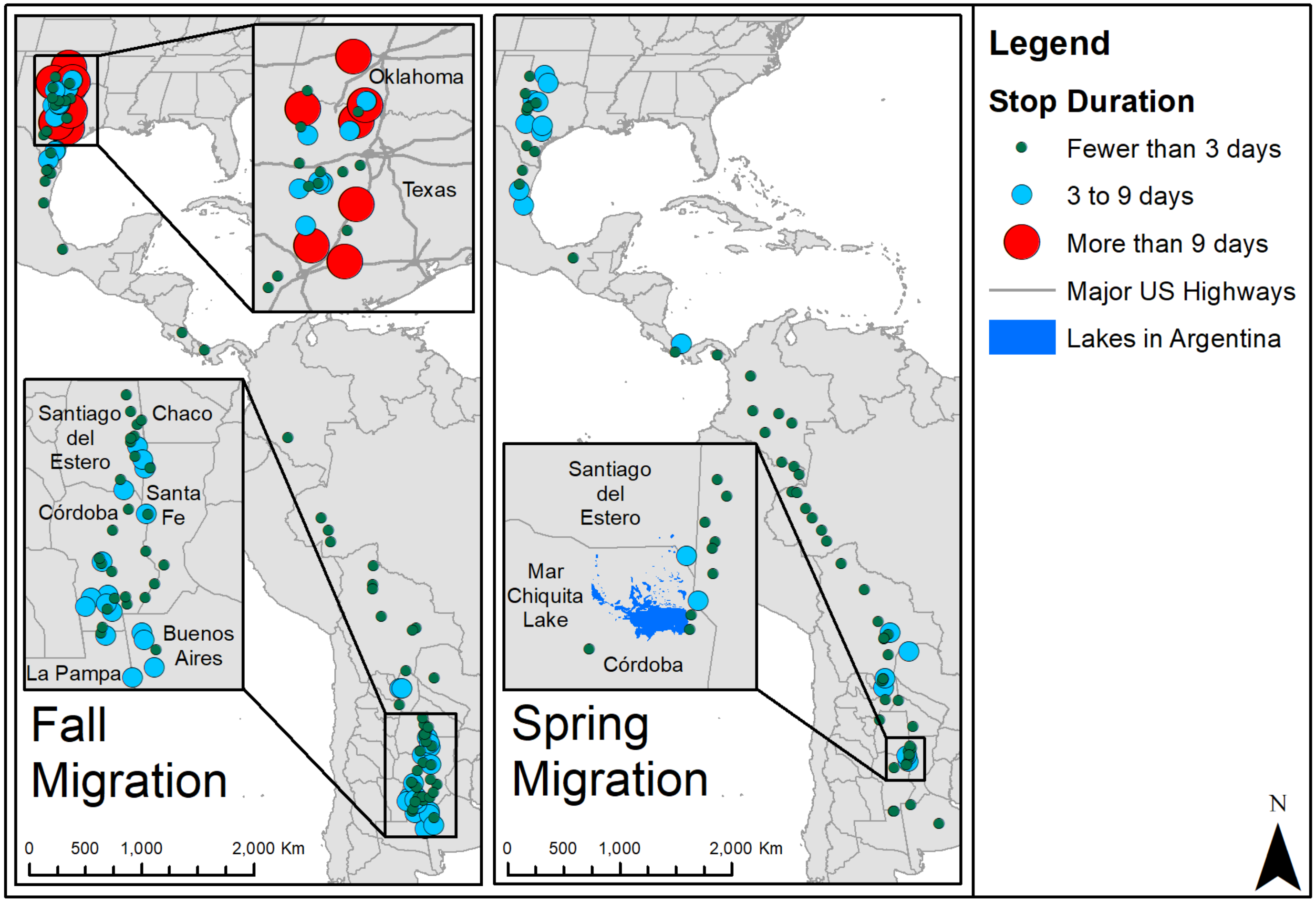

Figure 3.20. Stops made by migrating Swainson's hawks wearing satellite transmitters from 2012 to 2017. Points represent centroid of stop location and duration of stop. Inset maps highlight crowded areas to show centroid location within boundaries of states (USA, top) or provinces (Argentina, bottom), in reference to major US highways (top left), and within 150 km of Mar Chiquita Lake (bottom right).
Source: Berkeley Library Geodata, University of California, <https://geodata.lib.berkeley.edu>.

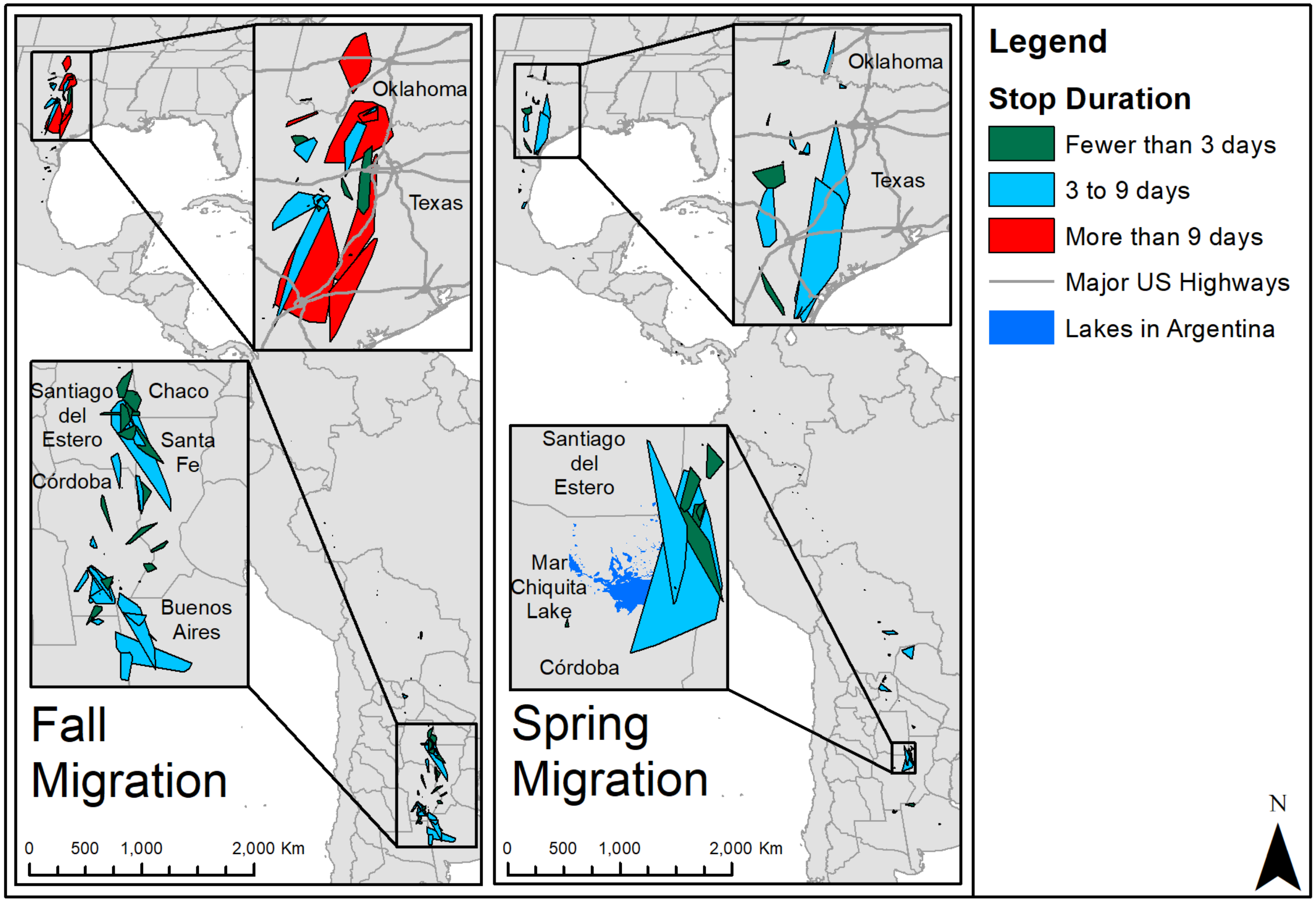

Figure 3.21. Stops made by migrating Swainson's Hawks wearing satellite transmitters from 2012 to 2017. Polygons represent minimum convex polygon around stop points, colored by duration of stop. Inset maps highlight crowded areas to show polygons within boundaries of states (USA, top) or provinces (Argentina, bottom), in reference to major US highways (top), and within 150 km of Mar Chiquita Lake (bottom right).
Source: Berkeley Library Geodata, University of California, <https://geodata.lib.berkeley.edu>.

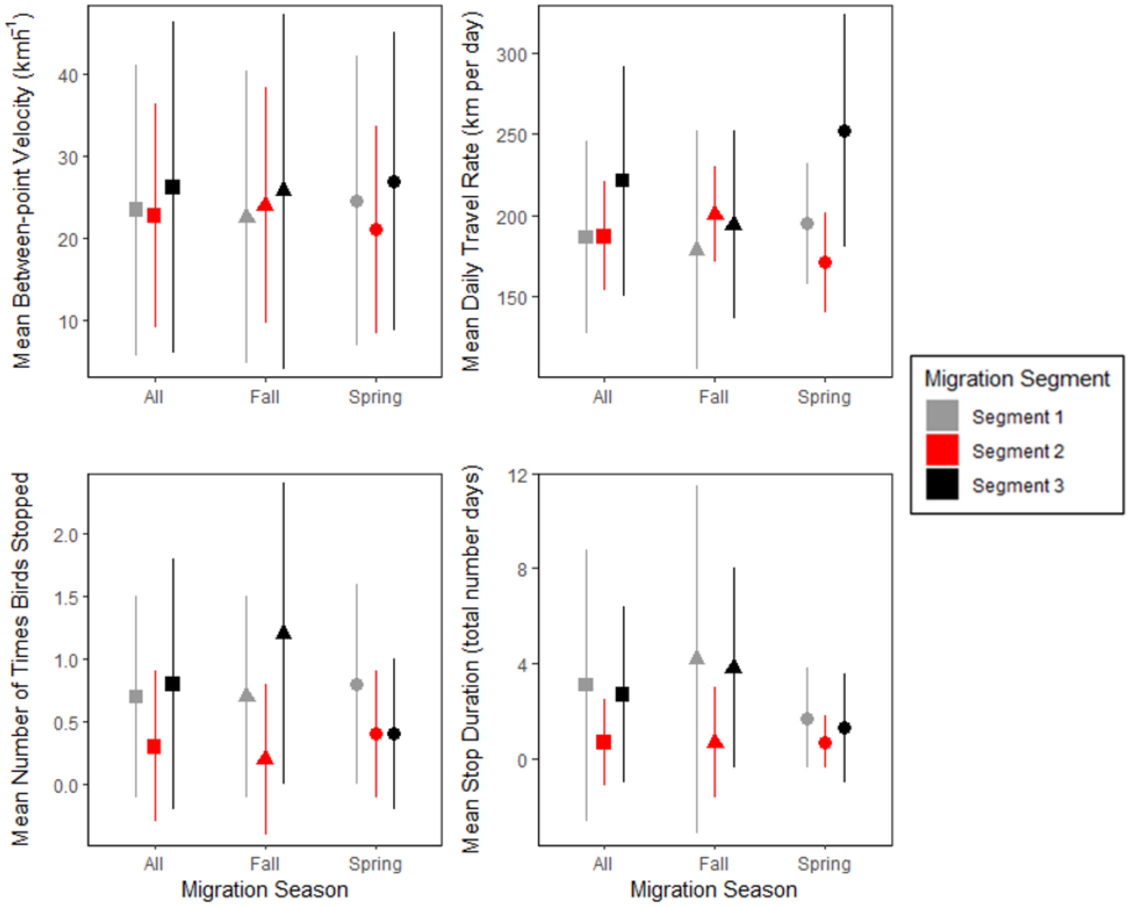

Figure 3.22. Mean between-point velocity, mean daily travel rate, mean number of times birds stopped, and mean number of days birds spent stopped per migration segment (segment 1 = first 1/3 of days spent travelling, segment 2 = middle 1/3, and segment 3 = last 1/3 of trip). Error bars show variability (standard deviation) among migration data. Data obtained from adult Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

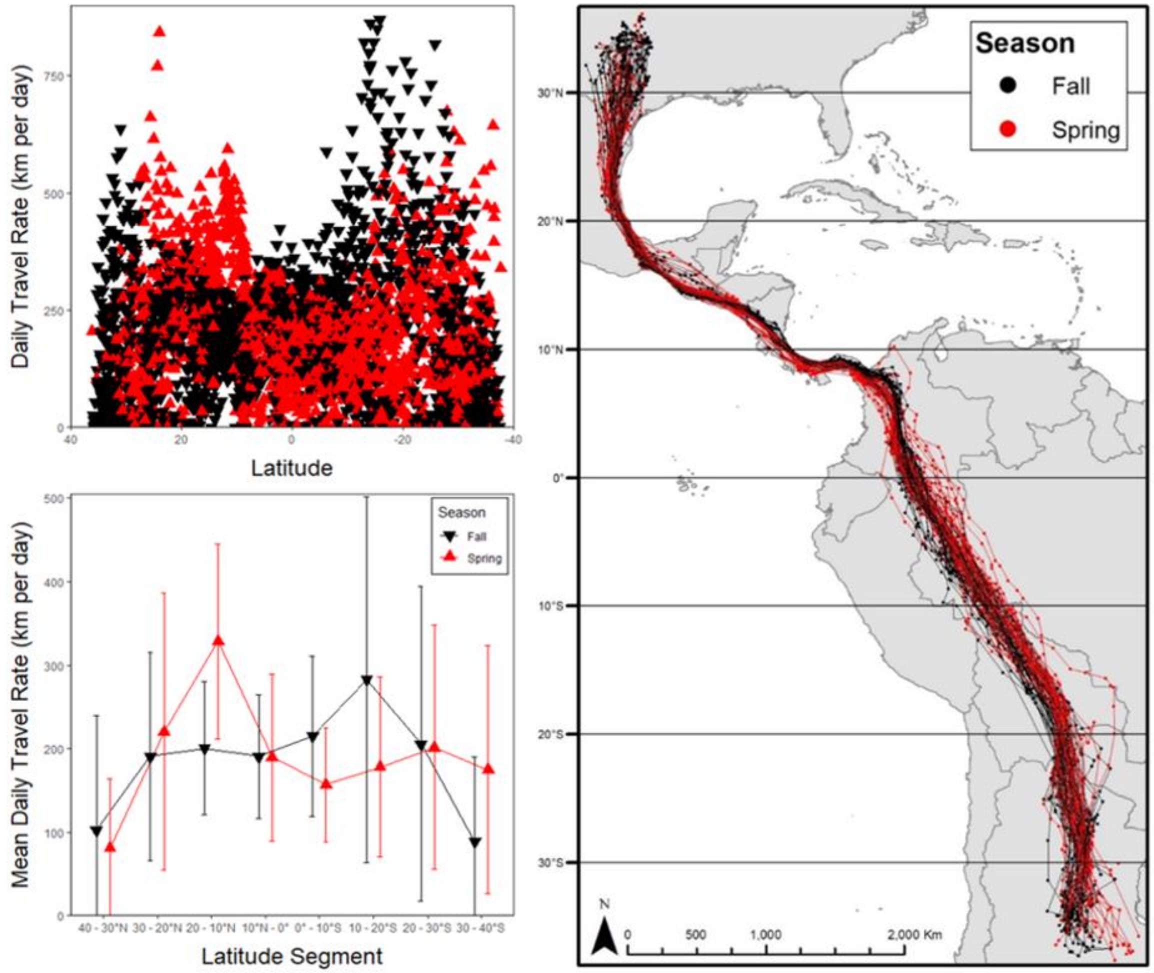

Figure 3.23. Daily travel rate compared to latitude (top) and mean travel rate across geographic segments (bottom) by season (fall = southward migration, spring = northward migration) with a map of roosting locations and vectors for reference. Data obtained from adult Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

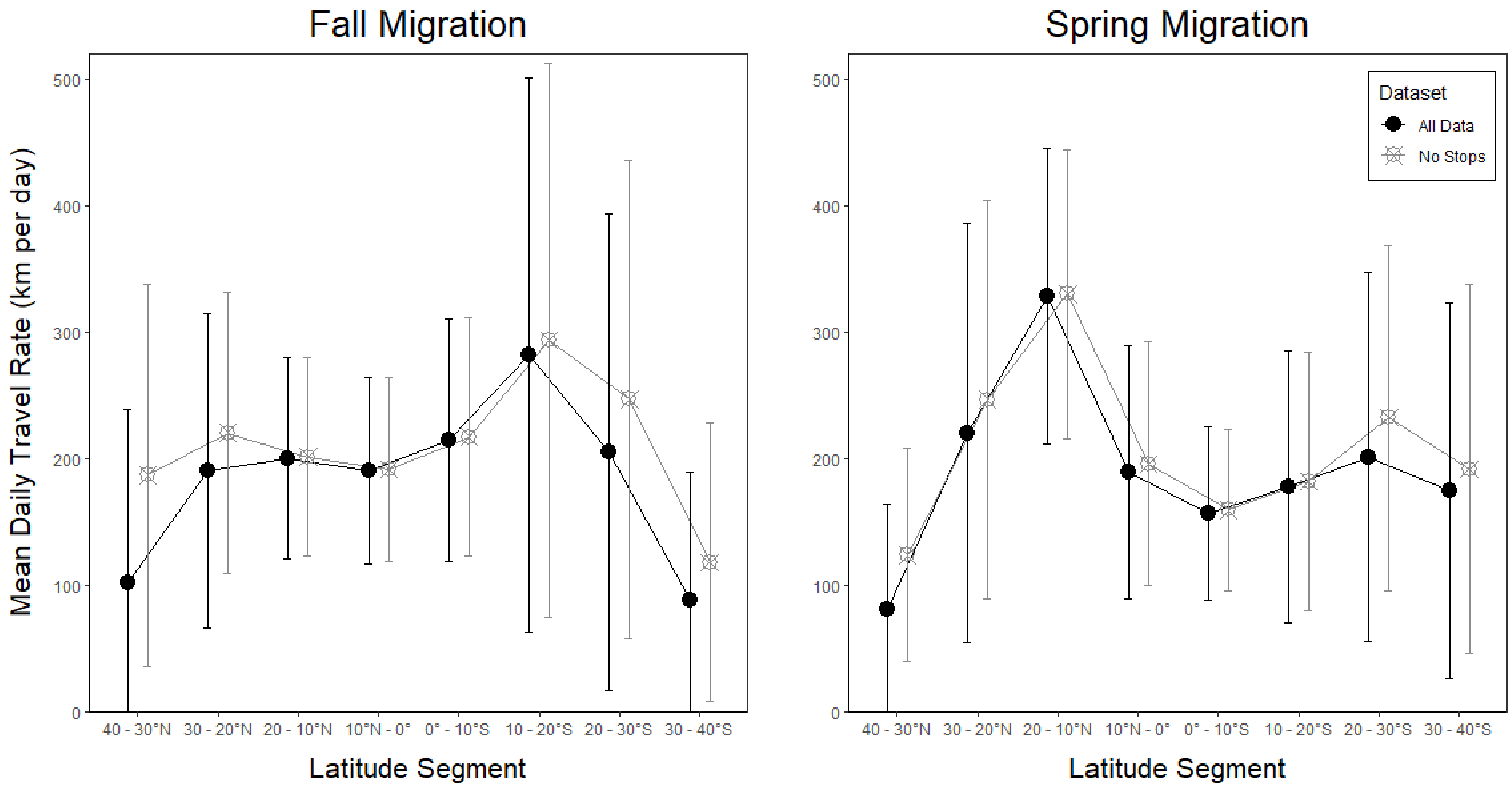

Figure 3.24. Difference in average daily travel rate when we examined all data compared to only data where hawks were actively migrating (i.e., we excluded days where hawks were stopped or otherwise not making forward migration progress). Data obtained from adult Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

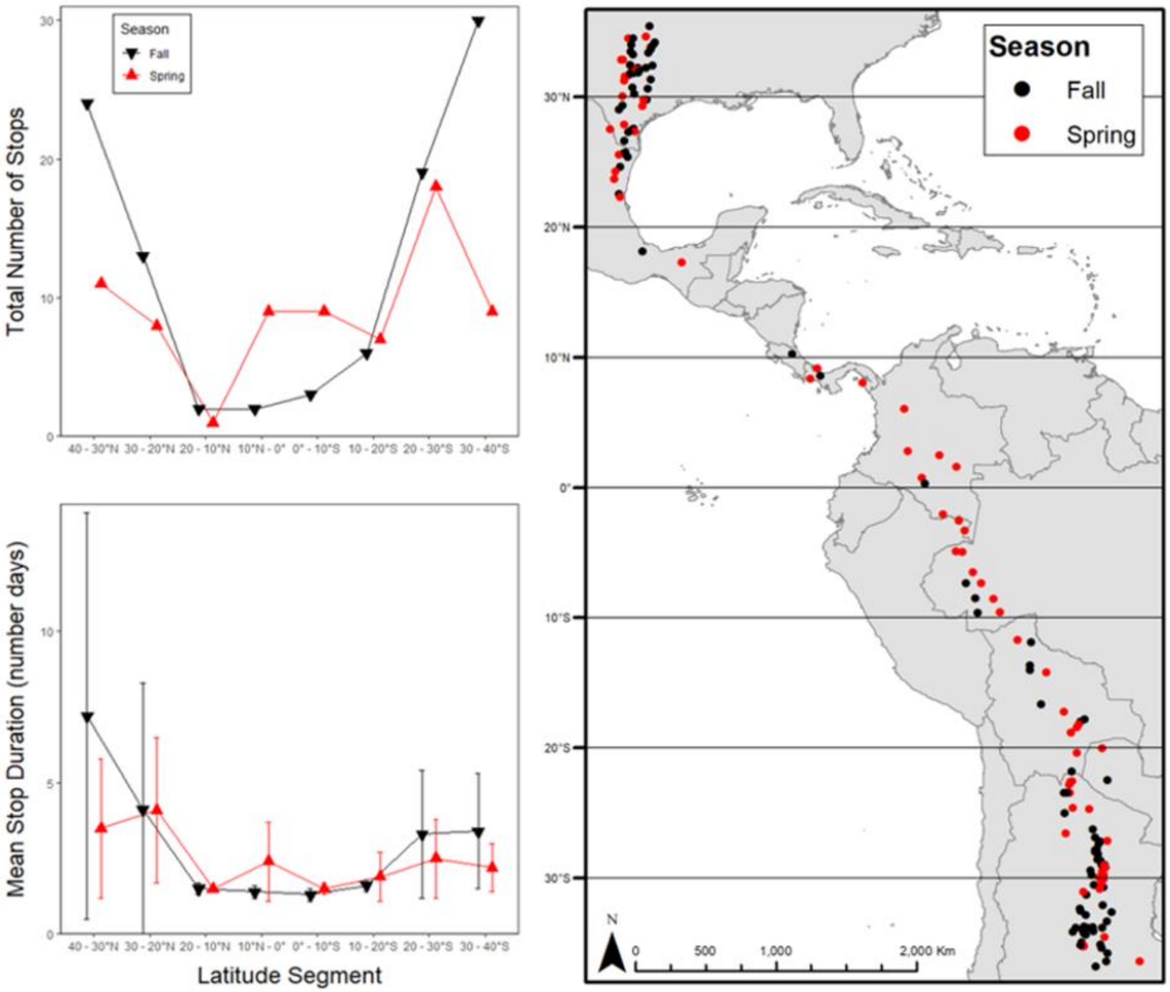

Figure 3.25. Total number of stops we recorded across all migration data and mean stop duration (number of days birds spent stopped) grouped by latitude segment (based on locations of centroids) and season (fall = southward migration, spring = northward migration) with a map of stop locations for reference. Data obtained from adult Swainson’s hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

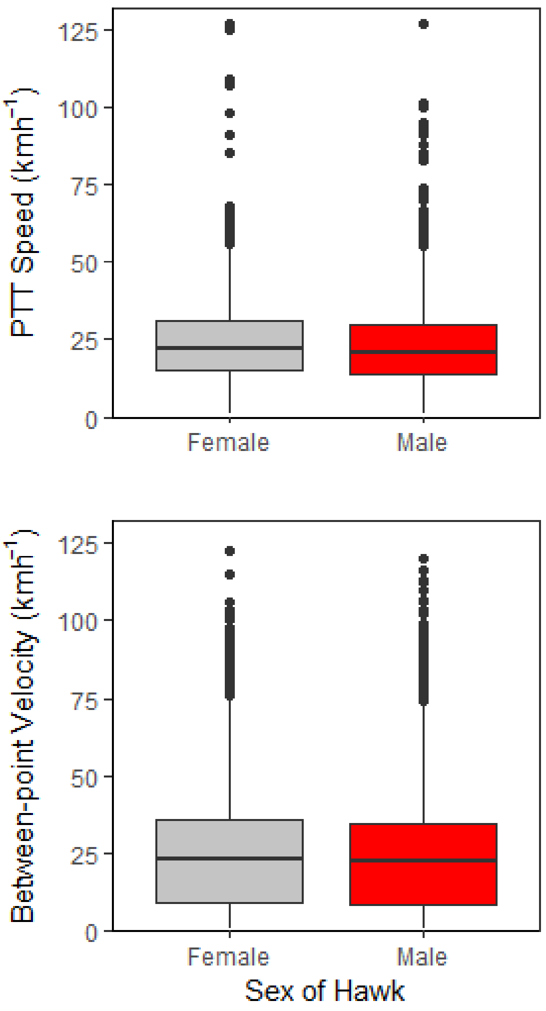

Figure 3.26. Speed reported by the transmitter during data transmission (PTT speed) and speed measured as distance between points divided by elapsed time (between-point velocity) by sex of hawk. Data obtained from adult Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

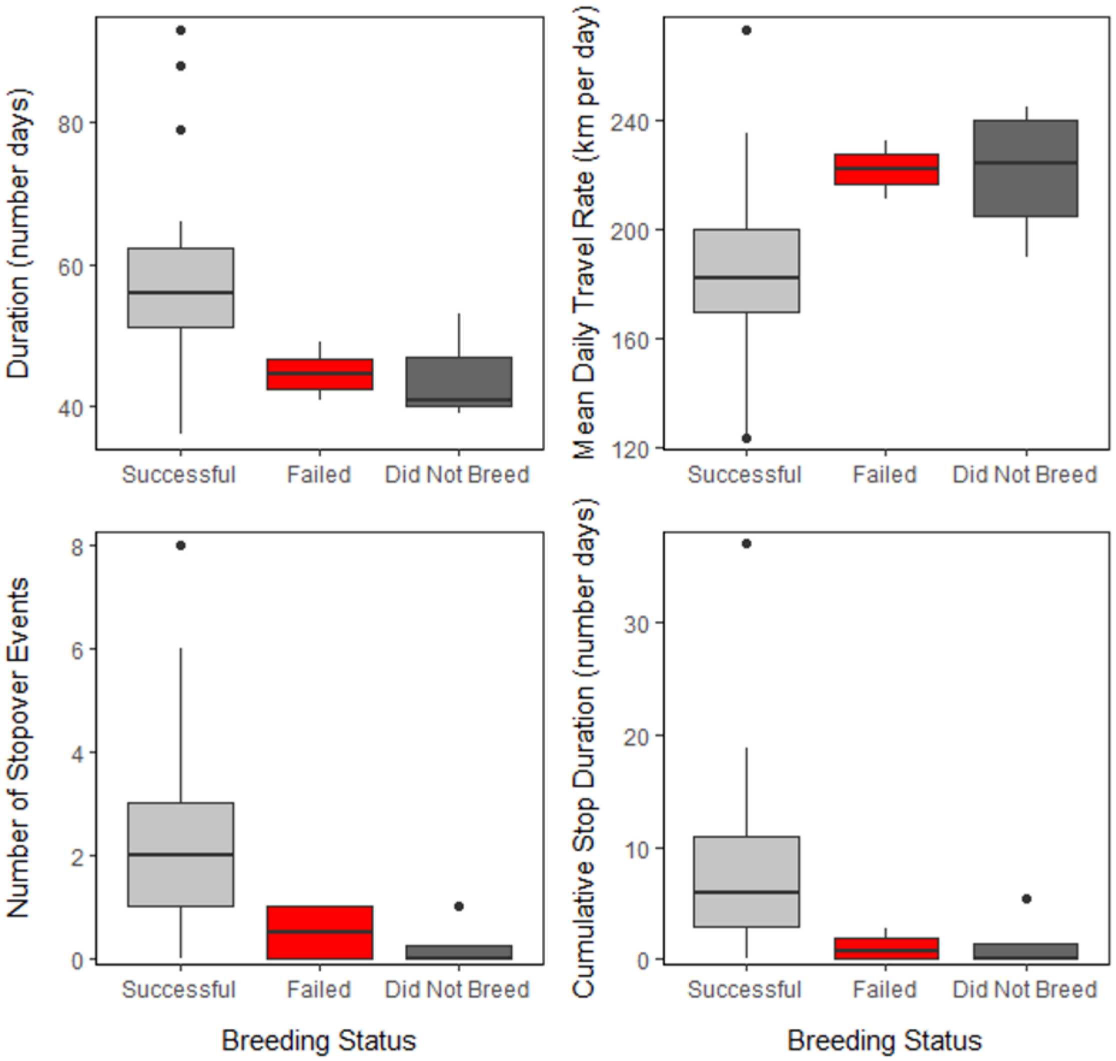

Figure 3.27. Various fall migration data compared to breeding status of hawks the previous summer. Data obtained from adult Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017, as well as monitoring of nesting activity in northern Texas from 2012 – 2018. *Source*: Chapter 2.

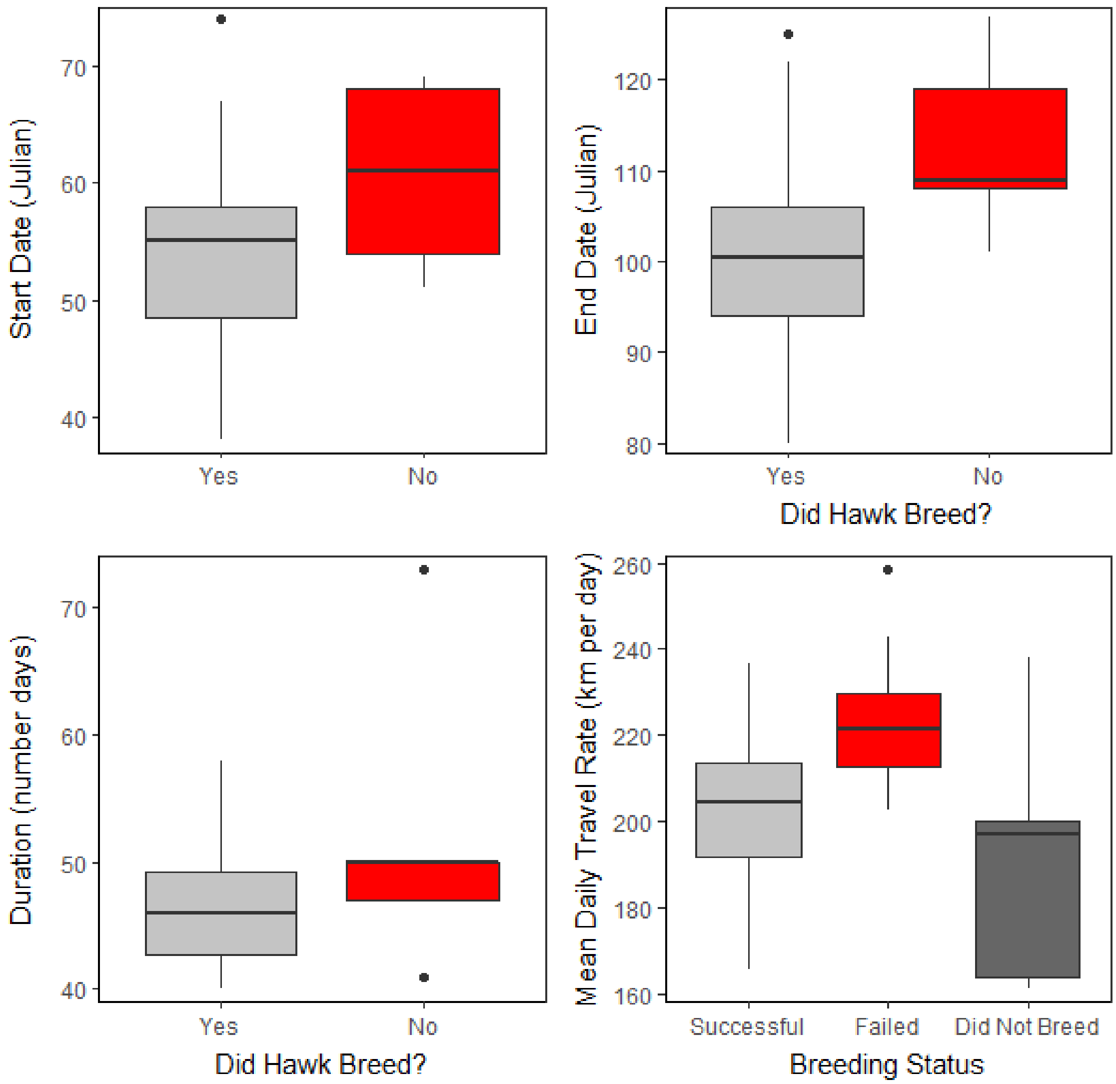

Figure 3.28. Various spring migration data compared to whether or not the hawk bred the following summer, and in the case of travel rate, if the hawk was successful or failed at their breeding attempt. Data obtained from adult Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017, as well as monitoring of nesting activity in northern Texas from 2012 – 2018.
Source: Chapter 2.

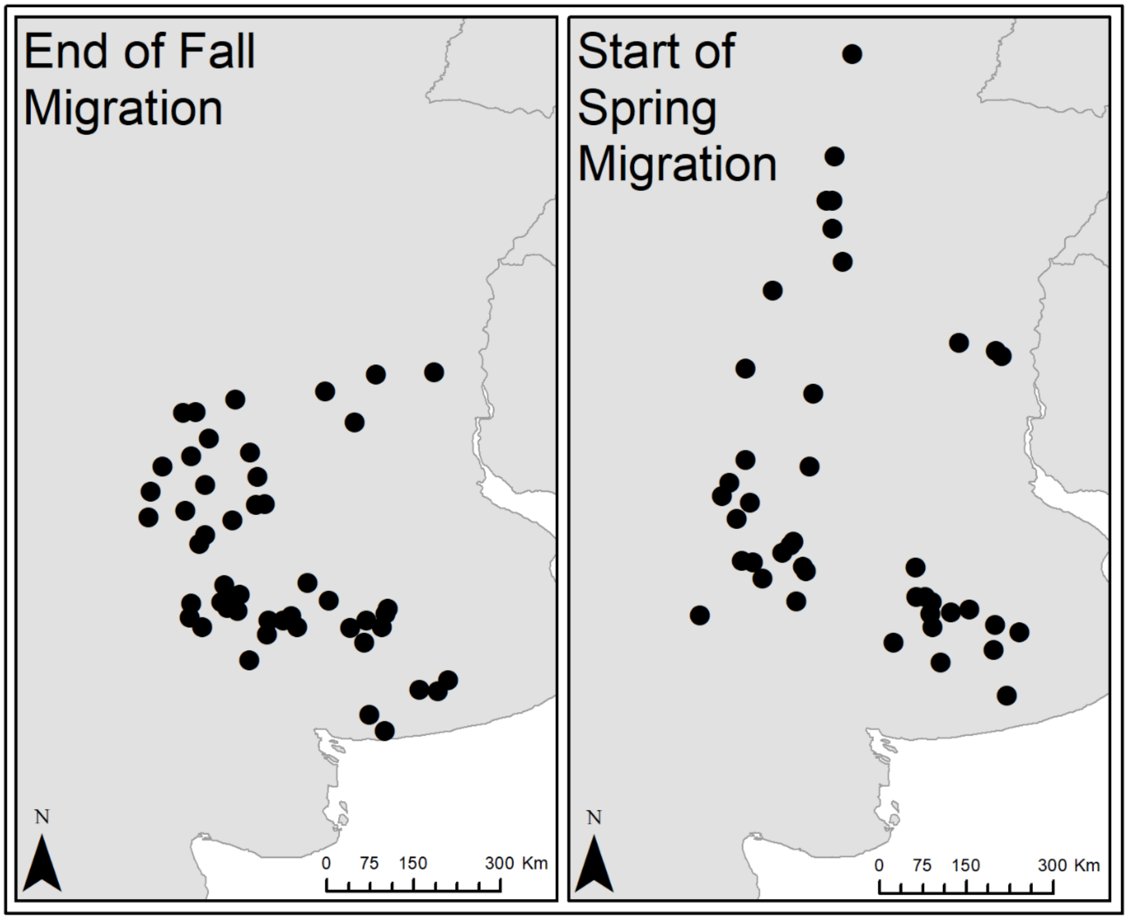

Figure 3.29. Locations in Argentina where Swainson's hawks ended their fall (southward or outbound) migrations compared to where hawks began their spring (northward or return) migrations. Data obtained from adult Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

CHAPTER IV

SWAINSON'S HAWKS' HABITAT USE AND SELECTION DURING MIGRATION

Abstract

Habitats are generally thought of as regions with resources that support occupancy by a species, but during migration, habitats play an important role in aiding survival of transitory individuals. Swainson's hawks (*Buteo swainsoni*) breed in western North America and migrate to Argentina for their wintering season. Habitats on the breeding and nonbreeding range are arid open country, such as grasslands, croplands, pastures, shrublands, and deserts. To our knowledge, landscape use has not been described for this species during migration outside of staging regions on the breeding range. We tracked 24 Swainson's hawks with satellite transmitters to describe landscape use and habitat selection during migration. Preferred migratory habitats were grasslands and croplands, similar to their breeding and wintering areas; these were especially important during pre-migratory staging periods when hawks forage to accumulate fat. Shrublands and deserts may represent further migratory habitat for hawks originating from other areas, but those land covers were underrepresented due to the breeding locations of hawks in this study. Forests of varying types were selected for or used in proportion with availability, likely due to hawk requirements of perches to roost at night, but we assume forests were not used during most migratory activities, as hawks can simply soar over them. Rainforests were used heavily, due to hawks having no other land covers across a 2,000-km stretch of migratory pathway. Importantly, avoidance of water

likely shapes the migratory pathway, causing a circuitous route that is longer than a straight line between starting and ending locations.

The term habitat means an area with the resources and environmental conditions to support occupancy (usually including survival and reproduction) of a member of one species (Hall et al. 1997, Darracq and Tandy 2019). In the case of migratory species, the term is extended to areas that additionally support survival during nonbreeding seasons (e.g., winter-range habitat; Hall et al. 1997, Darracq and Tandy 2019). While migrating, animals move through various land covers that may supply short-term feeding and resting locations or may serve little or no function, and possibly contain hazards, to transitory individuals. Migratory corridors, especially staging, stopover, and roosting locations, are therefore considered habitat in a broad sense, because they are selected and used to promote survival during hazardous and exhaustive migratory travel (Hall et al. 1997). To fully understand a species' life history, it is imperative to describe landscapes used during migration, so we may understand the year-round habitat needs of that species.

Swainson's hawks (*Buteo swainsoni*) breed in western North America and migrate to Argentina for their nonbreeding season (Bechard et al. 2010). Their habitat is described as arid open country: hawks may be found in grasslands, croplands, pastures, shrublands, and deserts throughout their breeding and nonbreeding ranges (Smallwood 1995, Rodríguez-Estrella 2000, Canavelli et al. 2003, Bechard et al. 2010, Nishida et al. 2013). Open landscapes provide ease of hunting from the wing, as well as the food Swainson's hawks require; small vertebrate animals, such as rodents, lizards, and snakes during the breeding season, and large invertebrates, such as grasshoppers, during the rest of the year (Woffinden 1986, Rodríguez-Estrella 2000, Canavelli et al. 2003, Giovanni et al. 2007, Bechard et al. 2010). Swainson's hawks will additionally hunt from perches, such as trees, utility poles, and fence posts, and can be found on the ground, a common behavior in Argentina where perches can be scarce in the core of their nonbreeding range (Canavelli et al. 2003, Sarasola and Negro 2006, Bechard et al. 2010, Littlefield and Johnson 2013).

Swainson's hawks migrate southwards from diverse breeding grounds, funneling into a relatively narrow pathway from southern Mexico to Argentina (Fuller et al. 1998, Bechard et al. 2010, Kochert et al. 2011). Hawks must travel over 10,000 km across coastlines, rivers, forests, and mountains to reach their nonbreeding destination, then return along the same pathway several months later (Fuller et al. 1998, Bechard et al. 2010, Kochert et al. 2011). As an obligate-soaring migrator, this species mostly uses thermal updrafts to travel efficiently, giving them a diurnal migration pattern (Kerlinger 1989, Hedenström 1993, Bildstein 2006, Bechard et al. 2010). Thus, Swainson's hawks must land and roost at night to conserve energy throughout a one-to-three-month journey (Smith 1985, Kerlinger 1989, Hedenström 1993, Bildstein 2006, Bechard et al. 2010). In addition, this species is known to stage, a behavior in which migratory birds spend time accumulating fat reserves and joining flocks, and is usually characterized by a movement away from a nesting territory but prior to full migration (Kerlinger 1989, Bildstein 2006, Warnock 2010). Moreover, Swainson's hawks make stopovers throughout the migratory pathway for unknown reasons; possible explanations include rest, opportunistically foraging, and being stalled by unavoidable weather conditions (Smith 1985, Woffinden 1986, Kirkley 1991, Kochert et al. 2011, Littlefield and Johnson 2013).

Habitat use and selection is well documented for Swainson's hawks on the breeding and nonbreeding grounds (Smallwood 1995, Rodríguez-Estrella 2000, Canavelli et al. 2003, Bechard et al. 2010, Nishida et al. 2013). Additionally, the migration pathway has been described in terms of geographic location (Schmutz 1996, Fuller et al. 1998, Kochert et al. 2011), but, to our knowledge, little information exists regarding landscape use and selection during this critical period in Swainson's hawk life history. Aggregations of staging hawks have been observed in recently harvested crop fields, grasslands, and deserts, which are similar to breeding habitat (Woffinden 1986, McGrath 1988, Houston 1990, Littlefield and Johnson 2013). Airola et al. (2019) tracked California Swainson's hawks to unusual wintering locations, many of which were along the pathway for hawks that would travel to Argentina; overwintering habitats at these short-stops were predominantly agriculture, grasslands, and shrublands, mixed with small amounts (around 15% or less) of forest and 'other' land covers. Stopover locations in California and Arizona, USA, and along the western coast of Mexico were described as mostly agriculture and shrublands, with smaller proportions (around 20%) of forest, grasslands, and 'other' land covers (Airola et al. 2019). Kochert et al. (2011) did not describe landscapes at staging and stopover sites reported in their study, but based on locations they provided, we estimate high use of grasslands, croplands, shrublands, and deserts within the USA and northern Mexico, a mixture of croplands/grasslands and forest/rainforests through Central America, many rainforest-dominated stopovers though South America, and a return to open landscapes when stopped in Argentina. The overall migration pathway suggests a strong avoidance of oceans (Houston 1990, Schmutz 1996, Fuller et al. 1998, Bechard et al. 2010, Kochert et al. 2011), and few descriptions exist suggesting use of aquatic and riparian areas on the breeding range (Smallwood 1995). Last, large flocks of migrating Swainson's hawks have been observed roosting in trees (Smith 1985, Smith et al. 1986, Kirkley 1991, Bechard et al. 2010), implying that use of forests and rainforests may be important during migration.

We used satellite transmitters to investigate land cover use and second-order habitat selection by Swainson's hawks during migration using Design III analyses (Manly et al. 2004). With an abundance of data, we divided the migration into several categories to assess potential differences in land use between migration seasons, time of day, whether hawks were actively migrating or stopped, and stop types (i.e., staging or mid-migration stopovers). Based on habitat use during breeding and nonbreeding seasons (Smallwood 1995, Rodríguez-Estrella 2000, Canavelli et al. 2003, Bechard et al. 2010, Nishida et al. 2013), and reports from staging, stopover, stopped-short overwintering locations, and the general geographic pathway (Bechard et al. 2010, Kochert et al. 2011, Littlefield and Johnson 2013, Airola et al. 2019), we expected hawks to select open landscapes and avoid water. We also expected hawks to select forested land covers proportional to availability, because trees provide opportunistic roosting locations (Smith et al. 1986, Kirkley 1991), but Swainson's hawks are not known to forage or otherwise spend time in forested areas during other seasons (Rodríguez-Estrella 2000, Canavelli et al. 2003, Bechard et al. 2010, Nishida et al. 2013, Airola et al. 2019).

Methods

We used bal-chatri and dho-gaza traps (Bloom et al. 2007) to capture 24 adult Swainson's hawks suspected or known to be breeding in the Amarillo area of Texas in

2012 and 2013. Each captured hawk weighing > 550 g was equipped with a solar-powered Global Positioning System (GPS) platform transmitter terminal (hereafter PTT; Solar PTT-100, Microwave Telemetry, Inc., Columbia, Maryland) on a backpack-style harness secured with Teflon® ribbon, as well as an aluminum leg band issued by the United States Geological Survey Bird Banding Laboratory (Meyburg and Fuller 2007); the weight restriction ensured transmitters added no more than 4% of a hawk's bodyweight (the transmitter weighed 22 g). PTTs were programmed to report 12 locations per day at 0000, 0500, 0700, 0900, 1100, 1200, 1300, 1500, 1700, 1800, 1900, and 2100 hours, local time. We followed hawks until transmissions ceased due to mortality, technical failure, or, in the case of two hawks, the end of the study, from April 2012 to September 2017. We omitted potential errors in collected data by first eliminating points reporting an error and identifying and removing post-mortality points. We then conducted an evaluation of implausible locations; points with orthodromic distance from last point > 100 km or velocity from last point > 80 kmh^{-1} were evaluated for plausibility based on elapsed time and deviation from pattern of previous and subsequent points (Chapter 3). Remaining locations were assumed to be accurate within ± 18 m (Microwave Telemetry, Inc., Columbia, Maryland). We visualized and analyzed data using Excel, ArcMap 10.7, and Program R 3.6.2 (packages 'ggplot2' and 'ggpubr'; Kassambara 2020, Wickham et al. 2020).

We separated migration data from other seasonal behaviors for analysis (similar to Kochert et al. 2011 and Chapter 3). Fall (southward or outbound) migration started at the first point > 150 km away from and south of (91° - 269° bearing) the hawk's capture location that began a pattern of points moving southward that showed no return to the buffer. Fall migration ended when the bird reached Argentina and stopped making progress in a southward direction for ≥ 10 days. Spring (northward or return) migration started at the first point in a series of consistently northward movements (preceded by ≥ 10 days of omnidirectional movement with no northward trend) and ended when the bird was located within 150 km of its capture location. In the case of one hawk that shifted to a nesting location 200 km south of the capture location in 2013, we subsequently used a 150-km buffer around the nest location to identify migration start and end dates.

We categorized locations as ‘all data’, ‘fall migration’, ‘spring migration’, ‘active hours’, ‘roosting hours’, ‘moving’, ‘stopped’, ‘staging’, and ‘stopover’ for various comparisons. We examined hourly behavior to classify points as “roosting” hours when > 25% of data indicated inactivity (i.e., speed reported by transmitters = 0 $\mathrm{kmh^{-1}}$; Chapter 3). We visually examined migration data for possible evidence of ‘stops’ (i.e., a lack of forward migration progress, though birds may have moved in omnidirectional patterns). We identified stops as when a bird spent two or more roosting periods at the same relative location (< 1 km between roost locations) or when a bird moved in a direction contrary to the pattern of migration for > 24 hours and including two or more roosting periods. Stops started at the first point going in the opposite direction of migration or the first point in a series of non-moving points, and stops ended when the bird resumed consistent movement in the direction of migration. When birds made short duration (< 24 hours) movements in the direction of migration followed by more stopping behaviors, we grouped those points as part of the same stop; we recorded multiple stop events when movements in the direction of migration > 24 hours separated them. Stops made within 1,000 km of trapping locations during fall migration were considered likely pre-migratory staging behaviors, where hawks presumably aggregate and accumulate fat reserves for migration (Bechard et al. 2010, Kochert et al. 2011, Littlefield and Johnson 2013). The remainder of stops throughout fall migration, and all stops made throughout spring migration, were considered mid-migratory stopovers, or periods when hawks may have been stalled by inclement weather or needed rest, and possible foraging (Smith 1985, Kirkley 1991), before proceeding; we determined early migratory stops during spring migration resembled stopovers from fall migration and the remainder of spring migration data and were therefore unlikely to be staging behaviors (Chapter 3).

We examined PTT-reported height to check our assumption that roosting and stopped locations represented periods when birds were most often near the ground (0 to 50 m) compared to other categories. PTTs reported estimated altitude above ellipsoid (± 22 m; Microwave Telemetry, Inc.), which we converted to altitude above sea level by subtracting values from a geoid undulation map (Poessel et al. 2018, Earth Gravitational Model EGM2008; National Geospatial-Intelligence Agency, https://earth-info.nga.mil/GandG/wgs84/gravitymod/egm2008/egm08_gis.html). We then estimated height above ground by subtracting values from an ASTER digital elevation map (National Aeronautics and Space Administration, https://search.earthdata.nasa.gov); specifically, Movebank (http://www.movebank.org) estimated elevation for each hawk location using an inverse-distance weighted interpolation, which averages the nearest elevation values on a grid while giving greater weight to nearer values.

We obtained land cover information from the GlobCover V2.3 2009 dataset (The European Space Agency, http://due.esrin.esa.int/page_globcover.php), which had a 300-m spatial resolution and 22 land cover categories. We reduced this dataset to seven land cover types by combining similar categories (when combining mixed categories, we chose whichever type was mentioned first, assuming that meant the majority of the mixture): “cropland”, “grassland”, “shrubland/desert”, “forest” (i.e., temperate-deciduous and -evergreen as well as tropical-dry forests), “rainforest” (this was such a large proportion of the migration pathway we decided to keep it a separate category), “water/riparian”, and “other” (Table 4.1). Rainforest was not available to the set of staging data, due to geographic limitation, so it was dropped from that analysis; we further dropped any land cover that showed no availability in our data collection.

We analyzed land use and selection at the second order (i.e., selection of a home range [or, in this case, a migration route] from a study area; Johnson 1980, Aebischer et al. 1993) using a Design III analysis; we compared real points (used) to random points (available) within a separate space for each individual migration (Manly et al. 2004). We defined a study area for tracked hawks with a 50-km buffer around all migration points, based on average (~25 kmh^{-1}) and maximum (99% of data were < 53 kmh^{-1}) flight speed described for this species in Chapter 3, to describe the general land cover composition of the migration pathway. We then created dynamic Brownian bridge movement models (code “brownian.bridge.dyn” in package “move” in program R; raster = 5,000, location error = 18 m, extent = 0.2, window size = 23, and margin = 3; Kranstauber et al. 2012, 2020) for each individual migration journey (i.e., all data from one individual moving from the breeding range to the nonbreeding range, or vice versa) to represent available spaces. We selected this model because it uses a sliding window to calculate a dynamic variance term, which makes it most appropriate for start-and-stop movements, such as Swainson’s hawk migration (Kranstauber et al. 2012). We extracted the 95% contour from each model within which to create random points equal to the number of PTT points examined for that migration journey, or equal to the number of points for each type of dataset. We extracted land cover information onto real and random points, and pooled real and random data by bird for selection analyses. For staging data, we limited available spaces to within 1,000 km of trapping locations using the ‘Buffer’ and ‘Clip’ tools prior to making random points equal to the number of staging locations for each migration journey (some migrations contained no staging locations and were omitted from this analysis). We then conducted Manly’s selection ratio analyses (w = use / available; code “widesIII” in package adehabitatHS; average known = false and alpha = 0.05; Aebischer et al. 1993, Manly et al. 2004, Calenge 2011) to test for selection for or against land covers in each dataset. We used Bonferroni 95% confidence intervals (CI) to interpret selection: if CI did not include and were > 1, we interpreted selection for the land cover, if CI did not include and were < 1, we interpreted selection against the land cover, and if CI included 1, we interpreted no selection (Manly et al. 2004).

Results

We recorded 93 migration journeys for 23 Swainson’s hawks. Hawks were observed on 1 to 10 migrations each (1 – 5 fall migrations and 1 – 5 spring migrations; mean = 2 migrations of each season); for the purposes of this study, we included eight incomplete migration tracks to maximize data. After filtering, we had 46,467 hawk locations that represented migration seasons (57% fall migration, 43% spring migration).

Rainforest comprised 38% of the overall migration pathway, grassland was 19%, cropland was 15%, forest was 11%, shrubland/desert was 9%, water/riparian was 8%, and ‘other’ was < 1% (Fig. 4.1). The portion of the pathway in the United States and Mexico was mostly grasslands and forest, southern Mexico through central Colombia was a mosaic of rainforests, grasslands, water, and croplands, southern Colombia through central Bolivia was nearly 100% rainforest, southern Bolivia through northern Argentina was forests with a mix of grasslands and shrublands, and the remainder of pathway through Argentina was croplands, grasslands, and shrublands (Fig. 4.1).

Based on speed data reported by transmitters, 0000 to 0700 and 1800 to 2100 hours represented periods when > 25% of locations were likely reflecting stationary birds (Fig. 4.2). We therefore labeled points between 0900 to 1700 as “active hours” and 1800 to 0700 as “roosting hours”. We recorded 172 stops: 99 during fall migration and 73 during spring migration (Fig. 4.3). Of those, 31 stops made by 16 hawks were classified as probable staging periods. Hawks stopped 0 to 8 times per migration (mean = 2 ± 2 stops) for 1 to 31 days (mean = 4 ± 4 days; Fig. 4.3). Our estimates of PTT height averaged 135 ± 363 m above ground (Chapter 6), with 13,105 locations (33% of all data > 0 m) occurring between 0 and 50 m above ground (mean = 25 ± 14 m above ground). Proportion of hawk locations that were near the ground was variable throughout datasets (15% – 62%), but in general, most locations were near ground during roosting hours (62%) and while hawks were not making forward progress (i.e., pre-migratory staging or mid-migration stopovers, 58-60%; Table 4.2).

We generated 46,467 random points to match the number of points considered in all migration data, which were 26,291 points for fall migration and 20,176 for spring migration. Among those were 27,113 for active hours, 19,354 for roosting hours, 40,302 for moving points, 6,165 for stopped points, 2,212 for staging points (created within

1,000 km of trapping areas), and 3,953 for stopover points (created across the entire migration pathway).

Across all migration data and during fall migration, hawks selected for grasslands and croplands, against rainforest and water/riparian land covers, and used shrubland/desert, forest, and ‘other’ land covers in proportion with availability (Fig. 4.4). During spring migration, hawks selected for croplands, against water/riparian land covers, and all other land covers were used in proportion to availability (Fig. 4.4). Selection ratios indicated croplands and grasslands were 1.1 to 6.2 times more likely to be selected than other land covers across all data, 1.1 to 7.6 times more likely across fall migration data, and 1.1 to 4.5 times more likely across spring migration data (Table 4.3). All land covers were selected 3 to 7 times more than water/riparian across these three datasets (Table 4.3).

Results of active hours were similar to those for all data (Fig. 4.5). During roosting hours, hawks selected for croplands and grasslands, against shrublands/deserts and water/riparian, and used forest, rainforest, and ‘other’ in proportion with availability (Fig. 4.5). Selection ratios indicated croplands and grasslands were 1.2 to 5.2 times more likely to be selected than other land covers during active hours and 0.9 to 9.4 times more likely during roosting hours (Table 4.4). All land covers were selected 2 to 9 times more than water/riparian across both datasets (Table 4.4).

When hawks were actively migrating north and south (‘moving’ data), they selected for croplands, grasslands, and rainforests, against water/riparian land covers, and used shrublands/deserts, forests, and ‘other’ land covers in proportion with availability (Fig. 4.6). When hawks were stopped (i.e., during staging and stopover periods combined), hawks selected for croplands and grasslands, against rainforests, water/riparian, and ‘other’ land covers, and used shrublands/deserts and forests in proportion with availability (Fig. 4.6). Selection ratios indicated croplands and grasslands were 1 to 5.3 times more likely to be selected than other land covers for moving data and 1.3 to 15.6 times more likely for stopped data (Table 4.5). All land covers were selected 3 to 11 times more than water/riparian across both datasets, except rainforest, in which case water was 1.4 times more likely to be selected (Table 4.5).

Pre-migratory staging (i.e., fall migration stops that occurred within 1,000 km of trapping locations) lacked rainforest land covers due to geographic location and lacked availability of ‘other’ and water/riparian land covers. During staging periods, hawks selected for croplands, against shrublands/deserts and forests, and used grasslands in proportion with availability (Fig. 4.7). During mid-migration stopover periods, hawks selected for croplands and grasslands, against rainforests, water/riparian, and ‘other’ land covers, and used shrublands/deserts and forests in proportion with availability (Fig. 4.7). Selection ratios indicated croplands and grasslands were 1.7 to 6.3 times more likely to be selected than other land covers for staging data and 1.1 to 11.7 times more likely for stopover data (Table 4.6). In the stopover dataset, all land covers were selected 4 to 9 times more than water/riparian, except rainforest, in which case water was 1.3 times more likely to be selected (Table 4.6).

Discussion

Swainson’s hawks consistently used and selected for croplands and grasslands over other land cover types throughout datasets examined in this study. The primary breeding- and nonbreeding-season habitats for Swainson’s hawks are grasslands and certain types of croplands, especially those that facilitate hunting of insects and small vertebrates, such as recently harvested fields (Bechard 1982, Smallwood 1995, Canavelli et al. 2003, Bechard et al. 2010, Littlefield and Johnson 2013), so this result was no surprise. Our results reinforce that these same open landscapes continue to be important throughout migration as well. Landscapes where hawks can easily find prey are likely most important during pre-migratory staging periods, when hawks accumulate fat to maintain energy throughout the journey (Kerlinger 1989, Bildstein 2006, Warnock 2010). Some bird species forage throughout migration, some forage at stopovers, and some fast until they reach their destination (Kerlinger 1989, Bildstein 2006, Warnock 2010), but we do not know to what extent, or even if, Swainson’s hawks forage during migration (see Smith et al. 1986, Kirkley 1991, and Bechard et al. 2006 for discussion of this question). The emphasis we found on grasslands and croplands, especially at stopovers, suggests hunting/foraging opportunities are likely available to Swainson’s hawks in many locations, if not throughout the entire route, supporting the arguments of Kirkley (1991) that opportunistic foraging likely occurs during migration for this species. These open landscapes may also promote more consistent thermal formation than other landscape types, facilitating soaring flight, which is essential to energy conservation for migrating Swainson’s hawks (Kerlinger 1989, Bildstein 2006, Bechard et al. 2010).

Shrublands and deserts are potential Swainson’s hawk habitat on the breeding and nonbreeding ranges, offering the open landscapes needed for their hunting style and prey, such as lizards, snakes, and rodents (Rodríguez-Estrella 2000, Bechard et al. 2010, Nishida et al. 2013). There was no evidence of selection for these landscapes in our results. However, our sample of hawks was biased in that all bred in northern Texas (a grassland/cropland mosaic), and never went further west than the border of Texas and New Mexico; thus, they encountered little shrubland and desert that would be available to more-western-breeding hawks (Bechard et al. 2010; Fig. 4.1). Staging locations and migration tracks of hawks trapped throughout the breeding range suggest use of western shrubland and desert regions (Kochert et al. 2011, Airola et al. 2019). Therefore, if our sample included a broader variety of breeding hawks, we may have found selection for this land cover type for similar reasons as for croplands and grasslands.

Hawks generally used forests proportional to availability during migration. Migrating Swainson’s hawks were expected to use forests to some extent, because flocks are known to roost in trees at night (Smith 1985, Smith et al. 1986, Kirkley 1991, Bechard et al. 2010). As a soaring-obligate species, forests would be difficult to maneuver through to find prey, so roosting may be their only ‘use’ during migration. In general, we assume Swainson’s hawks soared over thick patches of trees and only ‘used’ this land cover for short-term perching when more-open landscapes were unavailable. But opportunities to rest serve a purpose in survival (e.g., conservation of energy), so forests along the pathway do provide habitat, even if only for roosting.

Although availability of rainforests was generally high, hawks often selected against this land cover throughout various datasets. Rainforest comprised nearly 40% of the migratory pathway and was nearly 100% of the 2,000-km stretch from Colombia to Bolivia (Fig. 4.1); therefore, use of rainforest was unavoidable and expected, and we assume a similar pattern of use as for other forest types (i.e., only used for temporary perching and rest). However, hawk behavior was different when travelling this stretch;

migration tracks were often straighter, more-direct pathways with fewer and shorter-duration stopovers compared to all other sections of the migration route (Chapter 3; Fig. 4.3 and 4.8); this pattern was reflected by previous transmitter research as well (Kochert et al. 2011, Airola et al. 2019), supporting general selection against this land cover, especially during stopovers.

Hawks consistently selected against water/riparian landscapes compared to other land covers throughout migration. Swainson’s hawks drink water (Bechard et al. 2010) but can do so at water sources far smaller than what would appear on a 300-m resolution land cover map (e.g., ponds, pooled irrigation leaks, streams, etc.), so, our results really represented selection against large water sources, such as large lakes, wide rivers, and, most importantly, ocean. In addition, the GlobCover map had inappropriate resolution to identify all riparian land covers, and instead represented large blocks of flooded wetlands and estuaries. Swainson’s hawks do not use large bodies of water or expansive wetlands in breeding and nonbreeding seasons, and our results support that these areas are generally avoided throughout migration as well. Crossing oceanic waters is especially avoided because Swainson’s hawks heavily rely on thermal updrafts to conserve energy through soaring flight, and the temperature differential between cool water and warm tropical air promotes sinking downdrafts rather than rising updrafts (Kerlinger 1989, Bildstein 2006, Bechard et al. 2010). Therefore, flight across water is energy expensive for an obligate-soaring species (Kerlinger 1989, Bildstein 2006). In addition, water presents threat of mortality, because hawks cannot land to rest (Kerlinger 1989, Bildstein 2006). However, we were unsure if hawks truly avoided riparian land covers, because at the spatial resolution and geographic range of this study, there was too little of that land cover category to justify a separate examination from water pixels. In reality, riparian-associated trees may attract hawks during the breeding season, as sometimes the only trees in a landscape appropriate for nesting (Smallwood 1995). Furthermore, during migration, riparian trees may serve as important roosting locations in open landscapes. Therefore, the association with riparian land covers warrants further investigation than we were able to conduct in this study.

Hawks used the ‘other’ category (i.e., mostly urbanized landscapes throughout the migration pathway) so little that we had difficulty estimating selectivity. However, the spatial resolution of the land cover map was too large to capture most urbanized landscapes, with < 1% of the pathway being classified as either urban or permanent ice, missing most known city areas throughout the route. We were therefore unable to draw conclusions about use or selectivity of urban landscapes, though we assume little to no use and selection against areas of permanent ice, which would only represent high-elevation mountaintops in this migration pathway. James (1992), England et al. (1995), and Alsup (2012) suggested some breeding Swainson’s hawks use urban landscapes. We therefore see no reason to suggest that hawks would avoid passing over cities during migration, unless urban landscapes lack the thermal updrafts soaring hawks rely upon for efficient travel or present hazards to survival when roosting (Kerlinger 1989, Bildstein 2006); we found no final hawk locations within urban areas to suggest any specific survival hazard during migration or other seasons.

There were also only minor differences between fall and spring migrations. Fall migration reflected the same patterns as found when examining all data, perhaps because there were slightly more fall migrations recorded in this study (53%). During spring, hawks used rainforest proportional to availability, perhaps because there was no extended pre-migratory staging period to influence results. Additionally, during spring, hawks selected against shrubland/desert, which, as stated above, might be biased by the breeding destination of hawks in this study's sample and could change if we examined more-western-breeding hawks.

Hawks used landscapes differently during roosting hours than during the day, though, like other datasets, differences were minor. Active hours reflected the overall conclusions in this study: selection for croplands and grasslands, and against rainforest and water. Roosting hours showed similar positive selection, but use of rainforests proportional to availability, and selection against shrublands/desert and water. When hawks cross rainforested areas, they may have no choice in selection due to the lack of land cover diversity. Shrublands and deserts may not provide appropriate roosting perches for large flocks, so hawks may instead aim for areas with taller trees, but, again, more-western hawks may show different use of this land cover.

Migration data showed some differences when we separated stopped data from data of hawks actively moving north and south. The primary difference was when hawks were making consistent forward progress, they selected for rainforests, whereas when hawks were not making progress (i.e., hawks were either stationary or moving omnidirectionally), they selected against rainforests. The positive or neutral selection for all forest types may be due to roosting in trees at night (Smith et al. 1986, Kirkley 1991, Bechard et al. 2010); we did not find that selection in the roosting-hours dataset, but that dataset included stopped locations, which may have biased and nullified results. Selection against rainforest in the overall 'stopped' dataset likely reflected stopover locations, which occurred most often outside of rainforest areas, and longer-duration stops (especially staging periods) mostly occurred in the United States where rainforest was not available (Fig. 4.3).

Last, we found different results between staging and stopover periods. Staging data only suggested selection for croplands, which agreed with all recorded observations of mass staging flocks gorging on insects we found in the literature (Woffinden 1986, McGrath 1988, Houston 1990, Bechard et al. 2010, Littlefield and Johnson 2013). Cropland was readily available throughout the potential staging areas of hawks in this study (i.e., within 1,000 km of trap locations near breeding grounds), so the attraction to insects, such as grasshoppers, that increase in number in early autumn (Smith 1954) as an easy food source for pre-migratory fattening likely explains this result. Staging data also suggested selection against forests, perhaps because of a lack of appropriate prey. Stopover data, however, resembled the overall land use and selection of migration in this study. As stated above, we do not know if Swainson’s hawks forage during mid-migration stops (Smith et al. 1986, Kirkley 1991, Bechard et al. 2006); hawks might only make stops when halted by inclement weather conditions or a significant need to rest (Smith 1985). Stopovers, therefore, would be more likely to reflect use of landscapes proportional to availability, with only selectivity patterns as would be expected during any migratory activity. However, selection for croplands and grasslands also suggests possible opportunities to forage en route during stops, as stated above.

In conclusion, we suggest preferred migratory habitat for Swainson’s hawks is croplands and grasslands, similar to that used during the breeding and nonbreeding seasons (Smallwood 1995, Rodríguez-Estrella 2000, Canavelli et al. 2003, Bechard et al.

2010, Nishida et al. 2013). Our results showed that even when crossing forested regions, Swainson’s hawks seek out open landscapes where available, which likely plays a role in migration survival and success, such as allowing opportunities to forage en route. Trees throughout open and forested regions likely provide important nightly resting opportunities. The consistency we found across datasets suggests land cover is likely a less important factor to migrating Swainson’s hawks in terms of promoting survival compared to other factors of long-distance travel, such as flight efficiency, availability of thermal updrafts, wind and weather conditions, and selecting the pathway of least resistance (Kerlinger 1989, Bildstein 2006). Land cover and habitat are therefore most important during staging periods, when hawks need to find food for pre-migratory fattening, and, for the remainder of migration, likely only functions to maintain survival through resting opportunities, assuming hawks fast en route (Smith 1985, Smith et al. 1986, Kirkley 1991, Bechard et al. 2006).

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Tables

Table 4.1. We simplified the GlobCover V2.3 dataset into seven land cover types for analysis of Swainson's hawk landscape use during migration.

Land Cover	GlobCover Number	GlobCover Description
Cropland	11	Irrigated croplands
	14	Rainfed croplands
	20	Mosiac croplands/vegetation
Grassland	30	Mosaic vegetation/croplands
	120	Mosaic grassland/forest-shrubland
	140	Closed to open grassland
Shrubland/Desert	110	Mosaic forest-shrubland/grassland
	130	Closed to open shrubland
	150	Sparse vegetation
	200	Bare areas
Forest	50	Closed broadleaved deciduous forest
	60	Open broadleaved deciduous forest
	70	Closed needleleaved evergreen forest
	90	Open needleleaved deciduous or evergreed forest
	100	Closed to open mixed broadleaved and needleleaved forest
Rainforest	40	Closed to open broadleaved evergreen or semi-deciduous forest

Source: The European Space Agency (http://due.esrin.esa.int/page_globcover.php).

Table 4.1. Continued.

Land Cover	GlobCover number	GlobCover Description
Water/Riparian	160	Closed to open broadleaved forest regularly flooded (fresh-brackish water)
	170	Closed broadleaved forest permanently flooded (saline-brackish water)
	180	Closed to open vegetation regularly flooded
	210	Water bodies
Other	190	Artificial areas
	220	Permanent snow and ice

Table 4.2. Proportion of locations that suggested hawks were on or near the ground compared to higher altitudes across various datasets. We considered hawks to be near ground at heights of 0 – 50 m. Any locations > 50 m were considered hawks solely ‘flying above landscapes’, and for this assessment, we ignored any data < 0 m due to errors in estimating hawk height, measuring elevation, and data interpolation. Data obtained from adult Swainson’s hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

Dataset	% Near Ground	% Flying Above Landscapes
All migration data	33	67
Fall (outbound) migration	34	66
Spring (return) migration	31	69
Active hours (0900 – 1700)	15	85
Roosting hours (1800 – 0700)	62	38
Actively moving locations	29	71
Stopped locations	59	41
Staging locations	58	42
Stopover locations	60	40

Table 4.3. Ratios of Manly’s selectivity values (W) for all migration data of Swainson’s hawks equipped with GPS transmitters, as well as for fall (southward or outbound) and spring (northward or return) migration seasons. This indicates how much the land cover in the row was selected compared to the land cover in the column.

All migration data	Cropland	Grassland	Shrubland/Desert	Forest	Rainforest	Water/Riparian	Other
Cropland	1.0	1.2	1.6	1.4	1.6	6.2	1.7
Grassland	0.8	1.0	1.3	1.1	1.3	5.0	1.3
Shrubland/Desert	0.6	0.8	1.0	0.9	1.0	3.9	1.0
Forest	0.7	0.9	1.1	1.0	1.1	4.4	1.2
Rainforest	0.6	0.8	1.0	0.9	1.0	3.9	1.0
Water/Riparian	0.2	0.2	0.3	0.2	0.3	1.0	0.3
Other	0.6	0.8	1.0	0.8	1.0	3.7	1.0

Fall migration	Cropland	Grassland	Shrubland/Desert	Forest	Rainforest	Water/Riparian	Other
Cropland	1.0	1.3	1.7	1.5	1.8	7.6	2.0
Grassland	0.8	1.0	1.3	1.1	1.4	5.9	1.6
Shrubland/Desert	0.6	0.8	1.0	0.9	1.1	4.5	1.2
Forest	0.7	0.9	1.1	1.0	1.2	5.1	1.4
Rainforest	0.5	0.7	0.9	0.8	1.0	4.1	1.1
Water/Riparian	0.1	0.2	0.2	0.2	0.2	1.0	0.3
Other	0.5	0.6	0.8	0.7	0.9	3.7	1.0

Spring migration	Cropland	Grassland	Shrubland/Desert	Forest	Rainforest	Water/Riparian	Other
Cropland	1.0	1.2	1.5	1.3	1.3	4.5	1.2
Grassland	0.9	1.0	1.3	1.1	1.1	3.9	1.0
Shrubland/Desert	0.7	0.8	1.0	0.9	0.9	3.1	0.8
Forest	0.8	0.9	1.1	1.0	1.0	3.4	0.9
Rainforest	0.8	0.9	1.2	1.0	1.0	3.6	0.9
Water/Riparian	0.2	0.3	0.3	0.3	0.3	1.0	0.3
Other	0.9	1.0	1.3	1.1	1.1	3.9	1.0

Source: Manly et al. 2004

Table 4.4. Ratios of Manly's selectivity values (W) for migration data of Swainson's hawks equipped with GPS transmitters during 'active' migration hours (0900 – 1700 hours) or 'roosting' hours (1800 – 0700 hours). This indicates how much the land cover in the row was selected compared to the land cover in the column.

Active hours	Cropland	Grassland	Shrubland/Desert	Forest	Rainforest	Water/Riparian	Other
Cropland	1.0	1.2	1.5	1.7	1.8	5.2	2.1
Grassland	0.8	1.0	1.2	1.4	1.5	4.2	1.7
Shrubland/Desert	0.7	0.9	1.0	1.2	1.2	3.6	1.4
Forest	0.6	0.7	0.9	1.0	1.1	3.1	1.2
Rainforest	0.6	0.7	0.8	0.9	1.0	2.9	1.1
Water/Riparian	0.2	0.2	0.3	0.3	0.3	1.0	0.4
Other	0.5	0.6	0.7	0.8	0.9	2.6	1.0

Roosting hours	Cropland	Grassland	Shrubland/Desert	Forest	Rainforest	Water/Riparian	Other
Cropland	1.0	1.2	1.8	1.1	1.3	9.4	1.6
Grassland	0.8	1.0	1.5	0.9	1.1	7.9	1.4
Shrubland/Desert	0.6	0.7	1.0	0.6	0.7	5.2	0.9
Forest	0.9	1.1	1.7	1.0	1.2	8.7	1.5
Rainforest	0.7	0.9	1.3	0.8	1.0	7.0	1.2
Water/Riparian	0.1	0.1	0.2	0.1	0.1	1.0	0.2
Other	0.6	0.7	1.1	0.7	0.8	5.8	1.0

Source: Manly et al. 2004

Table 4.5. Ratios of Manly's selectivity values (W) of migrating Swainson's hawks equipped with GPS transmitters during periods when hawks were actively migrating north or south (i.e., 'moving' data) or during periods when hawks were not making forward migration progress (i.e., 'stopped' data). This indicates how much the land cover in the row was selected compared to the land cover in the column.

Moving data	Cropland	Grassland	Shrubland/Desert	Forest	Rainforest	Water/Riparian	Other
Cropland	1.0	1.2	1.5	1.2	1.2	5.3	1.0
Grassland	0.8	1.0	1.2	1.0	1.0	4.3	0.8
Shrubland/Desert	0.7	0.8	1.0	0.8	0.8	3.6	0.7
Forest	0.8	1.0	1.2	1.0	1.0	4.4	0.8
Rainforest	0.8	1.0	1.2	1.0	1.0	4.3	0.8
Water/Riparian	0.2	0.2	0.3	0.2	0.2	1.0	0.2
Other	1.0	1.3	1.5	1.2	1.3	5.4	1.0

Stopped data	Cropland	Grassland	Shrubland/Desert	Forest	Rainforest	Water/Riparian	Other
Cropland	1.0	1.5	2.0	2.4	15.6	11.1	-
Grassland	0.7	1.0	1.3	1.6	10.3	7.3	-
Shrubland/Desert	0.5	0.8	1.0	1.2	7.9	5.6	-
Forest	0.4	0.6	0.8	1.0	6.6	4.7	-
Rainforest	0.1	0.1	0.1	0.2	1.0	0.7	-
Water/Riparian	0.1	0.1	0.2	0.2	1.4	1.0	-
Other	-	-	-	-	-	-	-

Source: Manly et al. 2004

Table 4.6. Ratios of Manly's selectivity values (W) of migrating Swainson's hawks equipped with GPS transmitters during periods when hawks were staging prior to fall migration or during periods when hawks were on mid-migration stopovers. This indicates how much the land cover in the row was selected compared to the land cover in the column. Staging data lacked some land covers available in the stopover dataset.

Staging data	Cropland	Grassland	Shrubland/Desert	Forest
Cropland	1.0	2.7	4.6	6.3
Grassland	0.4	1.0	1.7	2.3
Shrubland/Desert	0.2	0.6	1.0	1.4
Forest	0.2	0.4	0.7	1.0

Stopover data	Cropland	Grassland	Shrubland/Desert	Forest	Rainforest	Water/Riparian	Other
Cropland	1.0	1.8	2.0	2.2	11.7	8.8	-
Grassland	0.6	1.0	1.1	1.3	6.6	5.0	-
Shrubland/Desert	0.5	0.9	1.0	1.1	5.8	4.4	-
Forest	0.5	0.8	0.9	1.0	5.3	4.0	-
Rainforest	0.1	0.2	0.2	0.2	1.0	0.8	-
Water/Riparian	0.1	0.2	0.2	0.3	1.3	1.0	-
Other	-	-	-	-	-	-	-

Source: Manly et al. 2004

Figures

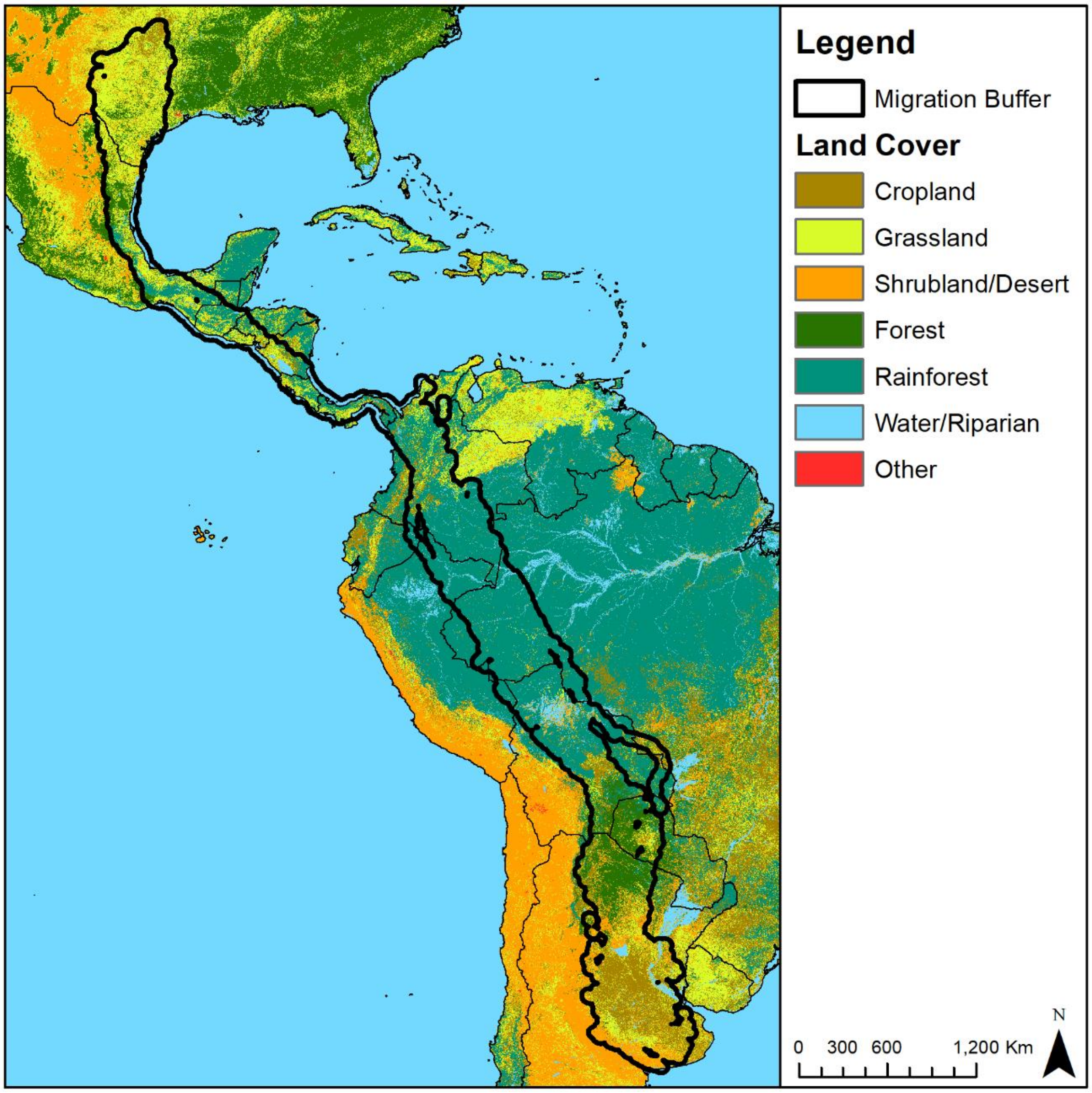

Figure 4.1. Land covers throughout the migration pathway of Swainson's hawks. The migration buffer depicted is a 50-km buffer added to migration locations of hawks tracked with GPS transmitters from 2012 – 2017. This buffer represents the migratory pathway for most hawks of this species from Central America through Argentina. North of Central America, western-breeding hawks may diverge onto a pathway following the pacific coastline or may diverge as they enter northern Mexico and the southern United States and would fan out into breeding areas north and west of the cut off of this buffer. *Adapted from*: The European Space Agency (http://due.esrin.esa.int/page_globcover.php).

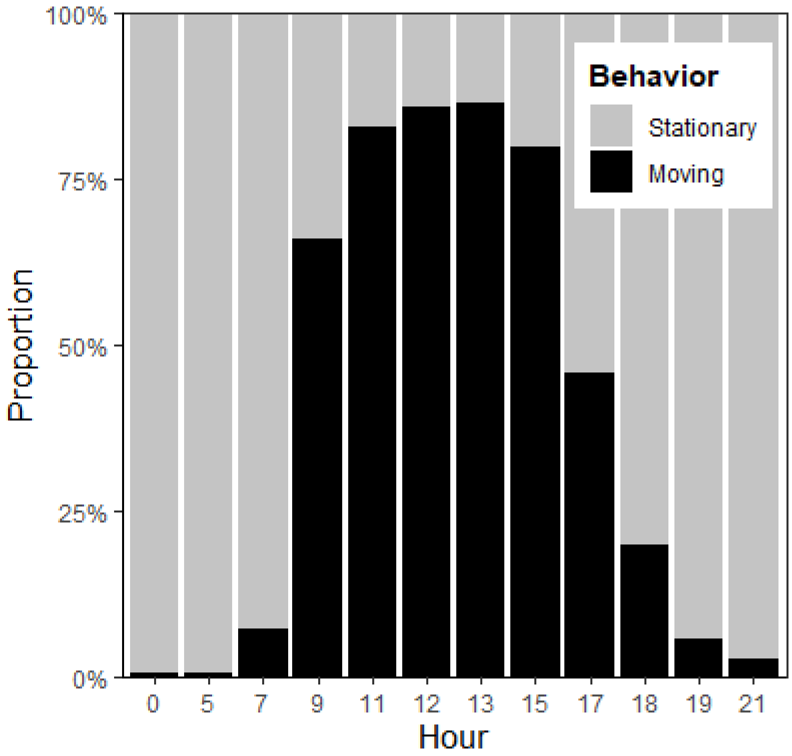

Figure 4.2. Proportion of transmitter locations that reported moving (speed > 0 kmh^{-1}) or stationary (speed = 0 kmh^{-1}) behaviors over time (hour of data transmission). Data obtained from adult Swainson's hawks breeding in northern Texas that were trapped from 2012 – 2013 and tracked with GPS transmitters until 2017.

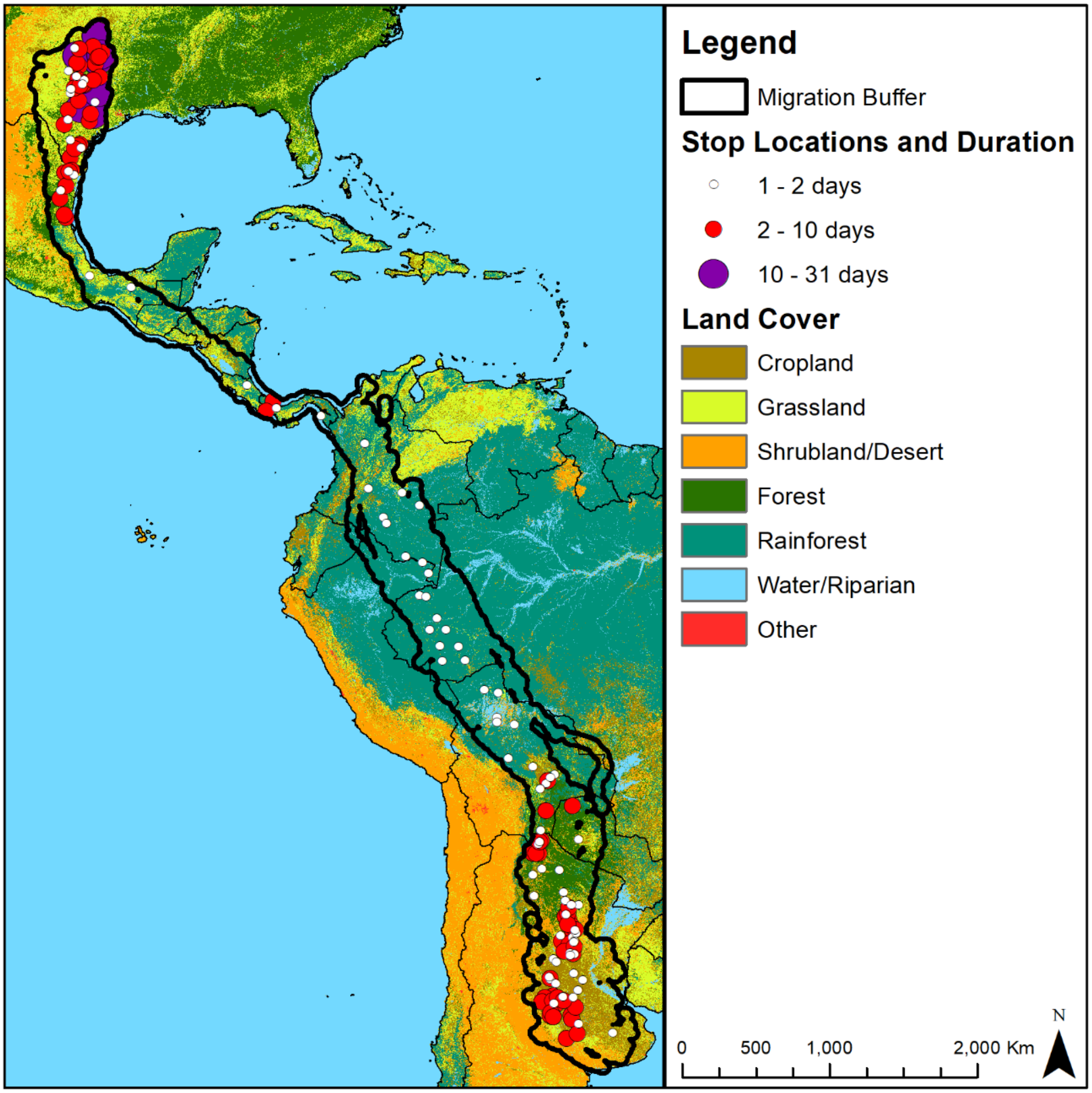

Figure 4.3. Periods when Swainson's hawks tracked with GPS transmitters were not making forward migration progress for > 24 hours. We called these periods 'stops', but hawks were often moving in omnidirectional patterns, especially during pre-migratory staging periods in the United States. The migration buffer represents a 50-km buffer around all migration data recorded for hawks in this study.
Adapted from: The European Space Agency (http://due.esrin.esa.int/page_globcover.php).

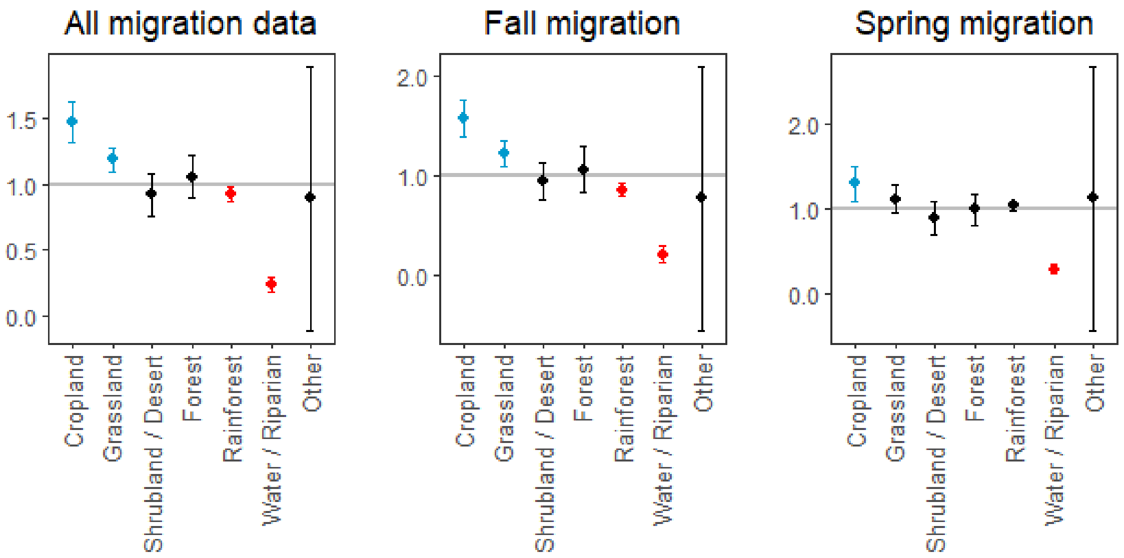

Figure 4.4. Manly's selectivity analyses comparing land cover selection (use versus available) of migrating Swainson's hawks equipped with GPS transmitters, including data from all combined migrations, fall (southward or outbound) migrations, and spring (northward or return) migrations. When error bars (95% confidence intervals) are above one (grey bar), the analysis suggests selection for the land cover (blue), below one suggests selection against that land cover (red), and crossing one suggests no selection (black).
Source: Manly et al. 2004

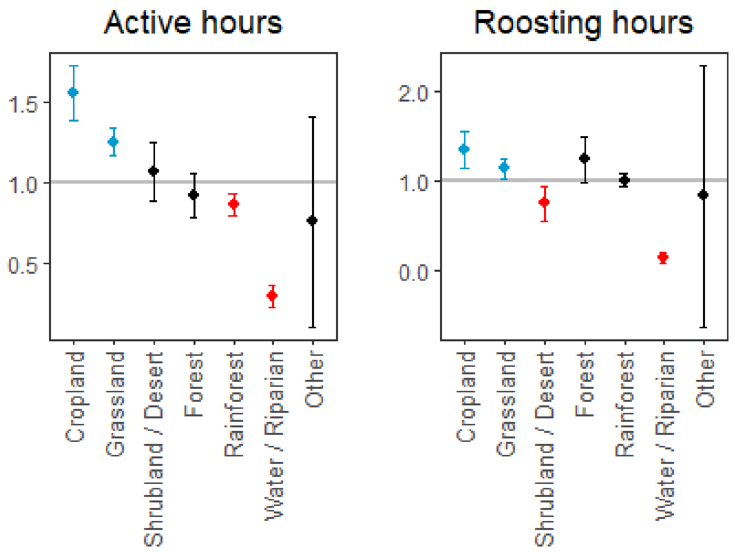

Figure 4.5. Manly's selectivity analyses comparing land cover selection (use versus available) of migrating Swainson's hawks equipped with GPS transmitters during 'active' migration hours (0900 – 1700 hours) or 'roosting' hours (1800 – 0700 hours). When error bars (95% confidence intervals) are above one (grey bar), the analysis suggests selection for the land cover (blue), below one suggests selection against that land cover (red), and crossing one suggests no selection (black).
Source: Manly et al. 2004

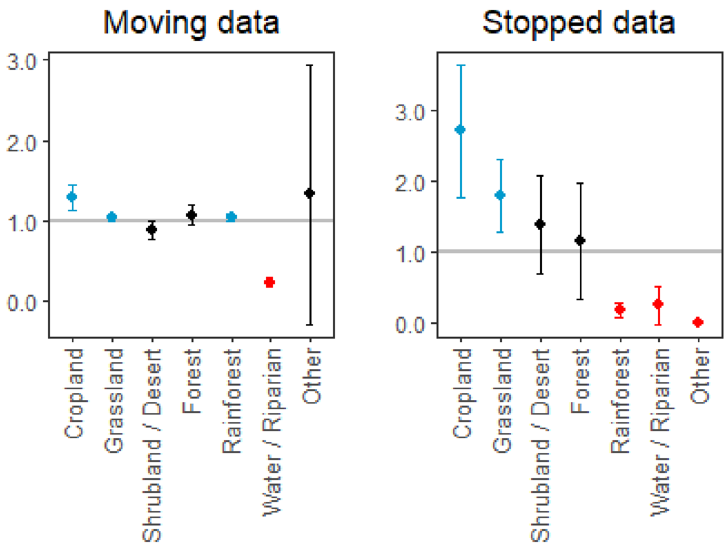

Figure 4.6. Manly's selectivity analyses comparing land cover selection (use versus available) of migrating Swainson's hawks equipped with GPS transmitters during periods when hawks were actively migrating north or south (i.e., 'moving' data) or when hawks were not making forward migration progress (i.e., 'stopped' data). When error bars (95% confidence intervals) are above one (grey bar), the analysis suggests selection for the land cover (blue), below one suggests selection against that land cover (red), and crossing one suggests no selection (black).
Source: Manly et al. 2004

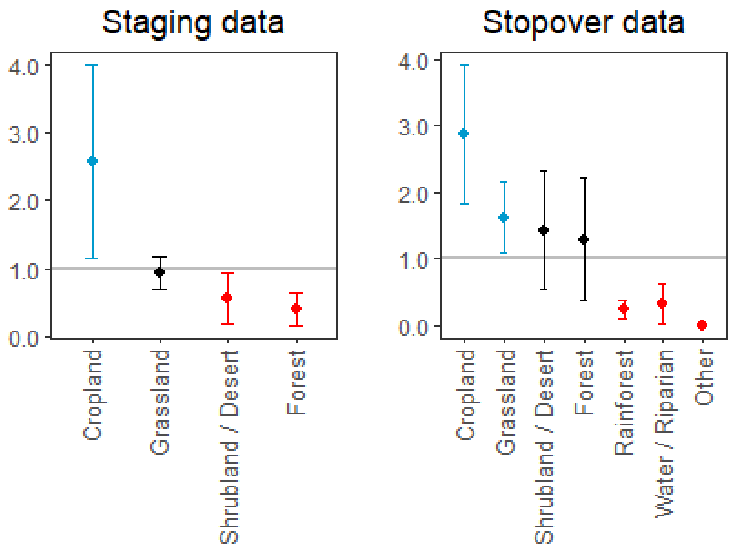

Figure 4.7. Manly's selectivity analyses comparing land cover selection (use versus available) of migrating Swainson's hawks equipped with GPS transmitters during periods when hawks were staging prior to fall migration or when hawks were on mid-migration stopovers. When error bars (95% confidence intervals) are above one (grey bar), the analysis suggests selection for the land cover (blue), below one suggests selection against that land cover (red), and crossing one suggests no selection (black).
Source: Manly et al. 2004

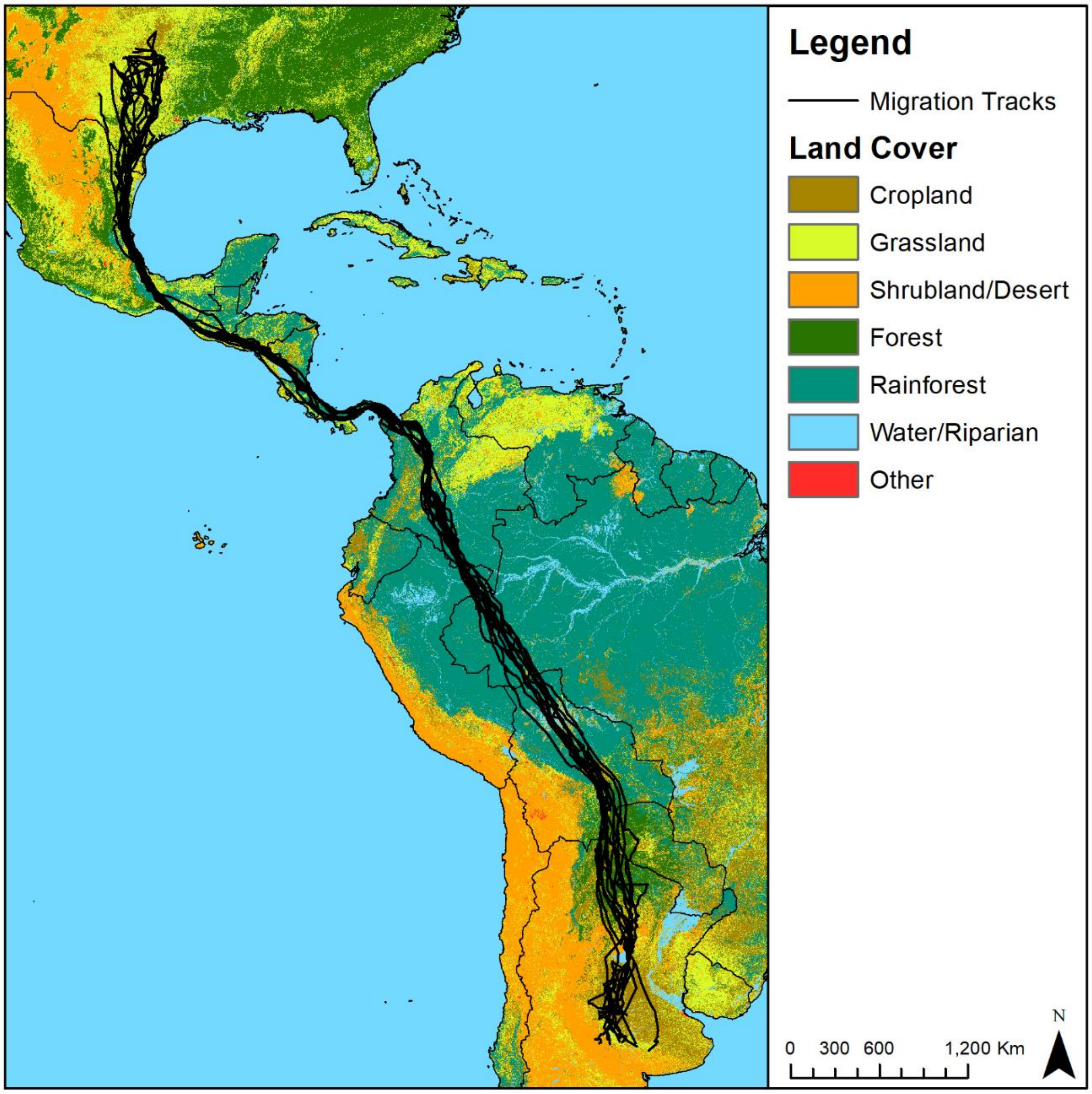

Figure 4.8. Migration tracks of fourteen representative Swainson's hawks tracked with GPS transmitters (8 fall/southward migrations and 6 spring/northward migrations), showing both variability and consistency of routes.
Adapted from: The European Space Agency (http://due.esrin.esa.int/page_globcover.php).

CHAPTER V

SURVIVAL AND BEHAVIORS OF JUVENILE AND SUBADULT SWAINSON'S HAWKS

Abstract

Swainson's hawks (*Buteo swainsoni*) are migratory raptors that breed in western North America and winter in the Pampas of Argentina. Most research on this species has focused on reproduction, habitats, foraging, and populations, with relatively little research on migration or wintering ecology, and, importantly, there is a lack of information about the juvenile and subadult period, which lasts three to five years. We equipped 17 fledgling hawks with satellite transmitters to describe ecology and survival during their first years of life. We observed a post-fledging-dependence period of 19 to 79 days. After gaining independence, hawks spent time wandering the breeding range until migration. Young hawks migrated south at the same time as adults, and first migration attempts showed high variability in routes; most hawks that deviated from the primary route presumably perished before reaching the wintering grounds. Some first-wintering periods were spent at a location northwest of the primary wintering grounds of adult hawks. Hawks that survived the first winter used expected pathways and had lower mortality during future migrations. Young hawks left for the northward migration later and arrived on the summering grounds later than adults, possibly because they were not intending on breeding upon return. On summering grounds, hawks wandered and explored; one hawk appeared to establish a home range in third and fourth summers. Survival was lowest immediately following fledging, and first migrations were another

common period for mortality. We never observed a breeding attempt among this sample, and therefore could not establish natal philopatry or dispersal.

Swainson's hawks (*Buteo swainsoni*) are Neotropical migratory raptors that breed in western North America and migrate to Argentina for the nonbreeding season (Bechard et al. 2010). Most research on this species has focused on reproduction (e.g., Dunkle 1977, Bechard 1983, Bednarz 1988, Houston and Zazelenchuk 2004, Briggs 2007), habitat (e.g., Green and Morrison 1983, Schmutz 1987, Babcock 1995, England et al. 1995, Bosakowski et al. 1996), foraging (e.g., Bechard 1982, Bechard et al. 1990, Rodríguez-Estrella 2000, Giovanni et al. 2007, Behney et al. 2010), and populations (e.g., Schmutz 1984, Smallwood 1995, Janes 2003, Schmutz et al. 2006, Hull et al. 2008) on the breeding range, with relatively little research into migration characteristics (e.g., Fuller et al. 1998, Kochert et al. 2011, Airola et al. 2019) or ecology on the nonbreeding range (e.g., Jaramillo 1993, Woodbridge et al. 1995b, Goldstein et al. 2000, Canavelli et al. 2003). Swainson's hawks may be three to five years old before they enter into breeding populations (Vennum 2017). Importantly, despite numerous studies of Swainson's hawks, there is little published information regarding the survival, ecology, and behaviors of juvenile and subadult age classes. In this study, we set out to compile published observations from the juvenile period and to provide new descriptions and interpretations of survival, locations, and behaviors of juvenile and subadult Swainson's hawks derived from fledglings equipped with satellite transmitters in northern Texas. We additionally compared data from young birds in this study to that for adult Swainson's hawks captured in the same region (Chapter 3) to compare and contrast seasonal behaviors.

The post-fledging parental-care period may be a critical time for young birds to improve body condition (through supplemental feeding and exercise) and learn life skills, such as flying and hunting, in preparation for independence (Grüebler and Naef-Daenzer 2010). In addition, longer post-fledging-care periods may correlate with higher juvenile survival (Grüebler and Naef-Daenzer 2010). Time to independence varies widely across and within species (Russell 2000). Among raptors, there is wide variance in the post-fledging parental-care period among species, but also among and within broods of a given species. For example, ferruginous hawks (*Buteo regalis*) have a post-fledging parental-care period of 10 to 40 days (Konrad and Gilmer 1986), red-tailed hawk (*Buteo jamaicensis*) fledglings stay with parents for 30 to 70 days (Johnson 1973), and eagles may extend post-fledging care beyond 100 days (Hunt et al. 1992) and some species up to a year (Brown 1966).

Swainson’s hawks have a post-fledging parental-care period that may last 11 to 38 days (Fitzner 1980, Bechard et al. 2010, Kolar and Bechard 2016). Juvenile hawks are thought to be dependent upon adults for food until > 17 days post-fledging (Fitzner 1980). The first observed hunting attempts were typically pursuits of insects on the ground, and fledglings tend to walk and perch more than adults (Fitzner 1980, Poole et al. 1988, Chapter 2). Even as hunting skills progressed, juvenile hawks continued to receive supplemental food until they left territories permanently (Fitzner 1980). Independent first-year hawks wearing leg bands have been found upwards of 240 km from their nest and formed groups of 8 to 150 juveniles prior to migration (Bechard et al. 2010). Fitzner

(1980) reported that fledglings appeared to leave the nesting territory unaccompanied and interpreted this as a cessation of family ties. Newton (1979) stated that it is unlikely for raptors to migrate in family groups, also implying that family ties generally end after the post-fledging-care period. Notable exceptions are species that hunt and/or breed cooperatively, such as Harris's hawks (*Parabuteo unicinctus*; Bednarz 1988) and Galapagos hawks (*Buteo galapagoensis*; Faaborg et al. 1995). Fitzner (1980) concluded that the limited time spent with adults and the few successful prey captures observed may result in poor survivorship for juvenile Swainson's hawks after they gain independence.

To our knowledge, there are no quantitative data published describing juvenile Swainson's hawk migration. Evidence from satellite transmitters has shown that migration behaviors, such as timing and speed, of male and female adult Swainson's hawks are similar (Kochert et al. 2011, Groen 2015, Chapter 3). A possibly erroneous assumption, however, is that migration of juvenile Swainson's hawks is the same as that of adults. There is substantial evidence from other raptors of age-specific differences in migration behavior. Martell et al. (2001) reported female osprey (*Pandion haliaetus*) began migration before fledglings had fully achieved independence, leaving males to care for the young. Juvenile sharp-shinned (*Accipiter striatus*) and Cooper's hawks (*Accipiter cooperii*) typically migrate before adults; DeLong and Hoffman (1999) proposed that the reduced hunting skills of juveniles drove the earlier departure for migration as prey availability declined. Early reports of northern harrier (*Circus hudsonius*) migration implied that females depart earlier than males, but because females are so difficult to distinguish from juvenile birds, Bildstein et al. (1984) argued that instead juvenile harriers might depart before adults, and that previous studies may have been misleading due to not separating female adults from juveniles. Mueller et al. (2000) reported juveniles of several raptor species initiated migration before adults in Wisconsin. In contrast, Peregrine falcons (*Falco peregrinus*), rough-legged hawks (*Buteo lagopus*), and northern goshawks (*Accipiter gentilis*) were reported to have roughly equal departure timing among both ages and sexes (Mueller et al. 2000). Juvenile golden eagles (*Aquila chrysaetos*) were reported as migrating before adults, because breeding adults have a long post-fledging-care period, while second- or third-year non-breeding eagles were free to begin migration when resources and internal pressures warranted the movements (Rus et al. 2017). Some long-distance migrant raptor species from other continents, such as honey buzzard (*Pernis apivorus*), Montagu’s harrier (*Circus pygargus*), osprey, and hobby (*Falco subbuteo*), demonstrate a pattern in which adults migrate ahead of juveniles during autumn migration (Kjellén 1992). This age-related difference may be due to adult competition for resources on the winter range, where improving body condition is essential for the following breeding season, while juveniles are merely focused on survival (Kjellén 1992). Alternatively, adults may be able to detect declining food resources on the breeding range earlier than juvenile birds, due to more experience with changing seasons (Kjellén 1992). Another alternative explanation is that adults may simply reach migrating body condition at a faster rate than juvenile birds (Newton 1979). Finally, these explanations may occur simultaneously, depending on the species and conditions.

There are data suggesting some components of migration may be different between adult and juvenile Swainson’s hawks. For example, evidence from leg band recoveries suggested that hatch-year Swainson’s hawks may initiate migration as much as a month later than adults (Schmutz 1996). In contrast, Littlefield and Johnson (2013) speculated juvenile Swainson's hawks might migrate before adults, based on concentrations of hawks with distinguishable plumage at a single staging site near Dimmitt, Texas. However, a single staging area is not enough evidence for migration differences, because Swainson's hawks occupy a large region of potential staging areas (Kochert et al. 2011, Chapter 3) and might move nomadically among areas, using locally abundant and ephemeral resources, before beginning full migration. During a peak in counting migrating raptors in Veracruz, Mexico, photographic evidence showed a consistent presence of juveniles among large flocks of Swainson's hawks, indicating similar migration timing when hawks reached that point in southward travel (Campbell and Inzunza 2017).

Overall, migration timing for different age classes is unclear for this species. Fitzner (1980) and Bechard et al. (2010) suggested that hatch-year hawks cease family ties and leave the natal area independently of siblings and adults, forming juvenile groups during a period of independent ranging and staging prior to their first migration. A lack of experience and growing bodies may cause fledglings to linger on the breeding grounds for a longer period than adults. It is possible that caring for fledglings leaves adults in poor body condition so that they must have a longer staging period and thus leave for migration later than juveniles. It is also possible that once juveniles leave the natal territory, adults are free to migrate as soon as needed, possibly resulting in earlier or equivalent migration initiation. In addition, older subadults may or may not behave differently than first-year birds. Due to the mass migratory behavior of Swainson's hawks (Fox 1956, Thiollay 1980, Bechard et al. 2010), and observations from raptor count sites mid-migration (Campbell and Inzunza 2017), we suspect age classes have similar migratory timing, which allows inexperienced juveniles to follow adults to the nonbreeding grounds. We also do not know which age group arrives back on the breeding grounds first (if any difference exists), as there is a lack of quantitative evidence in the literature.

Other than timing and pre-migratory staging, nothing is known about migration behaviors for young Swainson's hawks. Due to a lack of experience and reduced body condition, we suspected that juveniles, particularly hatch-year hawks, may take longer to complete migration than adults, possibly making more or longer stops for rest and feeding. Young hawks may follow routes that stray from the fairly-direct passageway that adults adhere to (Schmutz 1996, Fuller et al. 1998, Kochert et al. 2011, Chapter 3), again, due to lack of experience, and a higher potential for making mistakes, such as following the wrong migrating birds; Swainson's hawks share the migratory pathway, and flocks, with other raptor species, such as turkey vultures (*Cathartes aura*), Mississippi kites (*Ictinia mississippiensis*), and broad-winged hawks (*Buteo platypterus*) that are bound for different wintering areas (Smith 1985, Parker 1999, Haines et al. 2003, Bechard et al. 2010, Dodge et al. 2014). Finally, we anticipated that juveniles would show a later departure and slower northward migration in spring, especially during their first migration, because adult hawks may have a drive to return to and defend breeding territories as quickly as possible (Newton 1979), while young hawks are unlikely to breed upon return in this species (Vennum 2017).

Swainson's hawks are thought to primarily spend the boreal winter season in the Pampas (grasslands) region of Argentina during South America's austral summer

(Sarasola et al. 2008, Bechard et al. 2010, Kochert et al. 2011). Kochert et al. (2011) described adult Swainson's hawks tagged with satellite transmitters occupying six Argentinian provinces (Buenos Aires, Córdoba, Entre Rios, La Pampa, Santa Fe, and Santiago del Estero) and the western edge of Uruguay. This range represents the Dry and Humid Chaco, Espinal, Humid Pampas, Paraná Flooded Savanna and Uruguayan Savanna ecoregions, and the general landscape can be described as a mosaic of grasslands, pastures, and agriculture, similar to their breeding-range habitats (Canavelli et al. 2003, Bechard et al. 2010). Adult transmitter data from our related study supported the nonbreeding range spanning a large portion of Argentina, with tagged birds using all the previously described regions and some birds venturing into four additional provinces (San Luis, Mendoza, La Rioja, and Chaco), one additional ecoregion (Low Monte Desert), and further into Uruguay than previously described (Chapter 6). Jaramillo (1993) additionally observed > 5000 Swainson's hawks (mostly juveniles) near Puerto Piramide, Chubut province, Argentina, which, to our knowledge, is the most southerly observation of this species, and is > 400 km south of all adult data we collected (Chapter 3). Airola et al. (2019) tracked California hawks to short-stop wintering grounds along the migration pathway (and some areas east of the pathway) in Mexico, Guatemala, Nicaragua, Venezuela, Colombia, Bolivia, and northern Argentina. Furthermore, small numbers of Swainson's hawks have been reported overwintering in the United States, Cuba, Costa Rica, Panama, and Paraguay (Browning 1974, Herzog 1996, Bechard et al. 2010).

Juvenile Swainson's hawks have been observed on the primary wintering grounds with adults (Goldstein et al. 1999*a*, Canavelli 2000, Sarasola and Negro 2005, Bechard et al. 2006), but we do not know if all juveniles overwinter in the same Pampas region of

Argentina as adult hawks (Sarasola et al. 2008, Bechard et al. 2010, Kochert et al. 2011), or if juveniles can be found wintering in different areas. Juvenile Swainson's hawks have been equipped with very high frequency (VHF) radio transmitters and tracked on the wintering range, but research was limited to study sites on the primary wintering grounds in La Pampa and Santa Fe provinces (Canavelli 2000). Jaramillo (1993) found that almost all Swainson's hawks in Chubut province, Argentina (south of all previously reported wintering locations), were juveniles, and adult hawks were rarely found in that location. Jaramillo (1993) suggested that age-related segregation may occur on the wintering grounds, but, if true, such segregation might only occur on the periphery of the wintering range, because there are multiple reports of juveniles mixing with flocks of adults in their primary wintering areas (Goldstein et al. 1999*a*, Canavelli 2000, Sarasola and Negro 2005, Bechard et al. 2006). Here, we provide some of the first juvenile Swainson's hawk locations during the nonbreeding (winter) season obtained by satellite telemetry to compare to adult data we collected (Chapter 6) as well as what was reported in the literature.

Houston and Schmutz (1995*a*) reported the top causes of mortality of banded Swainson's hawks across the global range were shooting, vehicular collision, and electrocution, with smaller sources of mortality including depredation, starvation, drowning, and disease. Bechard et al. (2010) explained that persecution (shooting) was a common cause of mortality on the breeding range up to the 1950's, and has declined, but not disappeared, in modern times. Almost half of band recoveries south of the United States were the result of shooting, with specific notes from Columbia and Argentina (Bechard et al. 2010). Swainson's hawks suffered high mortality due to use of organophosphate pesticides, specifically Monocrotophos and Dimethoate, on the wintering range in the 1990's (Woodbridge et al. 1995*b*, 1996, Goldstein et al. 1999*b*, *c*, Bechard et al. 2010). Inclement weather, such as storms, wind, and hail, cause additional mortality for eggs, nestlings, and roosting birds throughout the global range (Gilmer and Stewart 1984, Sarasola et al. 2005, Bechard et al. 2010).

Little information is available on survival during the juvenile and subadult stage (fledging to recruitment) of Swainson's hawks. Research indicates a post-fledging survival (i.e., surviving from fledging to independence) of 80-98% in this species (Fitzner 1980, Poole et al. 1988, Woodbridge et al. 1995*a*, Kolar and Bechard 2016). Woodbridge et al. (1995*a*) noted that finding birds in juvenile plumage was rare in California, and Houston and Schmutz (1995*a*) suggested that juvenile Swainson's hawks may not return to their natal areas until recruitment. Therefore, we know little of survivability between fledglings gaining independence and reaching 3-5 years of age.

Genetic research across the breeding range showed a high level of intermixing and suggested no population structure, with only slight differences found in the population occupying the Central Valley of California (Hull et al. 2008). If adult Swainson's hawks have high site fidelity to nesting territories, as research suggests (Fitzner 1980, Schmutz et al. 2006, Bechard et al. 2010), then the mixing of genes likely results from natal dispersal. Multiple accounts of rarely resighting hawks until recruitment (Houston and Schmutz 1995*a*, Woodbridge et al. 1995*a*, Briggs 2007) suggests that Swainson's hawks spend their juvenile summers in separate areas or ranging across the landscape, possibly acting as floaters and locating future territories in which to attempt breeding. Variability in results and low resighting and recovery of leg bands indicates that the questions of juvenile survival and natal dispersal have yet to be answered for this species. By equipping fledgling Swainson's hawks with satellite transmitters and following them to recruitment, we hoped to better address the questions of survival, natal philopatry versus dispersal, and associated timing and behaviors.

Methods

We monitored nests and captured hawks in Armstrong, Carson, Hale, Hockley, Lubbock, Potter, Randall, and Swisher counties, Texas (Fig. 5.1). In 2016, 2017, and 2018 we deployed solar-powered platform transmitter terminals (hereafter PTT; Solar PTT-100, Microwave Telemetry, Inc., Columbia, Maryland) on young Swainson's hawks. We selected nests that were located on public property or on private property we were allowed to access. When nestlings were at least 38 days old (determined by plumage growth; Gossett and Makela 2005), we accessed the nest and captured birds by hand (Bloom et al. 2007; Table 5.1). In 2018, the region experienced a drought and there was a dearth of available fledglings to work with; those fledglings that were captured were often in poor and starving body condition, and thus we did not use them for transmitter deployment. To deploy more transmitters, we drove public roadways in Lubbock and surrounding counties to locate fledged juveniles (Wheeler and Clark 1995, Bechard et al. 2010) and attempted to capture them using a bal-chatri trap baited with a mouse (*Mus musculus*) from August to September 2018 (Bloom et al. 2007; Table 5.1). All fledglings captured were fitted with United States Geological Survey Bird Banding Laboratory aluminum leg bands. Each hawk in good body condition and weighing > 425 g was equipped with a PTT on a backpack-style harness secured with Teflon® ribbon

(Meyburg and Fuller 2007); the weight restriction ensured transmitters added no more than 4% of a hawk's bodyweight (the transmitter weighed 17 g) (Table 5.1). When multiple fledglings were available and met weight requirements, we placed transmitters on a maximum of two per nest; this gave us the opportunity to see how long siblings associated after fledging (Table 5.1).

We had two sets of PTTs; one set (hawks J1 – J14) only reported Argos (Doppler-shift) locations, and the other set (hawks J15 – J17) reported both Argos and Global Positioning System (GPS) locations (Table 5.1). Argos PTTs were programmed to report locations with a duty cycle of 10 hours on, attempting to contact a satellite every 60 seconds, and 24 hours off. Dual PTTs reported Argos locations on the same schedule and GPS locations every day at 0000, 0500, 0700, 0900, 1100, 1200, 1300, 1500, 1700, 1800, 1900, and 2100 hours, local time; the GPS schedule allowed for direct comparison with adult data in a related study (Chapter 3). Transmitters reported a location class (LC) with every Argos data point (LC 3, 2, 1, 0, A, B, and Z), which told us how much estimated error should be associated with each location based on the number of satellites the PTT connected with (< 250 m to > 1,500 m or unknown/unlimited error; Douglas et al. 2012; Table 5.2). We used the Douglas-Argos filter in Movebank (https://www.movebank.org) to increase our confidence that the dataset reflected reasonable location estimates; this filter marks implausible locations as outliers based on a series of user-defined parameters (Douglas et al. 2012). We altered the following four parameters from the default options available: Keep_LC = 3, Minrate = 90, Xmigrate = 5, and Xoverrun = 5 (Douglas et al. 2012; justifications provided in Table 5.3). We additionally retained all GPS locations, because they had higher and more-reliable accuracy (± 18 m error, Microwave Telemetry, Inc., Columbia, Maryland).

When a transmitter stopped sending data, we attempted to determine fate of the hawk. If the transmitter sent a series of points from the same location, we declared mortality and recorded the first date and location in the series as the last known location of the hawk (removing redundant post-mortality points). If the data suddenly stopped coming in, we recorded a presumed mortality and last known location. When last locations were within the study region, we attempted to visually locate the hawk or carcass.

We classified four seasons in the transmitter data to describe what juvenile hawks did during 'summer' on the breeding range, 'fall' or southward (outbound) migration, 'winter' on the nonbreeding range in South America, and 'spring' or northward (return) migration. We classified the beginning of the first fall migration as the first point when hawks moved > 150 km away from and southward of the PTT deployment location without returning (Kochert et al. 2011). Because hawks did not always return to the natal nest area on the summer range, we classified later fall migrations as beginning when hawks made consistent southward movements towards the winter range without returning to their summer-range locations. We classified the end of fall migration as the last point before hawks stopped moving southward for ≥ 10 days. We classified the beginning of spring migration as the first point when hawks began consistently moving northward without returning to wintering locations (Kochert et al. 2011). We classified the end of spring migration as the last point before hawks stopped making consistent northward progress for ≥ 10 days. Points between migratory movements were classified as summer when located in North America and winter when in South America.

We used Excel, ArcMap 10.7, and Program R 3.6.2 (packages 'stats' and 'ggplot2'; R Core Team 2019, Wickham et al. 2020) to explore and interpret data. We described behaviors interpreted from visual analysis of hawk locations. When examining summer-season movements, we compared hawk locations to the nest they fledged from, estimating great-circle distances to understand behaviors. We split the first summer into two periods. The 'post-fledging period', where 95% of locations were within a 2-km buffer around the nest; we selected an arbitrary distance of 2 km, because early-fledging data often exceeded 1 km from the nest but were typically contained within 2 km of each nest for long periods or until the bird began migration. The 'independent-ranging period', when fledglings presumably became independent of adults and moved away from the natal area (i.e., 95% of locations were outside of the 2-km buffer) but had not yet begun migratory movements. For all seasons after the first summer, we referenced adult Swainson's hawk GPS transmitter data when comparing migration dates, length of seasons, adherence to expected pathways, and locations on the breeding and nonbreeding ranges (Chapters 3 and 6).

To determine if migration dates and season lengths were similar between juveniles and adults (Chapter 3), we first performed an F test to determine if variances were equal, then we performed two-tailed Student's T-tests (for equal or unequal variance, depending on result of each F test) in Program R. Our hypothesis was that timing of fall migration would be equivalent between age classes (and thus all lengths of seasons would be equivalent), because of the importance of flocking during migration (i.e., we expected that juveniles follow in mixed-age flocks, as indicated by observations in Mexico [Campbell and Inzunza 2017], and therefore moved at the same time as adults); because that is a null hypothesis, we used the T-tests to examine the possibility of the alternative hypothesis that variables differed by age class. We expected to find a potentially longer spring migration season, with later return dates, because of the different drivers of hawks of breeding age and those that were not expected to breed upon return (i.e., juveniles and subadults). We otherwise expected season lengths to be similar among age classes unless differences in migration caused differences in lengths of winter and summer seasons. Additionally, we thought the first year of life might show more significant differences than later years, because young, inexperienced hawks may have variable migration timing and seasonal behaviors, while older hawks with the potential of recruitment might begin to resemble adults in their life cycles. We therefore examined the first year of a life (i.e., the first migrations, first winter, and first return to the breeding range), pooled data for subsequent years, and all data combined against pooled adult data (Chapter 3). To account for eight individual t-test comparisons within each dataset, we used a Bonferroni correction on the standard alpha value ($\alpha = 0.05$) to only suggest a significant difference if $P \leq 0.0063$, but also noted when P-values were between 0.05 and 0.0063 where possible. We provided the descriptive statistics of means and standard deviations for all metrics.

Results

We captured 27 juvenile Swainson’s hawks (25 on nests, 2 by trap), but only tagged 17 (including six pairs of siblings) that were in good body condition and met our mass criteria (Table 5.1). Transmitters reported data from 6 July 2016 to 18 April 2021 (Table 5.1). We collected seven days to 3.7 years of data on hawks tagged as fledglings, with an average data collection time of 293 ± 376 days. The Douglas-Argos filter identified 1,143 data outliers (which we removed), and the final dataset contained 36,874 Argos and GPS locations (Table 5.2).

No hawks were located alive after data transmissions ended; we assumed all data cessations indicated mortality. Survival of juvenile hawks declined post-fledging, with only 24% of hawks surviving to their second year, 12% surviving to their third year, and 6% surviving into a fourth year (Fig. 5.2). No hawks in this study were recruited into the breeding population. Three hawks presumably perished within 2 km of the nest, one hawk presumably perished 8 km from its nest, and one additional hawk did not make it to the first fall migration after reaching independence. Of 12 hawks that initiated their first fall migration, only seven made it to the winter range. Of those, six survived to attempt the first spring migration. Four hawks survived through a second summer, fall migration, and made it to the winter range for a second time. Two hawks survived through the second spring migration, third summer, fall migration, and winter seasons. Of these last two hawks, one presumably perished on the winter range, and one survived through a fourth year and was still alive as of this writing (18 April 2021).

Nine hawks suffered likely mortalities (i.e., many points were sent from the same location with no movement, however, this could also indicate transmitter drop), seven hawks had an unclear fate (e.g., PTT may have failed or mortality may have occurred; Table 5.1, Fig. 5.3). All five hawks that died in the US were only recently off the nest (Table 5.1, Fig. 5.3). Five hawks may have died during fall migration in Bolivia, Brazil, and Peru, two hawks may have died during spring migration in Panama and Mexico, and four hawks may have died during winter in Argentina and Uruguay (Table 5.1, Fig. 5.3). The last known location for the living hawk (J14) was Mexico during its fourth spring migration (Table 5.1, Fig. 5.3).

Summer (breeding) season

Hawks (n = 11) spent an average of 85 ± 7 days on the summer range prior to beginning migration (Table 5.4). During the post-fledging period, hawks stayed within 2 km of their nest for 45 ± 18 days (Table 5.5, Fig. 5.4). Locations during the post-fledging period averaged 2 ± 5 km from the nest, though some hawks made long distance movements (up to 79 km) for short periods before returning to the natal area (Table 5.6, Fig. 5.4). All hawks made movements > 50 km and 45% made movements > 250 km from the nest prior to beginning migration (Table 5.5, Fig. 5.5). When hawks entered the independent-ranging period, distance from nest increased to 178 ± 129 km with an overall northerly trend to movements (Table 5.6, Fig. 5.5 and 5.6). Four hawks returned to the 2-km buffer one or more times after beginning large movements away from the nest, while eight hawks never returned (Table 5.5). Hawk J17 was trapped and therefore not associated with a nest; after fitting this hawk with a transmitter, it moved 150 km northeast, where it remained until migration (Fig. 5.5).

Juvenile and subadult hawks spent 110 to 169 days (overall mean = 140 ± 23 days, n = 7, birds = 4; Table 5.4) on the summer range during their second, third, and fourth years. The first return to the breeding range was on average 35 days shorter than a typical adult summer (adult mean = 174 ± 12 days, $t = 4.7704$, $P < 0.0001$), and, while not statistically significant, the lengths of later summers for subadult hawks were on average 32 days shorter than adults (t = 1.8651, P = 0.1979; Table 5.7). Juvenile and subadult locations ranged from 1 to > 1,000 km (overall mean = 203 ± 207 km) from their natal nests (Table 5.8). Two hawks visited their natal areas multiple times, while two other hawks never returned to their natal region (Table 5.8, Fig. 5.7 – 5.9).

Overall, summer behaviors appeared to be exploratory and nomadic. In the second summer, hawk J3 wandered from southern Texas to New Mexico to northern Texas, moving 90 to 370 km between temporary settling locations (Fig. 5.7). Hawk J8 wandered from Colorado to Kansas, Oklahoma, northern Texas, and then circled within those areas, generally moving 60 to 130 km at a time (Fig. 5.7). Hawk J9 similarly circled from Colorado to Nebraska to New Mexico to Kansas, moving 90 to 570 km at a time (Fig. 5.7). Hawk J14 moved between Texas, Oklahoma, and Kansas at distances of 75 to 540 km (Fig. 5.7). During the third summer, hawk J3 moved from southern Texas to northeastern Mexico to Northern Texas, Kansas, and Oklahoma, moving 80 to 1,100 km at a time and moving in a similar pattern as the previous summer (Fig. 5.8). Hawk J14 also mimicked some of its previous summer’s pattern, moving between three locations in northern Texas at distances of 30 to 90 km (Fig. 5.8). During the fourth summer, hawk J14 moved 80 to 220 km between locations in northern Texas and Kansas (Fig. 5.9).

Fall migration

Hawks took 41 to 77 days (overall mean = 56 ± 11 days, n = 14, birds = 7) to complete fall migrations (Tables 5.4, 5.7, and 5.9). Overall, fall migration timing was similar to adult data, but the first time a hawk began migration, they did so on average 6 days later than adults (a result that was not statistically significant, but may be biologically meaningful; first-year mean = 8 Oct ± 7 days, adult mean = 2 Oct ± 9 days, t = -2.5951, P = 0.0163; Table 5.7). The first fall migration showed high variability and multiple deviations from expected routes (based on adult Swainson's hawk data; Chapter 3), while later migrations followed expected pathways (Table 5.9, Fig. 5.10 – 5.13).

During the first attempted migration, five hawks deviated from the expected route; four of those hawks experienced mortality en route (Table 5.9, Fig. 5.3 and 5.10 – 5.12). While other hawks crossed Costa Rica and Panama along the Atlantic coastline (the common pathway for adults; Chapter 3), hawk J4 detoured along the Pacific coastline, then crossed open water to spend 10 days on Coiba Island, Panama, before crossing back to resume southward travel (Fig. 5.11). Hawks J6 and J7 traveled a similar route from south Texas to eastern Colombia, where they both deviated from the expected route at around the same time (Fig. 5.12). The two hawks then separated near Arauca, Colombia on 5 Nov 2017 (Fig. 5.12). J6 went southeast and presumably perished in the Amazon rainforest in Grão-Pará province, Brazil, and J7 paralleled the expected route until it reached southern Brazil, where it turned north and east and presumably perished among croplands in São Paulo province (Fig. 5.12). Hawk J10 also went off course in Colombia, but then continue southward and survived (Fig. 5.10). Last, hawk J17 went southward into Peru, and ended up in the Andes Mountain range, 50 to 300 km west of all other routes (Fig. 5.10). The last known location for J17 indicated it had corrected its pathway and was about to enter the winter range when we lost contact with the transmitter (Fig. 5.3 and 5.10).

Winter (nonbreeding) season

Juvenile and subadult hawks spent 76 to 106 days (mean = 92 ± 10 days, n = 10, birds = 6) on the winter range, which was similar to adult data (adult mean = 89 ± 14 days, t = -0.7853, P = 0.4360; Tables 5.4 and 5.7). Like fall migration, some hawks showed unique behaviors during their first winter, while subsequent winters were spent in areas that overlapped adult data (Fig. 5.14 and 5.15). Hawks J3, J9, and J11 spent time in Salta and Tucuman provinces, Argentina, during the first winter season, the bulk of which was 350 to 400 km northwest of adult Swainson's hawk winter locations (Fig. 5.14).

Spring migration

Juvenile and subadult hawks took 48 to 102 days (overall mean = 73 ± 22 days, n = 7, birds = 4) to complete spring migrations (Tables 5.4, 5.7, and 5.10). The first spring migration began 8 days later (not statistically significant, but possibly biologically meaningful; first-year start mean = 3 Mar ± 4 days, t = -1.9903, P = 0.0525) and ended 34 days later than adult migrations (first-year end mean = 17 May ± 20 days, adult start mean = 23 Feb ± 10 days, adult end mean = 13 Apr ± 12 days, t = -5.2626, P < 0.0001; Table 5.7). Subsequent spring migrations showed similar patterns of starting and ending later (subadults on average began migration [mean = 5 Mar ± 6 days] 10 days later and ended [mean = 12 May ± 35 days] 29 days later than adults), but testing showed no statistical differences (Table 5.7); however, the overall average spring start date was significantly later than adults (mean = 4 Mar ± 5 days, t = -4.1078, P = 0.0003). Overall, spring migrations for juveniles and subadults were 25 days longer than adults (overall mean = 73 ± 22 days, adult mean = 48 ± 7 days), and though not statistically significant, this may be biologically meaningful (t = -2.9954, P = 0.0232; Table 5.7). One hawk deviated from expected routes during the first spring migration (Table 5.10, Fig. 5.16). Similar to fall data, juveniles on subsequent spring migrations followed the routes of adult hawks (Fig. 5.17).

Sibling locations and movements

Sibling hawks J1 and J2 were both depredated within two weeks of fledging and within 2 km of the nest. Sibling hawks J3 and J4 gained independence from adults 23 days apart. Hawk J3 continued to return to the nest site until migration and was within 2 km of its sibling on the last day hawk J4 was near the nest. However, when hawk J4 gained independence, it moved in a different direction from J3’s locations, and the birds started migration 4 days and 48 km apart (Fig. 5.12). Migration continued independently, with hawk J4 presumably perishing en route, and J3 making it to the wintering range in Salta province, Argentina (Fig. 5.12 and 5.14).

Sibling hawks J6 and J7 gained independence from adults 9 days apart. The birds started migratory movements 2 days and 237 km apart. Although the two hawks followed the same migration pathway, distance between pairs of points that were recorded within 2 hours of each other (mean 14 ± 33 minutes, median 2 minutes) ranged from 11 to 467 km (mean = 100 ± 80 km, median 85 km) from south Texas to eastern Colombia, where their pathways split and each bird continued moving until mortality (Fig. 5.12).

Sibling hawks J8 and J9 gained independence from adults 7 days apart. Both birds went northward into Oklahoma, Colorado, and Kansas during their independent-ranging period, but all locations and movements appeared to be independent (Fig. 5.5). The two hawks started fall migration on the same day but were 270 km apart at the first points identified as migratory movements (Fig. 5.12). However, similar to hawks J6 and J7, hawks J8 and J9 appeared to come together on the same migratory route (Fig. 5.12) in central Texas (where birds were 5 km apart on the second day of migration). Distances between pairs of points that were recorded within 2 hours of each other (mean 13 ± 22 minutes, median 2 minutes) ranged from 0 to 135 km (mean = 31 ± 29 km, median 23 km) from central Texas to western Brazil, and hawks appeared to continue travelling a nearly identical pathway to Argentina. Hawks J8 and J9 ended migration two days and 407 km apart (Fig. 5.12). Locations of the siblings were independent on the wintering grounds, with little overlap in locations and no indication they encountered each other (Fig. 5.14). Similar to fall migration, hawks J8 and J9 started spring migration on the same day, but 1,214 km apart (Fig. 5.16). Unlike fall migration, however, the birds never came together and instead maintained > 1,000 km distance throughout the migration pathway, ending migration 18 days and 77 km apart (Fig. 5.16). During the second summer season, the sibling hawk locations overlapped some, with birds potentially encountering each other once (i.e., one pair of points was 5 km and 30 minutes apart), but otherwise all locations and movements appeared independent (Fig. 5.7). Hawks J8 and J9 began their second fall migration 16 days and 241 km apart and, like spring migration, they maintained about 500-km distance through Bolivia, where they came within 13 km of each other on 1 Dec (Fig. 5.13). The birds continued independent movements, however, and ended migration 1 day and 650 km apart (Fig. 5.13). Both birds presumably perished during the same winter season; J9 in northern Argentina and J8 in Uruguay almost three months later (Fig. 5.3 and 5.15).

Sibling hawks J10 and J11 gained independence from adults 15 days apart. Hawk J11 spent most of its independent-ranging time in Oklahoma, whereas J12 spent the period entirely in western and central Texas (Fig. 5.5). The sibling hawks started fall migration 6 days and 641 km apart (Fig. 5.12). Migration continued independently along the same general pathway, and hawks ended migration 3 days and 1,795 km apart (Fig. 5.12). The sibling hawks spent the winter in different locations with no overlap and began spring migration 10 days and 1,720 km apart (Fig. 5.14 and 5.16). Hawks came within 78 km of one another on 12 March. The siblings presumably perished 3 days and almost 3,000 km apart: J10 in Panama and J11 in northern Mexico (Fig. 5.3).

Last, sibling hawks J12 and J13 gained independence from adults 4 days apart. Hawk J12 spent the remainder of its life ranging ≥ 100 km from its sibling, with no overlap of locations, and presumably perished 148 km from its nest prior to migratory movements, while J13 survived to attempt a first fall migration (Fig. 5.3 and 5.5).

Discussion

Behaviors

We observed longer post-fledging periods spent near the nest (19 – 79 days) than the 11 to 38 days described by Fitzner (1980). During late-season nest checks, we frequently observed fledgling hawks perching on the ground, likely taking advantage of abundant grasshopper prey (Chapter 2), similar to descriptions of fledgling Swainson’s hawks and red-tailed hawks (Johnson 1973, Fitzner 1980). During the post-fledging period, transmitters revealed short-duration movements away from the nest of up to 79 km, especially as birds grew older and, presumably, more independent. Similarly, Johnson (1973) reported some fledgling red-tailed hawks moved as much as 35 km from the nest and returned to continue interactions with adults, while other fledglings remained in the nest area until permanent departure. Yamaç and Bilgin (2012) reported that young cinereous vultures (*Aegypius monachus*) made daily trips of 10 to 60 km from the nest as they neared independence. In addition to the post-fledging dependency period, we also described a period of independent ranging in which juvenile hawks moved away from nests (up to 580 km) prior to the start of the first southward migration. Our descriptions are similar to gradual movements away from natal areas that Soutullo et al. (2006) described for fledged golden eagles. Movements occurred in all directions, but juvenile hawks generally went north of their natal range and large movements were common during this period. Our observations indicate that juveniles disappearing from their natal area does not mean they have initiated migratory travel, as Fitzner (1980) and Poole et al. (1988) assumed. We suspect independent ranging of juvenile hawks may serve a similar pre-migratory foraging function as staging for adult hawks (Warnock 2010). Swainson's hawks migrate en masse (Fox 1956, Smith 1985, Bechard et al. 2010) and independent ranging may additionally allow juvenile hawks to locate flocks to follow southward; the later first fall migration initiation dates we described suggests that hatch-year hawks likely wait to find a migratory flock before moving southward.

Juvenile Swainson's hawk fall migration was similar to migration behaviors of adults, with only a few notable exceptions. Most dates of migration departure and arrival by juvenile hawks were within the range reported for adult Swainson's hawks (Kochert et al. 2011, Airola et al. 2019, Chapter 3). We observed two instances of juveniles beginning fall migration later (Oct 16 and 22) than any adult departure date reported in transmitter literature (9 - 13 Oct [adults]; Kochert et al. 2011, Airola et al. 2019, Chapter 3). It is possible that some juvenile hawks don't find groups to join for southward migration, or that those that fledge later in the season begin in poorer body condition, may need more time to stage and prepare before starting migration. Adult Swainson's hawks from the unique California population (Hull et al. 2008) tracked by Airola et al. (2019) departed for fall migration exceptionally earlier than those in this and the Kochert et al. (2011) study; we suspect that our results are likely more representative of the general North American Swainson's hawk population. Our data for juvenile and adult Swainson's hawk migration timing is consistent with visual observations of mixed-age flocks passing through Mexico (Campbell and Inzunza 2017); the similar migration timing among adults and juveniles of this species likely facilitates success in inexperienced juveniles making it to the wintering grounds in their first year.

The first migration attempt (southward migration) was the most variable for juvenile hawks in this study, with 42% of individuals deviating from the route we expected them to take based on data collected from banded and transmitter-tagged adults (Schmutz 1996, Fuller et al. 1998, Kochert et al. 2011, Chapter 3). Deviation from the established route may come at a substantive cost; 80% of the juvenile hawks that went off the course experienced mortality. One significant deviation involved a hawk visiting Coiba Island, Panama, travelling a minimum of 19 km over open water each way. Adult hawks we tracked in a related study only occasionally crossed open water (Chapter 3), and none were recorded visiting Coiba Island, nor was this location reported in previous studies (Schmutz 1996, Kochert et al. 2011, Airola et al. 2019). *Buteo* hawks in general tend to avoid water during migration, but occasional trips over water, getting blown over water by cross-winds, and vagrants potentially exploring new areas do occur within most species (Kerlinger 1989, Bildstein 2006). In addition, Swainson's hawks have been observed in Cuba (Rodríguez-Santana 2010), and the closest relative of Hawaiian hawks (*Buteo solitarius*) and Galapagos hawks is thought to be the Swainson's hawk (Hull et al. 2008, Bechard et al. 2010), supporting that island vagrancy should be considered a rare, but unsurprising, behavior for this species.

Within the nest-monitoring study area, we did not typically begin observing hawks in juvenile plumage (Wheeler and Clark 1995) until late May to mid-June, which indicates that late spring arrival may be a common behavior. Three of four juveniles that survived to return to the summer range arrived later (18 May – 8 June) than the latest known adult arrival date (7 May; Chapter 3). Additionally, those same hawks spent longer migrating (77 – 102 days) during spring than did adults in our related study (maximum = 73 days; Chapter 3) and those tracked by Kochert et al. (2011; maximum = 72 days). Thus, some, but not all, juveniles may take longer to migrate northward and arrive later to the summering grounds. This may be due to individuals not expecting to attempt breeding that year and thus being in no hurry to arrive. Ueta and Higuchi (2002) suggested that young birds may take longer to migrate because they spend more time at stopover sites; we did not examine juvenile hawk stopovers in this study, but adult Swainson's hawks are known to make stops throughout migration (Kochert et al. 2011, Airola et al. 2019, Chapter 3).

Importantly, while the first fall and spring migrations showed variable routes and differential timing from adults, subsequent subadult migrations were generally indistinguishable from adult data. The only difference we found in later migrations of subadults was one instance of substantially later arrival on the summer range (20 June at the end of the second spring migration). We suspect that experience allows Swainson's hawks to improve navigation with age, which has support in literature on migrating osprey, honey buzzards, black kites (*Milvus migrans*), and whooping cranes (*Grus americana*) (Thorup et al. 2003, Mueller et al. 2013, Sergio et al. 2014).

We observed three juvenile Swainson's hawks wintering in Salta and Tucuman provinces, Argentina (Dry Chaco ecoregion), 350 to 400 km northwest of known wintering locations for most adult Swainson's hawks (Sarasola et al. 2008, Bechard et al. 2010, Kochert et al. 2011, Chapter 6). On Google Earth (Google Inc. 2017), this region appears to be a mosaic of croplands and forest, with most juvenile hawk locations occurring on apparent agricultural fields. This behavior only occurred during the first winter, with subsequent winters being spent within the typical range of adult hawks. We do not know why some juvenile hawks stopped short. It is possible this region is a common location for juvenile Swainson's hawks to spend their first winter. We found four records of Swainson's hawks in that region on the bird-sighting database, Ebird (Sullivan et al. 2009); one was a photographed adult that may have been finishing migration (date was 28 Dec, within the range of southward migration; Kochert et al. 2011) and no observations described a hawk in juvenile or subadult plumages. Interestingly, some California Swainson's hawks that were reported to stop short in unusual wintering locations also were found to overwinter in Salta province (Airola et al. 2019), which may have influenced the short-stop of juveniles we observed.

A likely explanation for the unusual juvenile winter locations is that juvenile hawks simply stopped short towards the end of migration, due to declining fat stores and finding the first reasonably suitable area to forage and survive (Goldstein et al. 1999*a*, Airola et al. 2019). Cues to stop at that location might include the behavior of other juveniles, but might also be aggregations of adult Swainson’s hawks stopping over for multiple days before they continue on to primary wintering areas (Kochert et al. 2011, Chapter 3), or even spending the winter in Salta province, such as some California hawks were recently observed doing (Airola et al. 2019). While we discovered an interesting winter location, this behavior may be no more common than Swainson’s hawks wintering in other unusual localities, such as Bolivia, Columbia, Costa Rica, Cuba, Guatemala, Mexico, Nicaragua, Panama, Paraguay, Venezuela, and the United States (Browning 1974, Herzog 1996, Bechard et al. 2010, Airola et al. 2019).

Jaramillo (1993) suggested that adult and juvenile Swainson’s hawks may segregate on the wintering range, and though their observations took place south of known adult wintering areas, our data lend support to the idea. However, we propose an additional explanation. Bechard et al. (2010) provided anecdotal evidence that hatch-year hawks group together on the summer range after gaining independence from adults. We found small groups of second-year hawks (6 – 12 birds) perching within 1 km, sometimes within 2 m, of each other on fence posts, electrical and irrigation structures, and on the ground. Sightings of groups were common throughout the summer season, but we did not track individuals and cannot determine if hawks stayed in groups or if aggregations were fluid, with hawks joining and leaving at will. We additionally observed solitary juveniles, indicating that the gregarious behavior is likely facultative and opportunistic. It is possible that Jaramillo's (1993) observations represent evidence that the juvenile aggregation behavior that began on the breeding range continues through the winter season, and perhaps year-round. Bechard et al. (2010) described Swainson’s hawks as an overall tolerant and moderately social species compared to other North American raptors, with breeding birds frequently foraging near conspecifics when away from the nest, and nonbreeding birds forming flocks upwards of 100 individuals in California. Gregarious behaviors of juvenile hawks may be driven by instinct, because the species is known to be gregarious during staging, migration, and on the wintering grounds (Johnson et al. 1987, Bechard et al. 2010, Littlefield and Johnson 2013). These behaviors may also be driven by extensive foraging on gregarious prey, such as patches of grasshopper outbreaks (Bechard 1982, Smallwood 1995, Canavelli et al. 2003, Bechard et al. 2010, Littlefield and Johnson 2013). Alternatively, for juvenile birds, forming aggregations may facilitate a learning-by-experience environment that gives a fitness advantage to social birds over solitary individuals. Smith et al. (2002) studied social learning in large mixed flocks of brown-headed cowbirds (*Molothrus ater*) and found that some associations proved to be important for fitness, such as juvenile males associating with adult males leading to increased courtship success. Aggregating may also increase survival of young birds, as seen in juvenile flocks of yellow-eyed juncos *(Junco phaeonotus*; Sullivan 1988).

Summering behaviors of juvenile hawks in this study indicated long-distance ranging and exploration. Researchers have reported ranging, exploratory, and nomadic behaviors among immature raptors in a variety of species, including ferruginous hawks (Watson 2003), golden eagles (Caro et al. 2011), Bonelli's eagles (*Aquila fasciata*, Real and Mañosa 2001, Caro et al. 2011), Spanish imperial eagles (*Aquila adalberti*, González et al. 1989), northern goshawks (Wiens et al. 2006), Cooper's hawks (Mannan 2010), and Eurasian eagle-owls (*Bubo bubo*, Delgado et al. 2009). The fitness advantages of juvenile ranging behaviors may include increased survival, because birds are free to move as resource availability changes, and increased reproductive potential, as young birds may stake out future breeding locations while acting as floaters and filling in breeding-population gaps when available (Morrison and Wood 2009).

Hawk J14 appeared to maintain a loose home range about 85 km northwest of its natal nest throughout the third and fourth summers. We visited the location of highest concentration of points on 28 May 2020; the hawk's core home range was patches of grassland surrounded by agricultural fields that lacked trees or any structure upon which a hawk might build a nest. Surrounding landscape patches contained at least four large stick nests, two of which we confirmed were occupied by unbanded adult Swainson's hawks, but only a few reported hawk locations were within 500 m of those nests (Fig. 5.18). Given that we assumed hawk J14 was female based on mass at capture, evidence of a breeding attempt would be a strong concentration of points at a nest location. Instead, the pattern of locations suggested a loose concentration over landscapes devoid of trees or other nesting structures until mid-June; the hawk then left the area and moved into similar landscapes in Kansas for a month and a half, then returned to this home range until migration. As this was the only hawk that lived long enough to potentially breed, we therefore concluded that no hawk we tracked recruited into the breeding population during this study.

Siblings in this study appeared to gain independence from each other once the post-fledging period ended. Similar to observations of family break up described by Fitzner (1980), Meyburg et al. (2005), and McIntyre et al. (2009), juvenile transmitter data indicated that siblings left the natal area individually and spent the independent-ranging period in different and varying locations. However, all siblings appeared to migrate in similar ways, following the same routes during the first fall migration, as would be expected given the mass-migration behavior of the species (Bechard et al. 2010).

Swainson's hawks migrate in large kettles with hundreds and thousands of birds of both the same species and in mixed flocks with broad-winged hawks, turkey vultures, and others (Bechard et al. 2010). Following mixed flocks of various species bound for different wintering areas may also explain why some juveniles departed from the expected Swainson's hawk migration route. While mass migration of multiple species may lead a small proportion of juveniles off track, one evolutionary significance of kettle migration lies in the ability of juvenile hawks to learn appropriate migration pathways and behaviors without the need for family groups to stay together after the nesting period (Newton 1979). Additionally, mass migration may increase survivability and efficiency at all life stages, because birds can locate air thermals to use energy-efficient soaring flight, birds can avoid obstacles (such as mountain ranges or storm systems) by observing the behaviors of other birds before encountering the obstacle itself, and birds may be able to find food and roosting locations by observing groupings of other birds (Smith 1985, Rotics et al. 2016).

Survival and dispersal

With a small sample size of 17 hawks and no evidence of recruitment, we chose to only generalize about juvenile survivorship and dispersal. Assumed mortality of juvenile hawks was highest during the first 6 months post-fledging, with four hawks presumably perishing near the nest, one presumably perishing just after gaining independence, and five additional hawks failing to complete the first migration. Out of remaining hawks, mortality occurred on the winter range and during spring migration seasons. Only 24% of marked individuals survived their first year, which is consistent with previous estimations of low survival among young hawks (Millsap and Allen 2006). After the first year, however, hawks in this study only (presumably) perished on the wintering grounds, which contrasts with adult mortality data from our related study; adult Swainson's hawks from the same region were assumed to have most often perished on the breeding grounds (Chapter 3).

Reports indicate 80 to 98% survival of Swainson's hawks during the post-fledging period (Fitzner 1980, Poole et al. 1988, Woodbridge et al. 1995*a*, Kolar and Bechard 2016). Depredation, electrocution, starvation or disease, and drowning were the apparent causes of mortality in previous reports (Fitzner 1980, Kolar and Bechard 2016). Assuming all data terminations meant mortality, we found a lower post-fledging survival rate of 77%. We only recovered one carcass, that had been depredated; the three other (presumed) mortalities were of unknown cause. It is possible that, rather than mortality, the transmitters failed (i.e., the data suddenly ended rather than sending us multiple single-location points) or were dropped (i.e., sending similar repetitive data as from a dead bird). In general, post-fledging survival is known to start out relatively low and increases rapidly with time (Naef-Daenzer and Grüebler 2016), and in the case of Swainson's hawks, we found it no surprise to encounter early (presumed) mortalities and a gradual increase in survivability as time went on.

Long-distance migration is also a vulnerable time for hatch-year Swainson's hawks. We found low first-migration survival at 58%; in contrast, annual migration survival of adult Swainson's hawks nesting in the High Plains of Texas ranged from 83 to 100% (Chapter 3). Oppel et al. (2015) similarly reported 50% first-migration survival among Egyptian vultures (*Neophron percnopterus*), Rotics et al. (2016) reported 78% first-migration survival among white storks (*Ciconia ciconia*), and Klaassen et al. (2014) suggested migration may be six times more risky than stationary periods for three old-world raptor species at adult life stages. Goldstein et al. (1999*a*) reported lower post-migration body mass in hatch-year Swainson's hawks compared to adults, which may have important consequences during the stressful and energetically expensive migration period. Body condition prior to travel is likely one of the most important aspects of surviving migration (Brown 1996, Cooper et al. 2015), which makes food resources during the post-fledging and independent-ranging periods especially important in this species. If Swainson's hawks only put on enough fat reserves to make it to the destination via the instinctually ingrained route, as suggested by Smith et al. (1986), then anything that increases energy expense, such as too much flapping flight (Rotics et al. 2016), or that delays travel, such as veering off route, spending extensive time at stopover locations (which may alternatively be opportunities to rest and refuel, if hawks forage en route; Kirkley 1991), or encountering inclement weather events (e.g., Sarasola and Negro 2006), may mean death for the individual hawk.

On the wintering range, pesticides have been found to be especially harmful; for example, the organophosphate Monocrotophos was linked to mass mortality events in Argentina during the 1990's (Woodbridge et al. 1995*b*, 1996, Goldstein et al. 1999*b*). However, efforts to reduce pesticide use were effective (Goldstein et al. 1999*c*). We assume survival threats on the wintering range today are likely similar to those on the breeding range (e.g., persecution, environmental toxins, collision with vehicles and stationary objects, electrocution, etc.; Bechard et al. 2010), so we have no clear explanation as to why we only found presumed mortality in Argentina and Uruguay after the first year in this sample of hawks; perhaps this was the result of random chance.

We failed to collect data for long enough to present results regarding natal philopatry or dispersal. With rare exception, Swainson's hawks do not breed until 3 to 5 years of age (Houston and Schmutz 1995*a*, Vennum 2017). Four birds in this study survived to the second summer, two survived to the third summer, and one survived to the fourth summer. Half the hawks visited their natal nest locations in summers subsequent to their hatch year, which may indicate natal philopatry. Only one bird settled into a seasonal home range 85 km from its natal nest, but no evidence of breeding was ever detected.

Recruitment rates from long-term banding and monitoring efforts in California indicated natal philopatry (dispersal no greater than 46 km), however their search area was limited, so they may have missed cases of greater dispersal (Woodbridge et al.

1995*a*, Briggs 2007, Vennum 2017). Houston and Schmutz (1995*a*) reported dispersal distances ranging from < 10 to > 300 km from natal areas, with a majority of hawks (70%) breeding near their natal territory, indicating that while dispersal appears to happen in this species, natal philopatry may be the more common behavior. Additionally, Bechard et al. (2010) reported 4 males banded in Alberta, Canada, breeding within 10 km of their natal sites, while 7 females were found 6 to 320 km away, indicating that perhaps females are more likely to disperse than males. Greenwood (1980) summarized philopatry and dispersal across many avian species and concluded that females are generally more likely to disperse. The available data suggests that dispersal is common in this species, but is not obligative, with young hawks both visiting and venturing far from nests, and adult hawks both returning to natal regions and nesting far from them (Houston and Schmutz 1995*a*, Woodbridge et al. 1995*a*, Briggs 2007, Bechard et al. 2010, Vennum 2017). This plasticity allows for high genetic mixing (Hull et al. 2008) and varied options of territory locations on the breeding range, and thus may have long-term population survival advantages (Morrison and Wood 2009).

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Tables

Table 5.1. Information about 17 fledgling Swainson's hawks captured in the High Plains of Texas from 2016 to 2018 and equipped with platform transmitter terminals (PTT). PTT 162229 was recovered post-mortality and reused on a second hawk (A and B). Sex was estimated based on mass: males (M) were smallest, females (F) were largest, and hawks with moderate masses were labeled as unknown (U). Nest names indicate location within study area region (P = Pantex Plant, A = near Amarillo, Texas, L = near Lubbock, Texas, and X = outside of main study areas used for monitoring nests) and order of nest discovery (Chapter 2). PTT burden was the mass of the transmitter compared to the hawk's mass. Fate was classified as mortality (carcass found [C] or mortality was suspected based on data pattern [M]), PTT failure (data suddenly stopped, which could indicate PTT failure or mortality [P]), or bird was known to still be alive (A) when we produced this table.

Hawk	PTT Number	Sex	Nest	Mass (g)	PTT burden	PTT Deployment Date	End date	Length of Data Collection (days)	Fate	Sibling
J1	162229A	U	P104	745	2.3%	6 July 2016	13 July 2016	7	C	J2
J2	162235	F	P104	830	2.0%	6 July 2016	19 July 2016	13	M	J1
J3	162227	M	P077	685	2.5%	6 July 2016	1 Mar 2019	968	P	J4
J4	162228	M	P077	736	2.3%	6 July 2016	28 Nov 2016	145	M	J3
J5	162238	U	A018	760	2.2%	8 July 2016	12 Dec 2016	157	M	-
J6	162236	M	P289	696	2.4%	12 July 2017	26 Nov 2017	137	M	J7
J7	162237	M	P289	665	2.6%	12 July 2017	12 Dec 2017	153	M	J6
J8	162234	M	A035	713	2.4%	12 July 2017	11 Mar 2019	607	P	J9
J9	162239	F	A035	895	1.9%	12 July 2017	24 Dec 2018	530	P	J8
J10	162231	F	L199	826	2.1%	16 July 2017	21 Apr 2018	279	M	J11
J11	162232	F	L199	899	1.9%	16 July 2017	24 Apr 2018	282	M	J10
J12	162233	U	A007	767	2.2%	26 July 2017	18 Sept 2017	54	P	J13
J13	162230	F	A007	829	2.1%	26 July 2017	10 Nov 2017	107	P	J12
J14	162229B	U	P025	749	2.3%	26 July 2017	18 Apr 2021	1,362	A	-
J15	175368	U	X302	737	2.3%	23 July 2018	13 Aug 2018	21	P	-
J16	175370	F	X303	790	2.2%	26 July 2018	8 Oct 2018	74	P	-
J17	175369	U	Trapped	749	2.3%	15 Sept 2018	1 Dec 2018	77	M	-

Table 5.2. Number of juvenile Swainson's hawk transmitter points within Argos location-class categories that were retained after filtering. Estimated error is standard for Argos location classes. Global positioning system (GPS) represents another type of location obtained on some transmitters, which we included here to show the totality of locations that were used in analyses.

Argos Location Class	Estimated Error (m)	Number of Points
3	< 250	13,121
2	250 – 500	5,408
1	500 – 1,500	4,453
0	> 1,500	4,459
A	Unknown	2,916
B	Unknown	5,512
Z	Invalid Location	5
GPS	18	1,000
Total		36,874

Source: Douglas et al. (2012), Microwave Telemetry, Inc. (Columbia, Maryland).

Table 5.3. The Douglas-Argos filter was used to remove implausible locations from satellite transmitter data, and here we provide our selections for the following parameters in Movebank and our justification; all other parameters were left as default.

Parameter	Selection	Justification
Filter Method	‘Best Hybrid’	Douglas et al. (2012) suggested this setting for migratory species
Keep_LC	LC 3	Allows filter to identify implausible locations from all location classes except location class 3 (the points with the smallest error radius)
Minrate	90 kmh^{-1}	Maximum speed used in data filtering by Kochert et al. (2011)
Xmigrate	5 km	A median of 95% of breeding-season adult Swainson’s hawk transmitter locations were within 5 km of their nest (Chapter 3)
Xoverrun	5 km	We set this equal to the Xmigrate value

Source: Movebank <https://www.movebank.org>, Kochert et al. (2011), Douglas et al. (2012), Chapter 3.

Table 5.4. Number of days juvenile Swainson’s hawks spent in each complete season: summer (Su) represents locations on the breeding range in North America, fall (F) represents southward (outbound) migration, winter (W) represents locations on the non-breeding range in South America, and spring (Sp) represents northward (return) migration. Data obtained from transmitters worn by Swainson’s hawks captured as fledglings in the High Plains of Texas from 2016 – 2018. Sample size (n) is number of datasets used to calculate means and standard deviations (SD).

	1st Year				2nd Year				3rd Year				4th Year		
Hawk	Su	F	W	Sp	Su	F	W	Sp	Su	F	W	Sp	Su	F	W
J1	*														
J2	*														
J3	86	44	106	50	167	62	76	48	169	41	*				
J4	83	*													
J5	80	73	*												
J6	89	*													
J7	86	*													
J8	87	45	101	96	122	62	*								
J9	86	47	99	77	125	77	*								
J10	91	51	82	*											
J11	98	48	89	*											
J12	*														
J13	75	*													
J14	72	56	85	80	141	60	90	102	110	50	96	56	145	65	99
J15	*														
J16	*														
J17	+	*													
n	11	7	6	4	4	4	2	2	2	2	1	1	1	1	1
Mean	84.8	52.0	93.7	75.8	138.8	65.3	83.0	75.0	139.5	45.5	-	-	-	-	-
SD	7.3	10.1	9.7	19.1	20.6	7.9	9.9	38.2	41.7	6.4	-	-	-	-	-

* Bird did not survive season.

+ Data was incomplete, because bird was trapped away from its natal nest.

Table 5.5. Number of days it took for each fledgling hawk to make the first movement of varying distances (km) from their natal nest, total length of the post-fledging period (when 95% of locations were within 2 km of the nest), and whether the hawk returned to the 2-km natal-area buffer after beginning independent ranging (when 95% of locations were away from the nest, but migration had not started). Data obtained from transmitters worn by Swainson’s hawks captured as fledglings in the High Plains of Texas from 2016 – 2018. Sample size (n) is number of datasets used to calculate means and standard deviations (SD).

	Distance from natal nest (km)					Post-fledging	Returned to
Hawk	> 2	> 10	> 50	> 100	> 250	period (days)	natal area?
J1	*						
J2	3	*					
J3	1	1	73	84	88[+]	56	Yes
J4	3	7	69	83[+]	84[+]	79	Yes
J5	3	41	74	81[+]	85[+]	72	Yes
J6	2	30	39	39	89[+]	28	Yes
J7	10	20	22	25	65	19	No
J8	1	38	44	45	59	43	No
J9	3	9	40	40	51	37	No
J10	6	41	55	55	58	54	No
J11	4	27	41	43	46	39	No
J12	3	37	37	37	*	35	No
J13	3	24	34	34	75[+]	33	No
J14	1	15	52	56	74[+]	48	No
J15	7	7	*				
J16	7	14	*				
n	15	14	12	12	11	12	
Mean	3.8	22.2	48.3	51.8	70.4	45.3	
SD	2.6	13.8	16.5	20.4	15.4	17.6	

* Bird died before moving this distance from the nest.

[+] Bird did not move this distance until migration.

Table 5.6. Average and maximum distances (km) hawks moved from their natal nest locations during the first summer. The ‘post-fledging period’ represents when 95% of hawk locations were within 2 km of the nest and the ‘independent-ranging period’ represents when birds moved away from the natal area but had not yet begun migration. Data obtained from transmitters worn by Swainson’s hawks captured as fledglings in the High Plains of Texas from 2016 – 2018. Sample size (n) represents number of points used to calculate means, standard deviations (SD), and maximum values (Max).

	All data			Post-fledging period				Independent-ranging period			
Hawk	n	Mean	SD	n	Mean	SD	Max	n	Mean	SD	Max
J1*	45	0.6	0.6	45	0.6	0.6	2.4	0			
J2*	86	0.9	1.4	86	0.9	1.4	10.5	0			
J3	739	7.7	19.0	498	1.2	2.2	16.3	241	21.2	28.8	122.8
J4	610	6.4	18.6	581	3.9	12.4	78.7	29	56.6	39.6	96.2
J5	654	7.2	21.2	587	1.0	1.7	19.5	67	61.4	33.0	102.4
J6	673	65.6	55.9	209	1.3	0.9	5.9	464	94.6	42.7	133.0
J7	725	138.7	107.0	163	0.7	0.6	4.8	562	178.7	87.3	325.4
J8	732	99.8	106.7	374	1.1	2.0	20.3	358	203.0	49.3	273.0
J9	654	158.0	147.5	251	2.7	6.5	31.6	403	254.7	104.3	366.9
J10	723	61.3	111.3	406	1.6	1.9	16.7	317	137.7	133.6	435.5
J11	781	232.2	203.4	304	1.3	1.6	17.1	477	379.3	109.9	579.5
J12*	274	41.3	64.1	195	0.6	0.8	5.5	79	141.9	0.4	144.0
J13	568	59.8	54.4	220	1.1	2.5	26.4	348	96.9	35.6	211.1
J14	482	62.1	86.5	285	1.6	2.5	14.9	197	149.6	72.9	215.0
J15*	210	0.4	1.4	210	0.4	1.4	13.6	0			
J16*	343	1.6	1.2	343	1.6	1.2	13.4	0			
Overall	8,299	76.8	121.3	4,757	1.6	5.0	78.7	3,542	177.7	129.1	579.5

* Bird did not survive season.

Table 5.7. Comparison of average start and end dates and length of seasons (number days) between the first year of juvenile Swainson's hawks life, later (second, third, and fourth) years of juvenile data, and all juvenile data combined, with all data (1 – 5 years) available from adult Swainson's hawks tagged with Argos and GPS satellite transmitters from 2012 – 2021. Fall and spring refer to southbound and northbound migrations, summer refers to the breeding season in North America, and winter refers to the nonbreeding season in South America. In the case of the first-year dataset, we did not count the summer birds fledged from nests; instead we considered their first return to the breeding range in comparison with a typical adult summer. Sample size 'N' represents number of birds and 'n' represents number of data sets considered when calculating means and standard deviations (SD). T-tests were performed to determine if datasets differed, and the test statistic (t), degrees of freedom (df) and P-value are provided; we used an F test to determine if T-test for equal or unequal variance should be performed. All calculations excluded incomplete data. We accounted for eight comparisons within each group of juvenile data by adjusting the alpha using a Bonferroni correction.

Juvenile		Juvenile Hawks			Adult Hawks			T-test Results		
Dataset	Data Type	N	n	Mean ± SD	N	n	Mean ± SD	t	df	P-value
First year	Fall start	12	12	8 Oct ± 6.6	23	46	2 Oct ± 9.0	-2.5951	23	0.0163
	Fall end	7	7	1 Dec ± 10.0	23	49	27 Nov ± 10.5	-0.9002	54	0.3720
	Spring start	6	6	3 Mar ± 3.9	19	42	23 Feb ± 9.5	-1.9903	46	0.0525
	Spring end	4	4	17 May ± 19.7	18	39	13 Apr ± 11.7	-5.2626	41	< 0.0001**
	Length of fall	7	7	52.0 ± 10.1	23	46	56.3 ± 14.3	0.7587	51	0.4515
	Length of spring	4	4	75.8 ± 19.1	18	39	47.7 ± 6.6	-2.9196*	3	0.0597
	Length of winter	6	6	93.7 ± 9.7	19	42	88.5 ± 13.6	-0.8562	46	0.3963
	Length of summer	4	4	138.8 ± 20.6	15	24	173.7 ± 12.3	4.7704	26	< 0.0001**
Later years	Fall start	4	7	30 Sept ± 16.7	23	46	2 Oct ± 9.0	0.3321*	7	0.7502
	Fall end	4	7	4 Dec ± 11.0	23	49	27 Nov ± 10.5	-1.6921	54	0.0964
	Spring start	2	4	5 Mar ± 6.2	19	42	23 Feb ± 9.5	-1.9920	44	0.0526
	Spring end	2	3	12 May ± 35.2	18	39	13 Apr ± 11.7	-1.4272*	2	0.2877
	Length of fall	4	7	59.6 ± 11.4	23	46	56.3 ± 14.3	-0.5777	51	0.5660

Source: Chapter 3.

Table 5.7. Continued.

Juvenile		Juvenile Hawks			Adult Hawks			T-test Results		
Dataset	Data Type	N	n	Mean ± SD	N	n	Mean ± SD	t	df	P-value
	Length of spring	2	3	68.7 ± 29.1	18	39	47.7 ± 6.6	-1.2426*	2	0.3391
	Length of winter	2	4	90.3 ± 10.2	19	42	88.5 ± 13.6	-0.2187	44	0.8279
	Length of summer	2	3	141.3 ± 29.7	15	24	173.7 ± 12.3	1.8651*	2	0.1979
All data	Fall start	12	19	5 Oct ± 11.7	23	46	2 Oct ± 9.0	-1.0100	27	0.3214
	Fall end	7	14	2 Dec ± 10.2	23	49	27 Nov ± 10.5	-1.7406	61	0.0868
	Spring start	6	10	4 Mar ± 4.7	19	42	23 Feb ± 9.5	-4.1078*	29	0.0003**
	Spring end	4	7	15 May ± 24.8	18	39	13 Apr ± 11.7	-3.3636*	7	0.0135
	Length of fall	7	14	55.8 ± 11.1	23	46	56.3 ± 14.3	0.1190	58	0.9057
	Length of spring	4	7	72.7 ± 21.9	18	39	47.7 ± 6.6	-2.9954*	6	0.0232
	Length of winter	6	10	92.3 ± 9.5	19	42	88.5 ± 13.6	-0.7853	50	0.4360
	Length of summer	4	7	139.9 ± 22.5	15	24	173.7 ± 12.3	3.8035*	7	0.0066

* T-test for unequal variances was performed.

** Statistically significant at α = 0.0063.

Table 5.8. Average, minimum, and maximum distances (km) from natal nests to hawk locations during three summers after hatch year. Data obtained from transmitters worn by Swainson's hawks captured as fledglings in the High Plains of Texas from 2016 – 2018. Sample size (n) represents number of points used to calculate means and standard deviations (SD).

Summer	Hawk	n	Mean	SD	Min	Max
Second	J3	1,393	290.4	266.0	0.5	999.0
	J8	863	224.1	64.1	49.4	335.8
	J9	748	348.3	86.2	200.8	647.9
	J14	1,049	172.3	198.6	1.9	568.1
Third	J3	1,263	177.1	307.3	1.6	1,110.8
	J14	1,054	90.3	26.8	1.6	117.7
Fourth	J14	1,358	155.8	112.4	1.3	354.2
Overall		7,728	203.1	207.0	0.5	1,110.8

Table 5.9. Departure dates, arrival dates, and route information for hawks that attempted up to four fall (southward or outbound) migrations. Data obtained from transmitters worn by Swainson's hawks captured as fledglings in the High Plains of Texas from 2016 – 2018. Standard deviation (SD) is provided with means.

Migration	Hawk	Departure Date	End Date	Did bird depart from the expected route?
First	J3	1 Oct 2016	14 Nov 2016	No
	J4*	28 Sept 2016		Yes
	J5	27 Sept 2016	9 Dec 2016	No
	J6*	9 Oct 2017		Yes
	J7*	7 Oct 2017		Yes
	J8	7 Oct 2017	21 Nov 2017	No
	J9	7 Oct 2017	23 Nov 2017	No
	J10	16 Oct 2017	6 Dec 2017	Yes
	J11	22 Oct 2017	9 Dec 2017	No
	J13*	9 Oct 2017		No
	J14	8 Oct 2017	3 Dec 2017	No
	J17*	9 Oct 2018		Yes
	Mean	7 Oct	30 Nov	
	SD	6.6	9.8	
Second	J3	8 Oct 2017	9 Dec 2017	No
	J8	10 Oct 2018	11 Dec 2018	No
	J9	24 Sept 2018	10 Dec 2018	No
	J14	9 Oct 2018	8 Dec 2018	No
	Mean	5 Oct	10 Dec	
	SD	7.5	1.3	
Third	J3	2 Oct 2018	12 Nov 2018	No
	J14	10 Oct 2019	29 Nov 2019	No
	Mean	6 Oct	20 Nov	
	SD	5.7	12.0	
Fourth	J14	24 Sept 2020	28 Nov 2020	No
Overall	Mean	5 Oct	2 Dec	
	SD	11.7	10.2	

* Bird did not survive season.

Table 5.10. Departure dates, arrival dates, and route information for hawks that attempted up to four spring (northward or return) migrations. Data obtained from transmitters worn by Swainson's hawks captured as fledglings in the High Plains of Texas from 2016 – 2018. Standard deviation (SD) is provided with means.

Migration	Hawk	Departure Date	End Date	Did bird depart from the expected route?
First	J3	2 Mar 2017	21 Apr 2017	No
	J8	4 Mar 2018	8 June 2018	Yes
	J9	4 Mar 2018	20 May 2018	No
	J10*	28 Feb 2018		No
	J11*	10 Mar 2018		No
	J14	27 Feb 2018	18 May 2018	No
	Mean	3 Mar	16 May	
	SD	3.9	19.7	
Second	J3	24 Feb 2018	13 Apr 2018	No
	J14	10 Mar 2019	20 June 2019	No
	Mean	3 Mar	17 May	
	SD	9.9	48.1	
Third	J14	5 Mar 2020	30 Apr 2020	No
Fourth	J14	8 Mar 2021		
Overall	Mean	4 Mar	16 May	
	SD	4.7	24.6	

* Bird did not survive season.

Figures

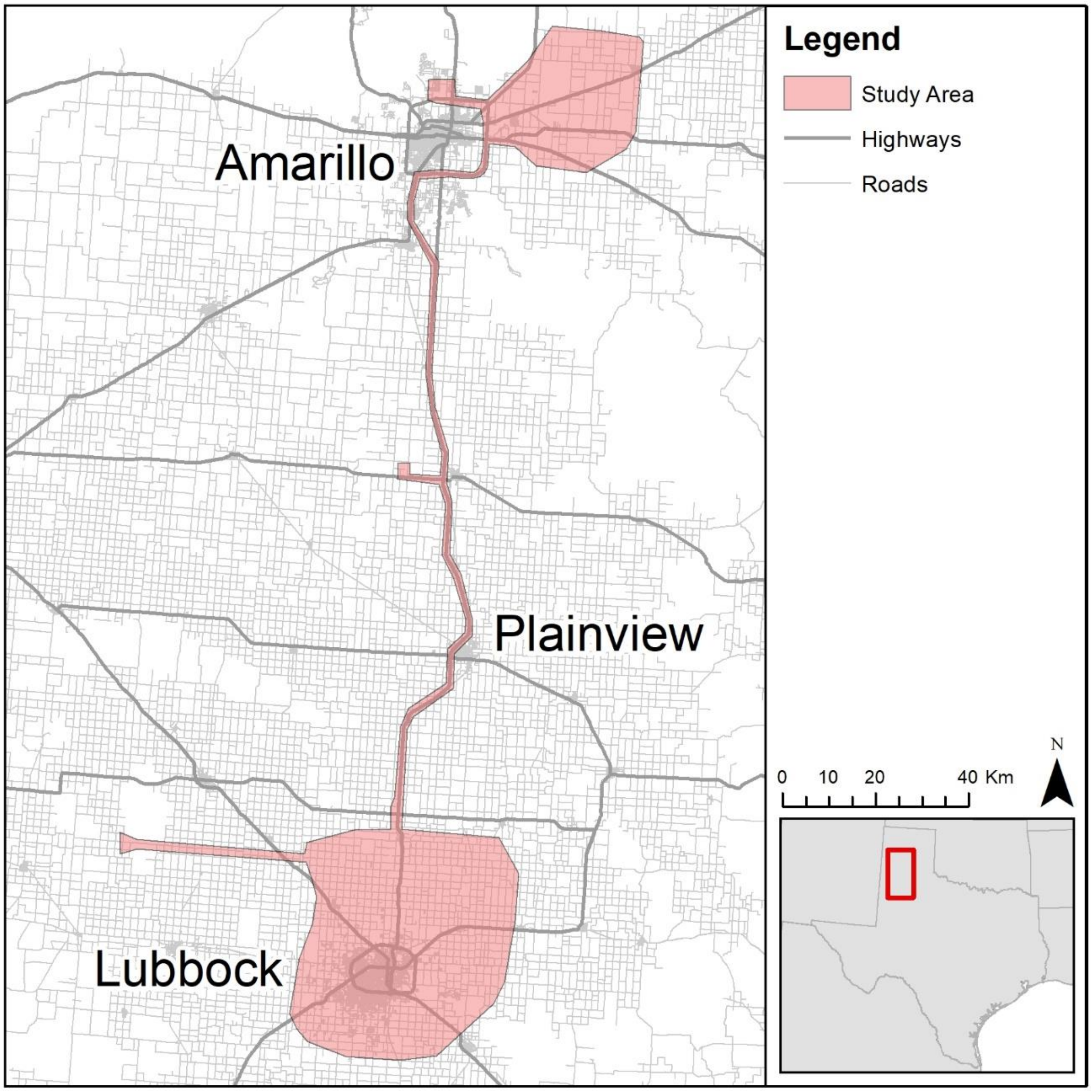

Figure 5.1. Study area where juvenile Swainson's hawks were captured on nests and by trap and equipped with satellite transmitters from 2016 – 2018. Inset map shows location within Texas.
Source: Texas Natural Resources Information System, <https://tnris.org>.

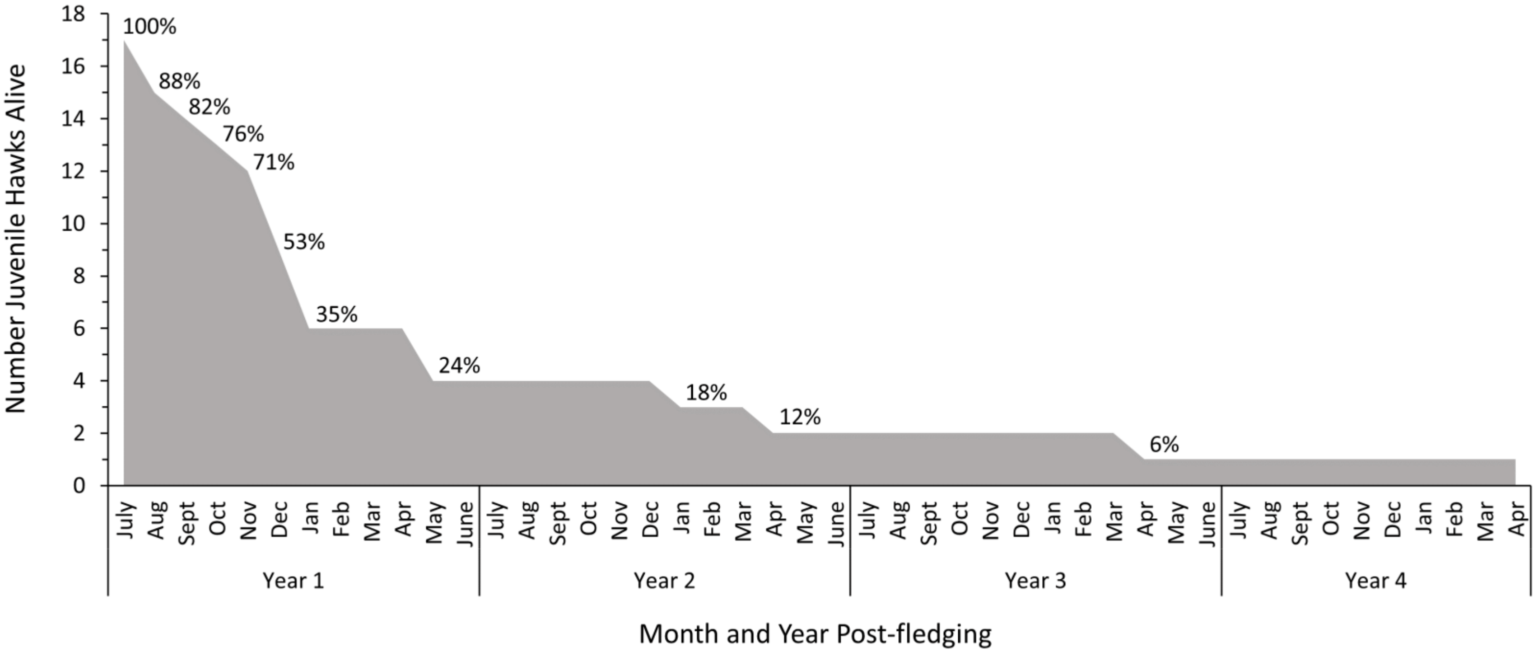

Figure 5.2. Number and proportion of juvenile Swainson's hawks that survived each month post-fledging. Each proportion indicates a change in number of birds known to be alive. Data obtained from transmitters worn by Swainson's hawks captured as fledglings in the High Plains of Texas from 2016 – 2018.

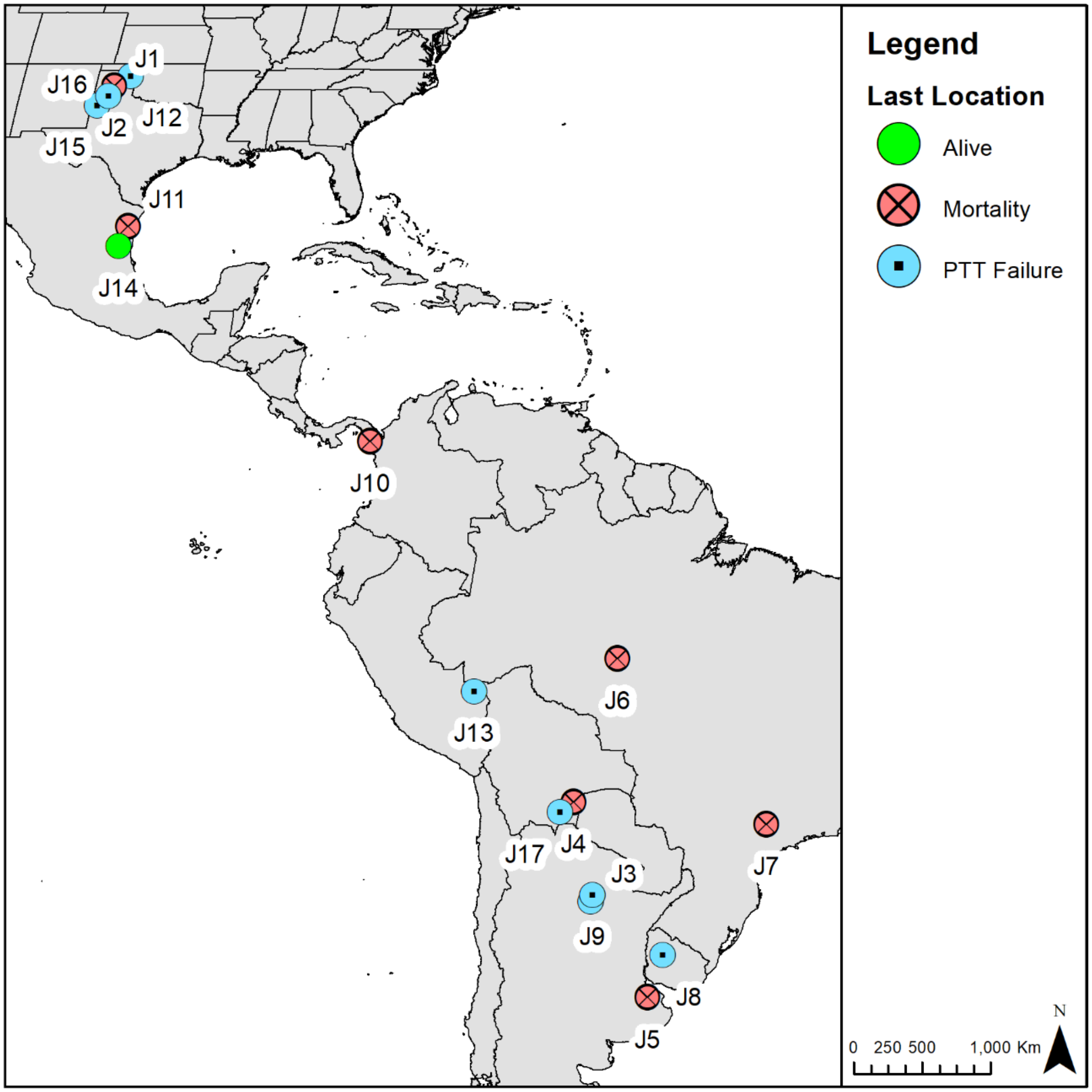

Figure 5.3. Last known locations for juvenile Swainson's hawks; 'mortality' was confirmed by finding a carcass or assumed when a series of points occurred in one location before transmissions ended, 'PTT failure' occurred when data transmission suddenly stopped (bird was presumed dead), and one PTT was continuing to send movement data (Alive) at the time this figure was made. Data obtained from transmitters worn by Swainson's hawks captured as fledglings in the High Plains of Texas from 2016 – 2018.

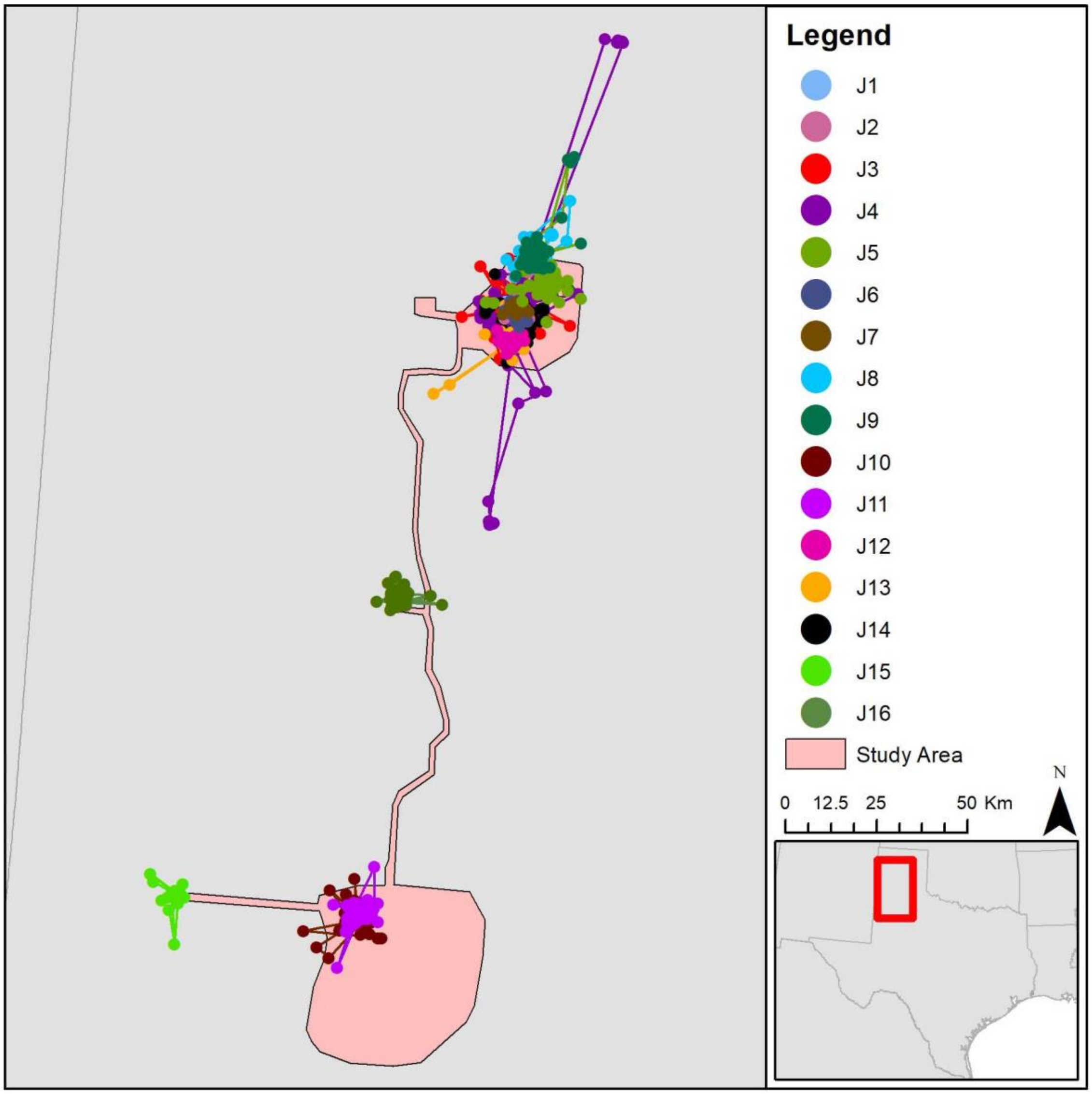

Figure 5.4. Locations of Swainson's hawks during the post-fledging period, when 95% of locations were within 2 km of the nest. Inset map shows location within Texas. Data obtained from transmitters worn by Swainson's hawks captured as fledglings in the High Plains of Texas from 2016 – 2018.

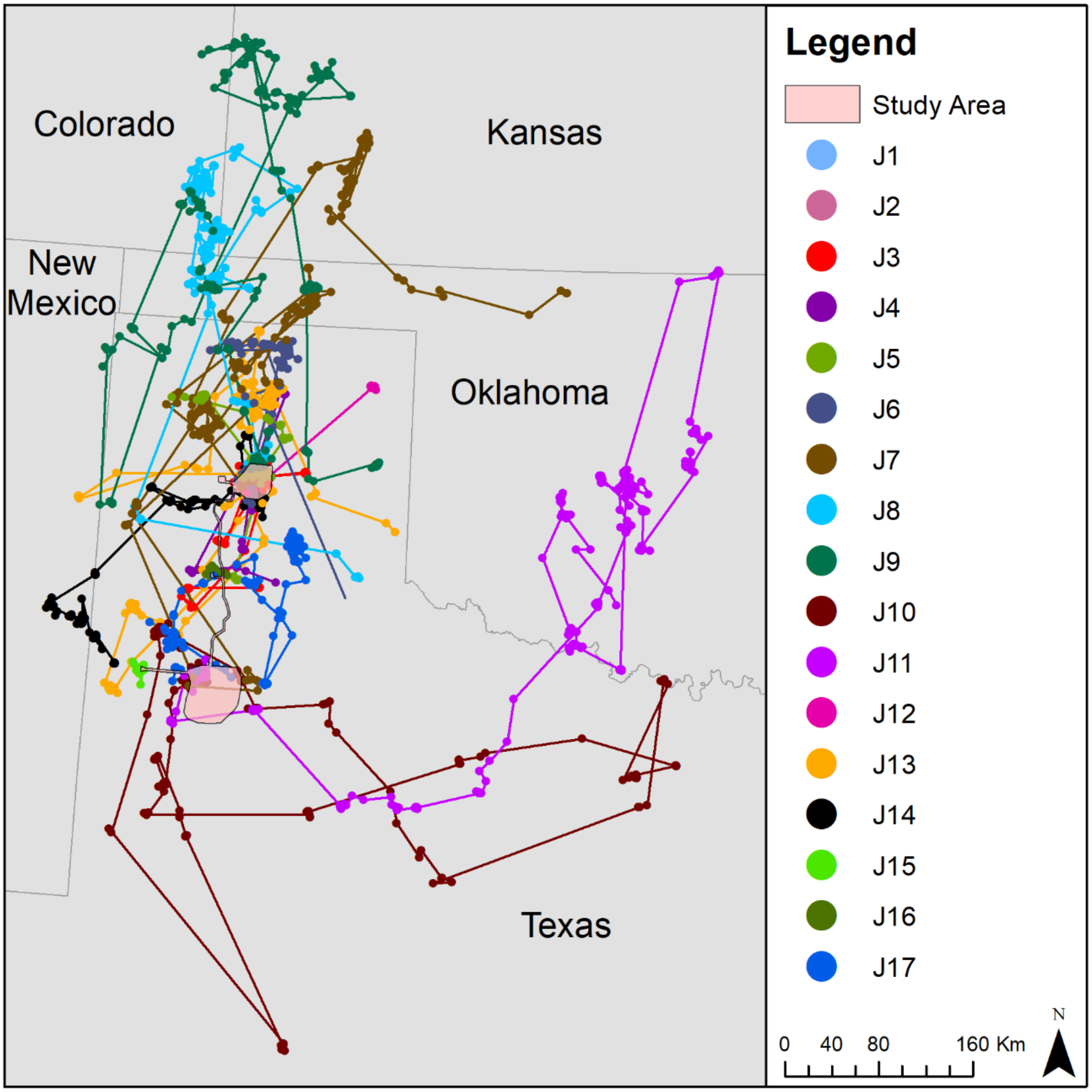

Figure 5.5. First summer locations of juvenile Swainson’s hawks prior to migration. Study area is included for reference to locations where birds were captured on nests. Data obtained from transmitters worn by Swainson’s hawks captured as fledglings in the High Plains of Texas from 2016 – 2018.

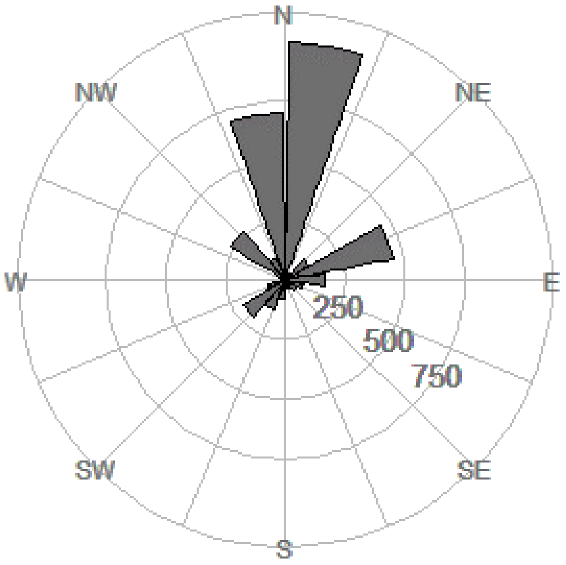

Figure 5.6. Aggregation of points in various directions from each bird’s natal nest during the independent-ranging period (i.e., after hawks left the natal area, but before migration). Data obtained from transmitters worn by Swainson’s hawks captured as fledglings in the High Plains of Texas from 2016 – 2018.

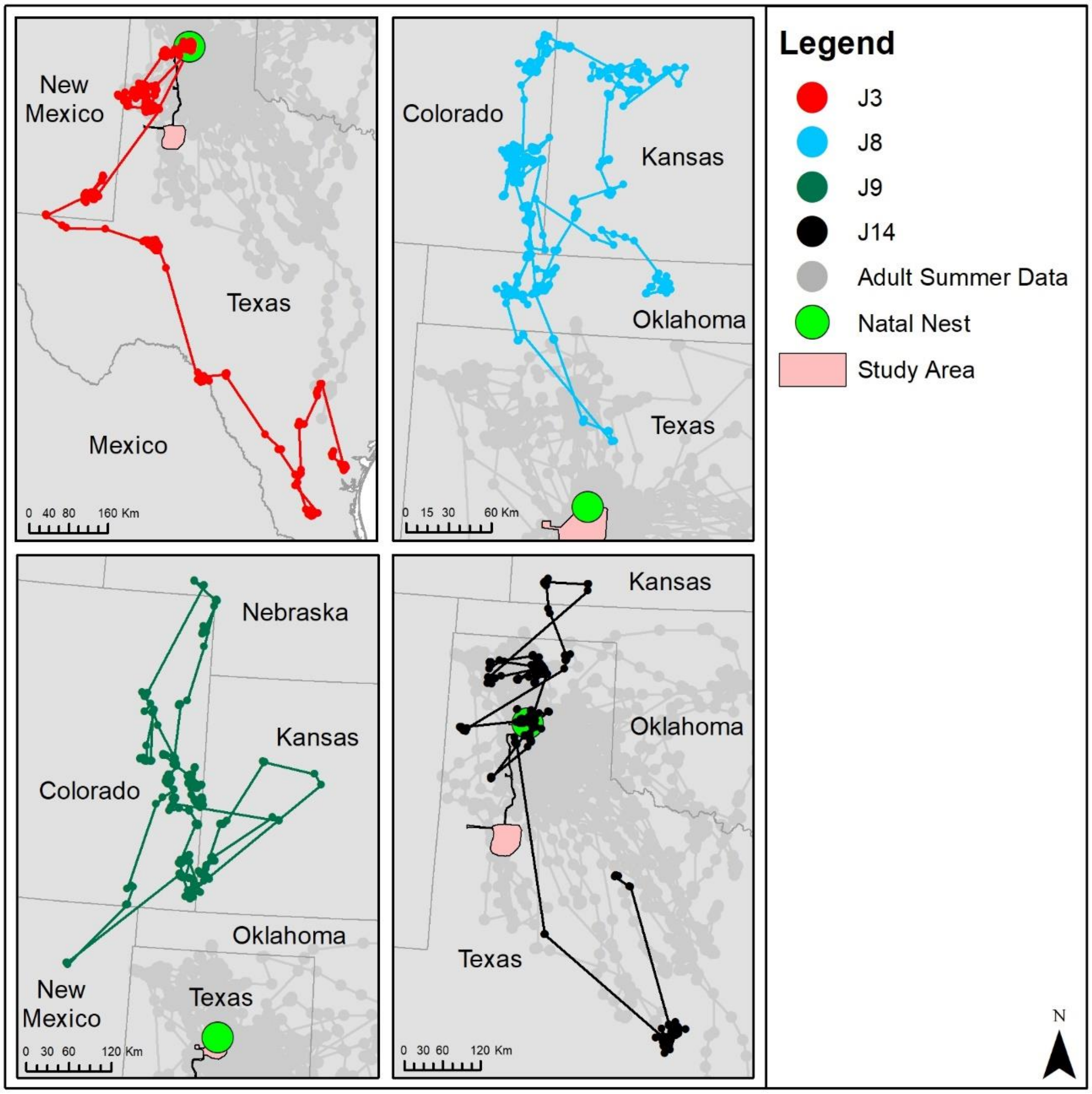

Figure 5.7. Movements on the summer range during juvenile Swainson's hawks' first return in reference to the study area, each bird's natal nest, and adult GPS data from a related study. Data obtained from transmitters worn by juvenile and adult Swainson's hawks captured in the High Plains of Texas from 2012 – 2018.
Source: Chapter 3.

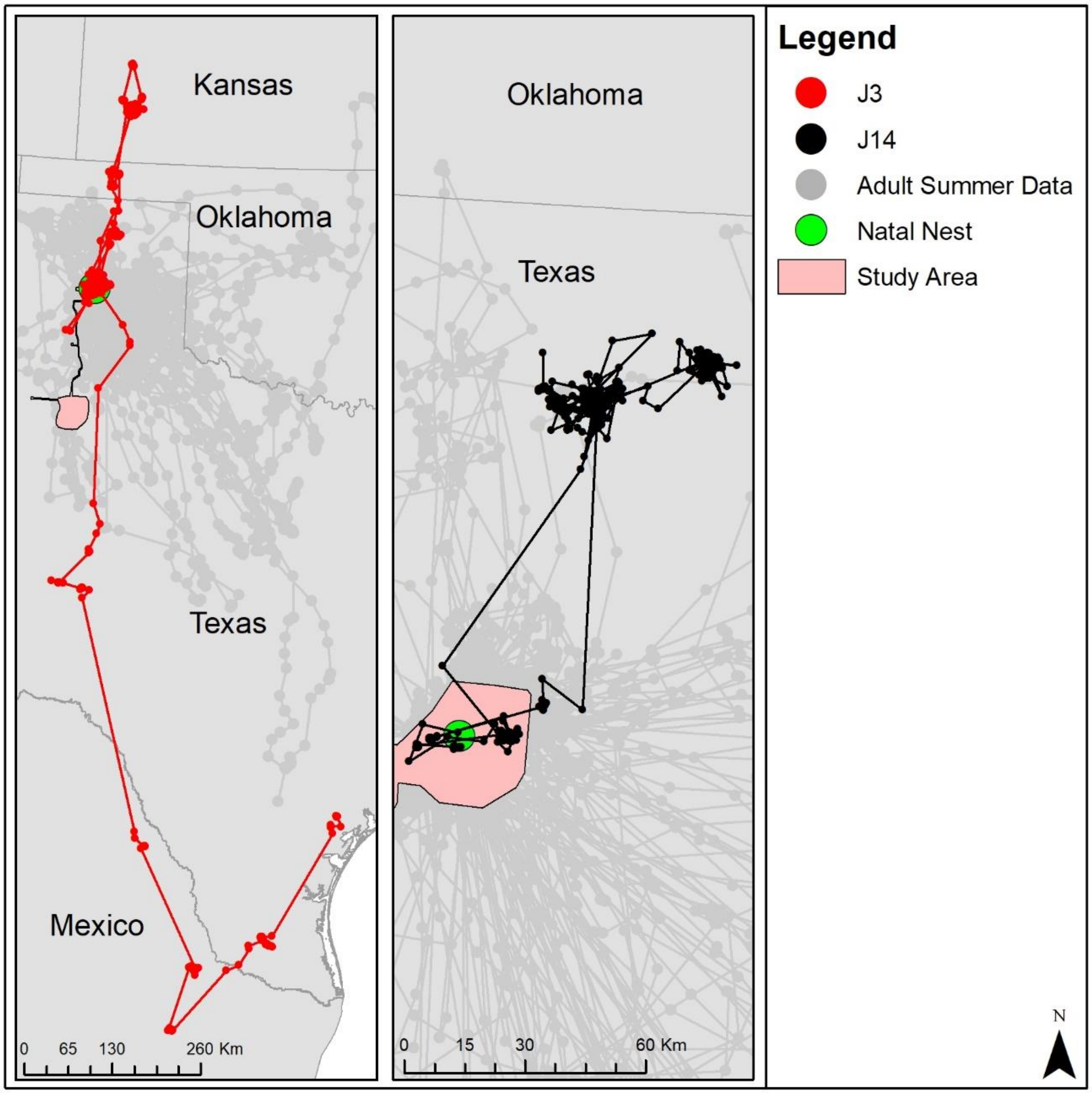

Figure 5.8. Movements on the summer range during juvenile Swainson's hawks' second return in reference to the study area, each bird's natal nest, and adult GPS data from a related study. Data obtained from transmitters worn by juvenile and adult Swainson's hawks captured in the High Plains of Texas from 2012 – 2018.
Source: Chapter 3.

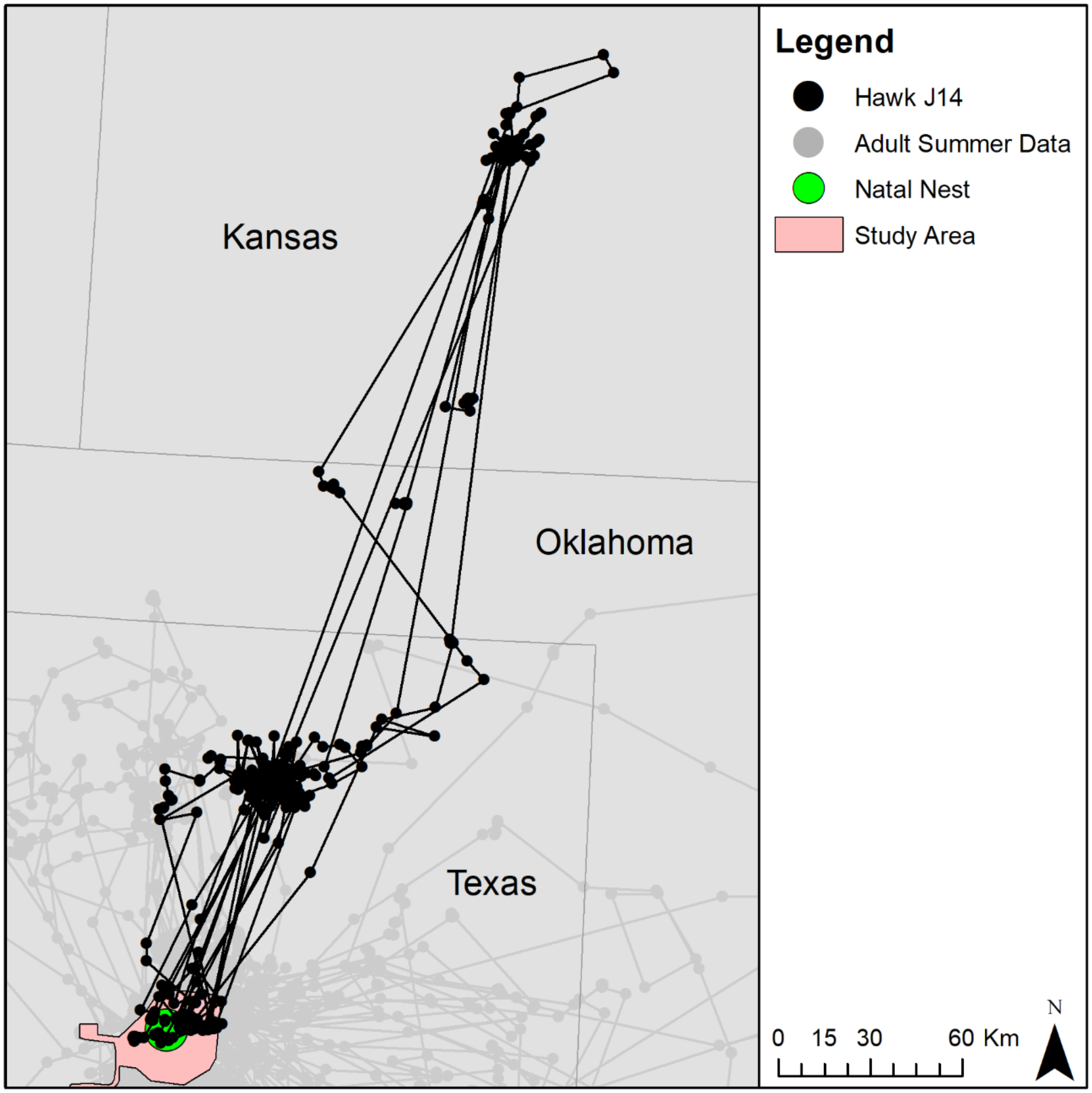

Figure 5.9. Movements on the summer range during one Swainson's hawk's third return in reference to the study area, the natal nest, and adult GPS data from a related study. Locations were obtained from a platform transmitter terminal attached to the hawk just prior to fledging from a nest near Amarillo, Texas, in 2017.
Source: Chapter 3.

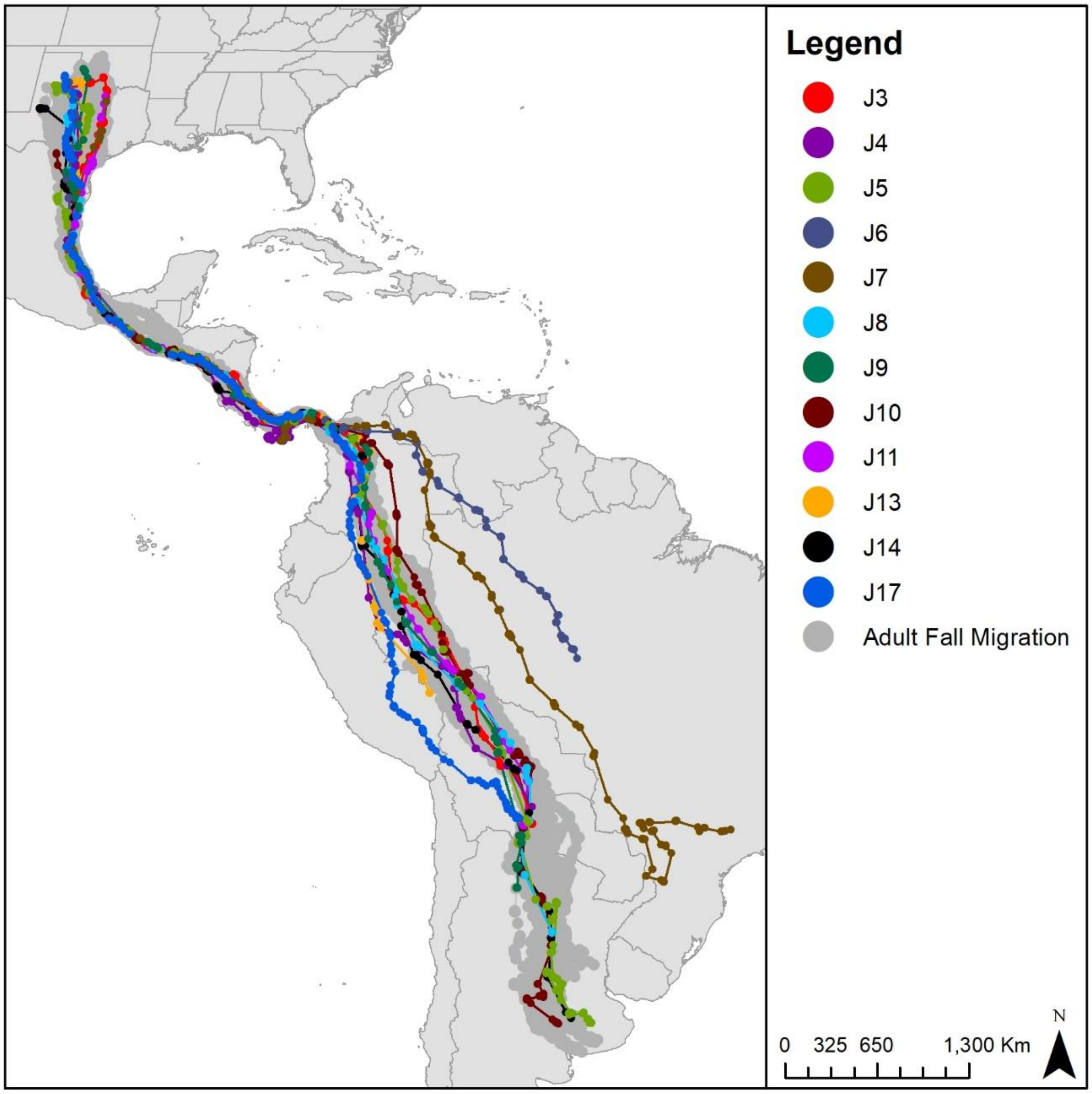

Figure 5.10. First fall (southward or outbound) migration of juvenile Swainson’s hawks compared to adult GPS data from a related study. Data obtained from transmitters worn by juvenile and adult Swainson’s hawks captured in the High Plains of Texas from 2012 – 2018.
Source: Chapter 3.

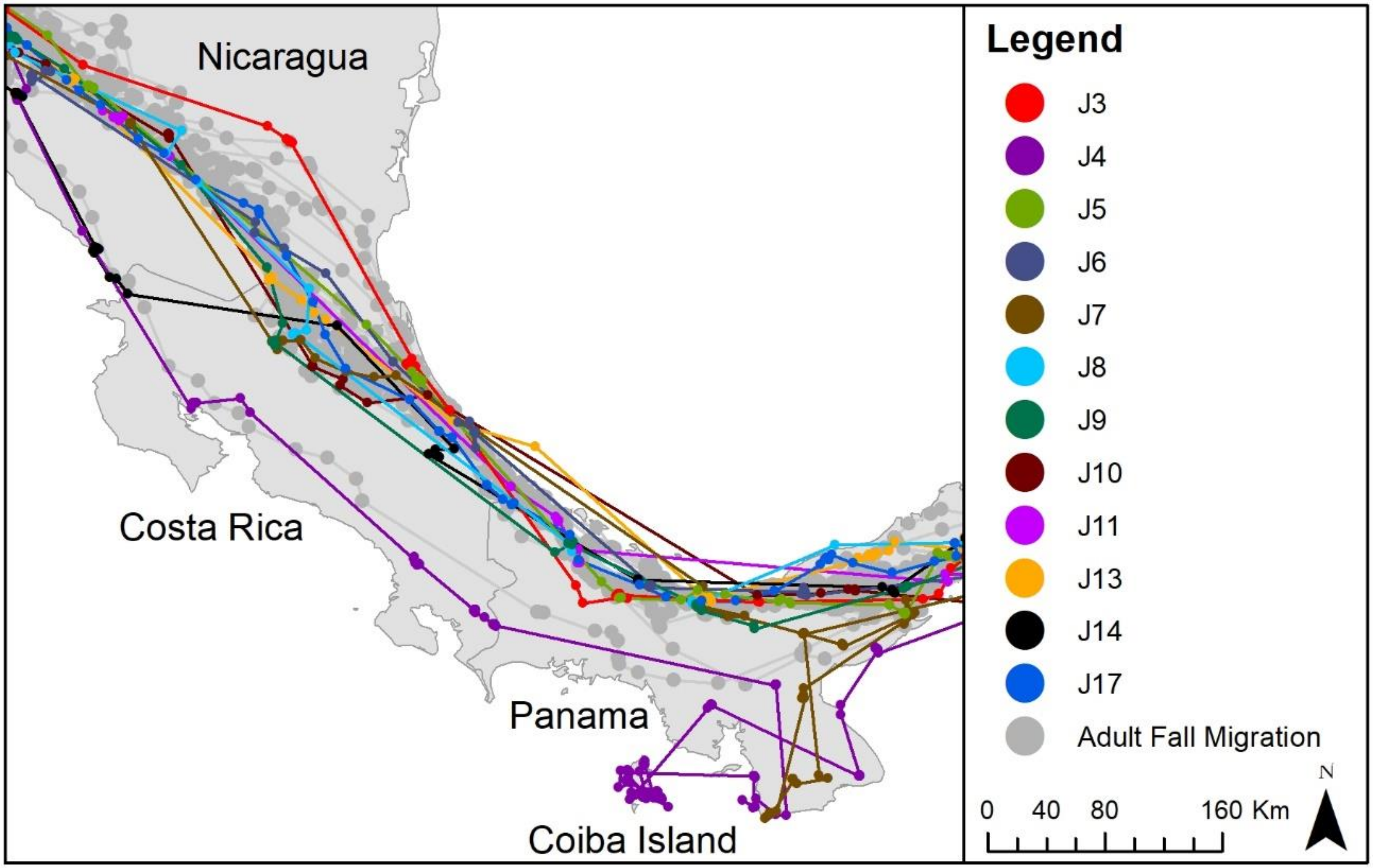

Figure 5.11. First fall (southward) migration of juvenile Swainson's hawks through Nicaragua, Costa Rica, and Panama compared to adult GPS data from a related study. Bird J4 spent 10 days on Coiba Island, before resuming migration. Data obtained from transmitters worn by juvenile and adult Swainson's hawks captured in the High Plains of Texas from 2012 – 2018.
Source: Chapter 3.

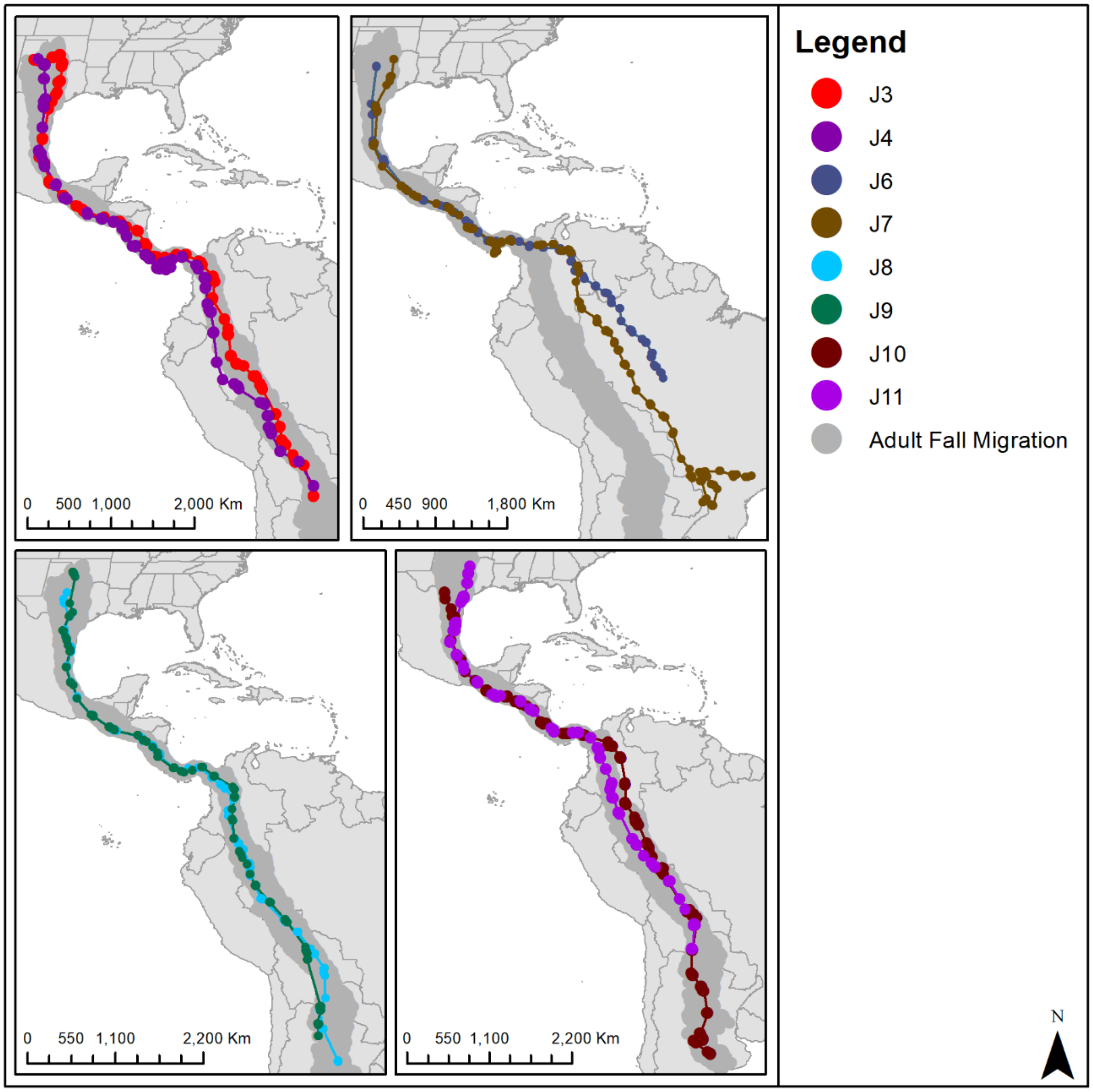

Figure 5.12. Sibling Swainson's hawks often showed similar migratory patterns during their first fall (southward or outbound) migration. Adult GPS data from a related study is provided for reference. Data obtained from transmitters worn by juvenile and adult Swainson's hawks captured in the High Plains of Texas from 2012 – 2018.
Source: Chapter 3.

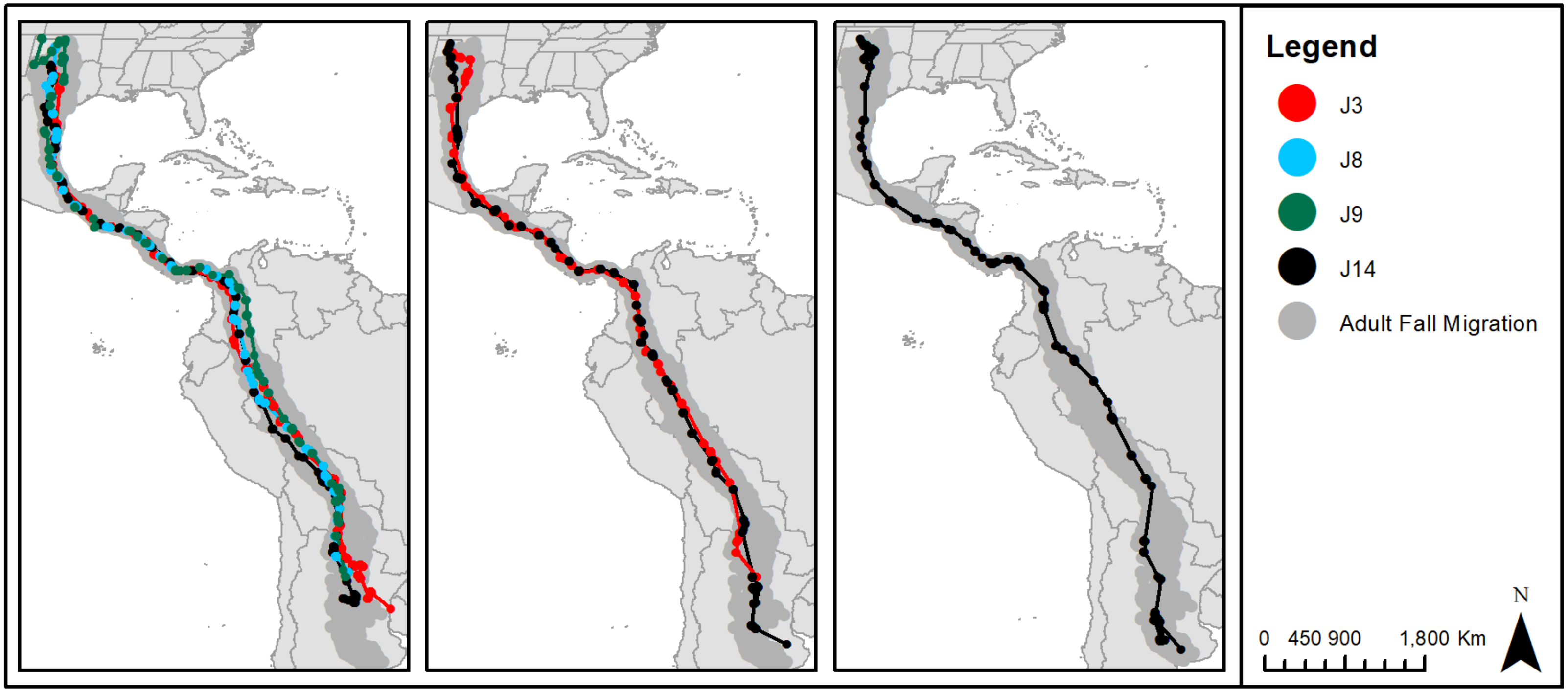

Figure 5.13. Second (left), third (middle), and fourth (right) fall (southward or outbound) migrations of juvenile Swainson’s hawks compared to adult GPS data from a related study. Data obtained from transmitters worn by juvenile and adult Swainson’s hawks captured in the High Plains of Texas from 2012 – 2018.
Source: Chapter 3.

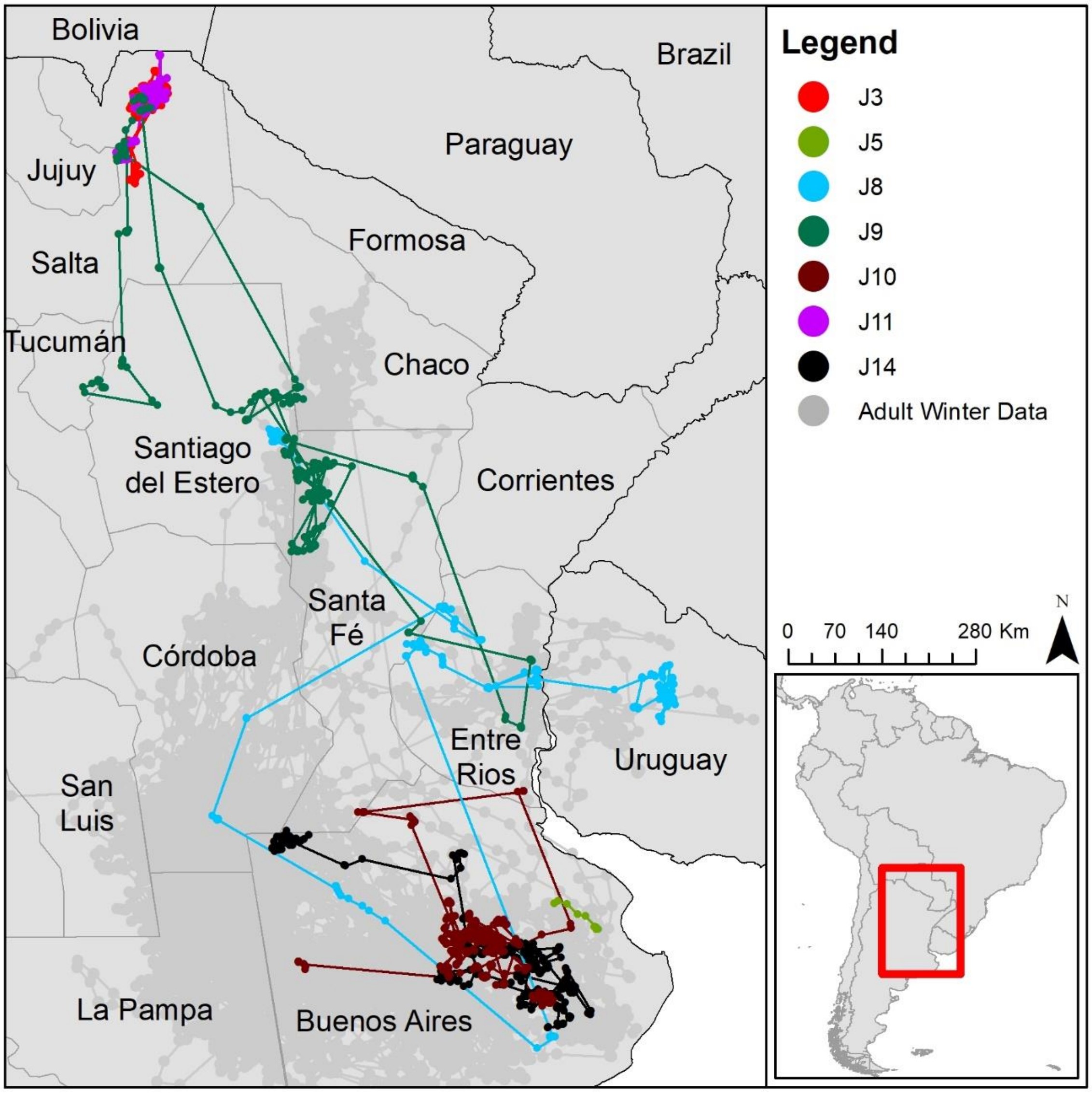

Figure 5.14. Juvenile Swainson's hawk locations during their first winter season compared to adult GPS data from a related study. Inset map shows location within South America. Data obtained from transmitters worn by juvenile and adult Swainson's hawks captured in the High Plains of Texas from 2012 – 2018.
Source: Chapter 3.

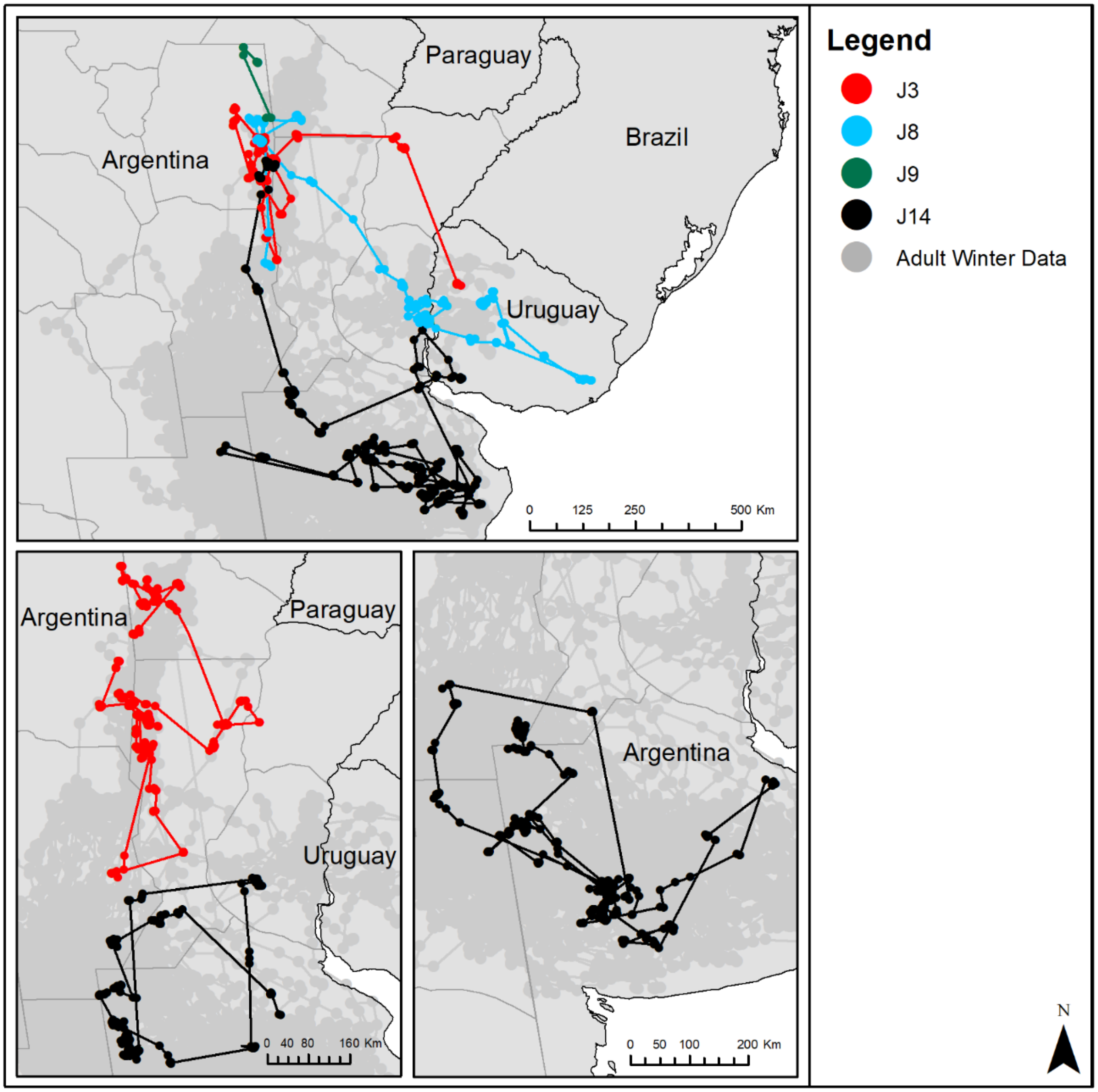

Figure 5.15. Juvenile Swainson's hawk locations during their second (top), third (bottom left), and fourth (bottom right) winter (nonbreeding) seasons compared to adult GPS data from a related study. Data obtained from transmitters worn by juvenile and adult Swainson's hawks captured in the High Plains of Texas from 2012 – 2018.
Source: Chapter 3.

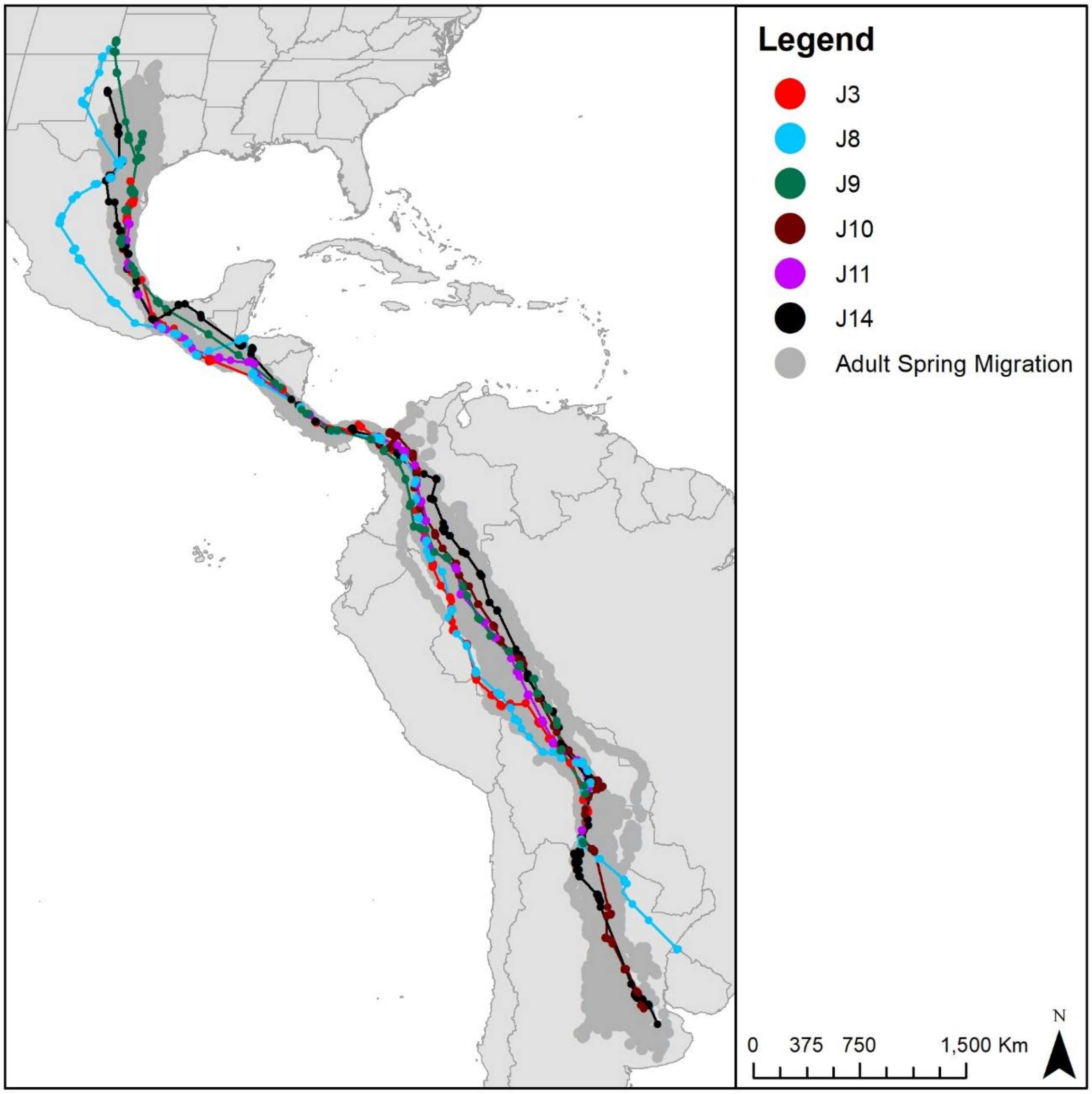

Figure 5.16. First spring (northward or return) migration of juvenile Swainson's hawks compared to adult GPS data from a related study. Data obtained from transmitters worn by juvenile and adult Swainson's hawks captured in the High Plains of Texas from 2012 – 2018.
Source: Chapter 3.

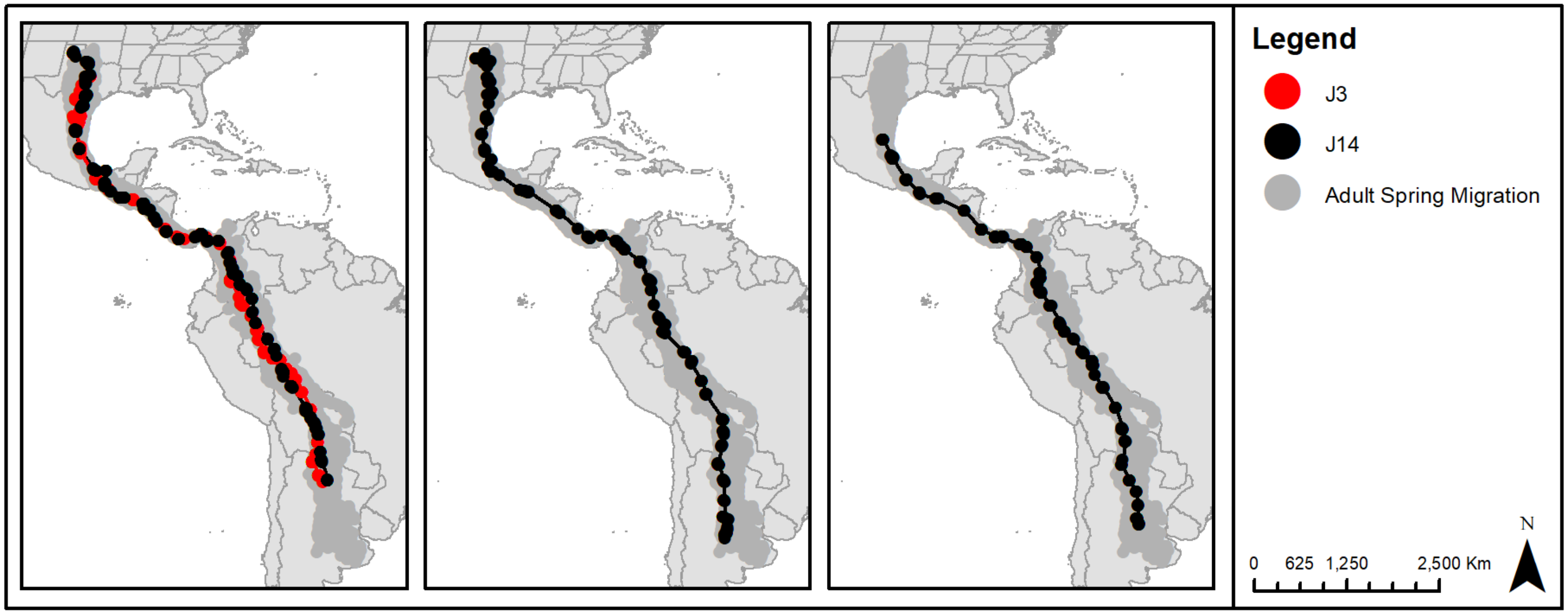

Figure 5.17. Second (left), third (middle), and fourth (right) spring (northward or return) migrations of juvenile Swainson's hawks compared to adult GPS data from a related study. The fourth spring migration is incomplete, because the hawk was still migrating when we made this figure. Data obtained from transmitters worn by juvenile and adult Swainson's hawks captured in the High Plains of Texas from 2012 – 2018.
Source: Chapter 3.

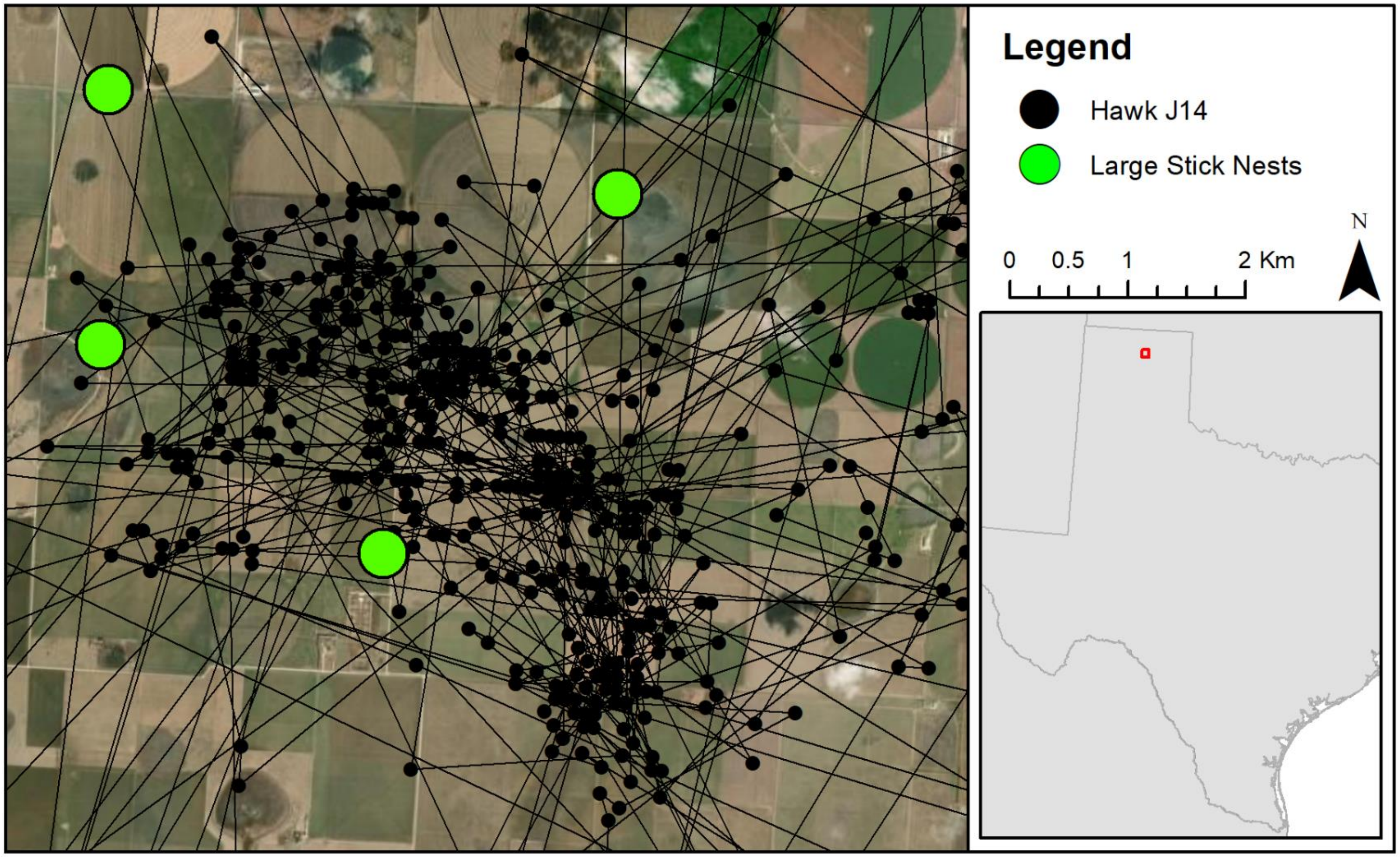

Figure 5.18. Region of highest concentration of summer 2020 locations for hawk J14 in reference to the approximate locations of four large stick nests (most of which were occupied by unbanded adult Swainson’s hawks) observed by researchers on 28 May 2020. Inset map shows location within Texas. Hawk locations were obtained from a platform transmitter terminal attached to the hawk just prior to fledging from a nest near Amarillo, Texas, in 2017.
Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, the GIS User Community.

CHAPTER VI

RISK OF SWAINSON'S HAWKS ENCOUNTERING WIND TURBINES ACROSS THEIR GLOBAL RANGE

Abstract

Wind energy is a known hazard for many avian species, with raptors being especially vulnerable due to flight characteristics, low fecundity, and small population sizes. Swainson's hawks (*Buteo swainsoni*) are migratory raptors that inhabit regions of North and South America that may be prime areas for building wind energy facilities. However, little information exists regarding vulnerability of this species to wind turbine mortality, displacement, or other impacts. We equipped 41 adult and juvenile Swainson's hawks with satellite transmitters and tracked them throughout life; we compared transmitter data to locations of wind energy facilities to assess risk. We could not find reliable locations internationally, so we used satellite imagery to identify suspected and confirmable wind turbines throughout the migration route and wintering range. To further assess risk, we used transmitter and wind turbine locations to model resource selection and resource selection probability functions throughout the global range relevant to our sampled hawks. We found 26,258 wind turbines that might present a hazard to tracked hawks, with most turbine facilities being located on the breeding range. However, most hawk locations (90%) did not occur in collision-risk buffers, and those that did were mostly (98%) on the breeding range; models agreed with the result that the breeding range presents the most significant risk from this industry. Swainson's hawks have rarely been found dead at turbine facilities, though, perhaps because of their hunting style (i.e.,

flights low to the ground, perching on the ground, and diving from perches) and adaptability to changing landscape conditions.

Wind energy is one of several options for producing electricity from renewable resources to help move society towards a sustainable future (Alrikabi 2014). However, it is important to understand the unintended impacts of current wind technology on the natural world, so we may mitigate for negative effects and improve technology and placement to promote positive outcomes as the industry expands (Wang and Wang 2015). Wind energy structures (i.e., turbines) are built in locations with consistent and strong winds; these locations also tend to be habitats and migratory pathways for birds and bats (Shaffer and Buhl 2016, Nourani and Yamaguchi 2017). The wind energy industry causes mortality for volant animals due to collision with blades and towers, collision with and electrocution from associated power lines and other structures, collision with vehicles along turbine-related roadways, and pulmonary barotrauma (i.e., rapid air pressure change near spinning turbine blades damages bat lungs, causing mortality without collision) (Erickson et al. 2001, Kuvlesky et al. 2007, Baerwald et al. 2008); however, most avian research focuses on the risk from collision with spinning rotor blades (e.g., Madders and Whitfield 2005, Kuvlesky et al. 2007, Smallwood and Thelander 2008, de Lucas et al. 2012). While wind energy is not yet considered a significant threat to most avian species (e.g., cats, windows, automobiles, power lines, and communication towers have each been estimated to kill millions more birds than turbine blades in the United States; Erickson et al. 2001, Loss et al. 2015), the industry is expanding rapidly, and it is becoming increasingly important to understand risk for particular species that may be more susceptible to turbine mortality and population effects (Beston et al. 2016).

While passerines may suffer greater collision numbers overall, raptors are more likely to suffer population-level impacts from turbine mortality due to long lifespans, low fecundity, and low population sizes (Kuvlesky et al. 2007, Beston et al. 2016). Raptors may or may not perceive turbines as a hazard. Regardless, distractions while hunting (i.e., searching the ground for prey while maintaining flight; especially common for soaring species) and agonistic interactions, horizontal wind gusts, and the use of thermals (i.e., circling in rising columns of air to assist lift) and orographic updrafts (i.e., using an updraft along a ridge with turbines near the edge) may lead to accidental blade collision that results in injury and mortality (Smallwood et al. 2009, Wang and Wang 2015, Nourani and Yamaguchi 2017). Raptors have been the primary focus of onshore wind energy research, because large-bodied birds are the easiest animal to find beneath turbines (i.e., raptors leave more-visible carcasses) and several charismatic species of conservation concern have been identified as particularly vulnerable to turbine collision, including bald eagles (*Haliaeetus leucocephalus*; e.g., Mojica et al. 2016), golden eagles (*Aquila chrysaetos*; e.g., Katzner et al. 2017), Egyptian vultures (*Neophron percnopterus*; e.g., Carrete et al. 2009), and griffon vultures (*Gyps fulvus*; e.g., de Lucas et al. 2012).

Swainson’s hawks (*Buteo swainsoni*) are a Neotropical migratory species that inhabits grasslands, shrublands, and agricultural fields in North America and Argentina. This species migrates over 10,000 km between hemispheres, making it potentially vulnerable to landscape changes across much of North, Central, and South America. We selected this species for study of wind energy risks, because Swainson’s hawks migrate long distances, allowing us to examine wind energy impacts across international borders, and, to our knowledge, little information exists on turbine-related mortality even though Swainson's hawks have been documented to inhabit wind farms (Watson et al. 2018*a*) and share many behavioral characteristics, such as soaring flight, with other species frequently reported in turbine-mortality literature. Additionally, Beston et al. (2016) identified Swainson's hawks as a species with a relatively high risk of suffering turbine-related population decline over time.

Wind turbine blades only pose a risk to hawks when they fly near turbines and within the rotor-sweep zone (i.e., the 3-dimensional space where rotor blades spin). Barclay et al. (2007) suggested a correlation between bird fatalities and turbine height (i.e., taller turbines kill more birds). Depending on the design, turbine rotors may have a diameter of 15 to 180 m on a pole 24 to 135 m tall (Barclay et al. 2007, Campbell 2016). The largest turbines are being built offshore and, to our knowledge, the largest onshore turbine design to date has a rotor diameter of 127 m and a tip height of 199 m (Campbell 2016). However, Poessel and colleagues (2018) stated that most turbine tip heights are < 150 m. For this study, we used a conservative estimate of the total vertical zone where a bird may have the potential to collide with a turbine blade as 0 to 200 m above ground, to account for the combined errors in estimating bird height and our lack of information on individual turbine designs (Barclay et al. 2007, Tachikawa et al. 2011, Campbell 2016, Poessel et al. 2018). Smith (1985) described typical flight altitudes of migrating Swainson's hawks and other soaring species moving through Panama as 375 to 2,650 m above ground; when birds are above 200 m, there is essentially no risk of encountering wind turbines no matter the location (assuming heights are calculated correctly, which can be difficult to determine; Poessel et al. 2018). However, the risk of collision with a turbine exists when birds are flying at low height, which occurs throughout daily activities during the breeding and nonbreeding seasons, actions such as hunting and interactions with conspecifics and other species, and during migration when birds enter and leave nightly roost areas or when slope-soaring if turbines are present on ridges (e.g., migrating eagles flew closer to the ground when slope soaring than when gliding between thermal updrafts; Miller et al. 2014), and when birds stop during migration (e.g., due to inclement weather or a need to rest and forage; Smith 1985) and perform low-height activities, such as hunting. An additional hazard is posed during inclement weather; Erickson et al. (2001) reported that lighting on turbines meant to warn airplanes at night can attract birds during fog and storm events, which increases risk of collision when visibility is poor.

During migration, Swainson’s hawks use soaring flight for movement and hunting, roost every night, and make up to 26 stopovers throughout each migratory journey. In addition, normal migratory flight may include heights within 200 m of the ground depending on wind conditions, topography, and time of day (Duerr et al. 2012). All of these behaviors put Swainson’s hawks at risk of colliding with wind turbine blades if turbines are present. However, where turbines are being built and whether or not Swainson’s hawks collide with them has been studied little to date. We located 24 Swainson’s hawk fatalities caused by collision with turbine blades in wind energy literature (Howell 1997, Johnson and Erickson 2011, Loss et al. 2013, Graff et al. 2016, Watson et al. 2018*a*). However, the relatively few turbine-collision reports we could find give us a poor basis to understand the level of risk wind turbines pose for this species;

perhaps the lack of data indicates that Swainson’s hawks avoid turbine mortality more successfully than other soaring species. Additionally, there is little information available about global wind energy locations, and therefore we have a poor understanding of how frequently Swainson’s hawks encounter this hazard outside of breeding areas. We set out to answer some of these questions by attaching satellite transmitters to Swainson’s hawks to track movements year-round and by using satellite imagery and modelling to estimate risk posed by turbine presence and how frequently Swainson’s hawks might overlap the industry throughout the global range. Furthermore, all Swainson’s hawks may be at risk from wind energy development; experience (e.g., adult, fledgling) and behavior (e.g., holding territories, exploration, migration) may expose different birds to varying levels of risk. For example, non-breeding birds may be more mobile and exploratory in their movements, hence increasing risk of encountering wind energy facilities. Juvenile birds may increase risk due to inexperience controlling flight in wind gusts or by paying poor attention to surroundings while hunting. To examine risk to this species as a whole, we included adults (both breeders and non-breeders) and juveniles of both sexes in our analysis.

Methods

Hawk data

From 2012 to 2018, we captured adult Swainson’s hawks in the High Plains ecoregion of Texas and fitted them with satellite transmitters to understand movement ecology and the risk of encountering wind turbines throughout the species’ global range (with a focus on the global range relevant to our transmitter data). In 2012 and 2013, we captured adult hawks using bal-chatri and dho-gaza traps in Potter, Carson, and Armstrong counties, Texas (Bloom et al. 2007). Each captured adult hawk weighing > 550 g was equipped with a solar-powered Global Positioning System (GPS) platform transmitter terminal (hereafter PTT; Solar PTT-100, Microwave Telemetry, Inc., Columbia, Maryland) on a backpack-style harness secured with Teflon® ribbon, as well as an aluminum leg band issued by the United States Geological Survey Bird Banding Laboratory (Meyburg and Fuller 2007); the weight restriction ensured transmitters added no more than 4% of a hawk's bodyweight (the transmitter weighed 22 g). In 2016 to 2018, we captured juvenile hawks on nests or with a bal-chatri trap in Carson, Hockley, Lubbock, and Swisher counties, Texas (Bloom et al. 2007). We equipped juveniles weighing > 425 g with lower-weight Doppler-shift PTTs (Solar PTT-100, Microwave Telemetry, Inc., Columbia, Maryland; 17 g) and leg bands.

GPS PTTs were programmed to report daily hawk locations (± 18 m error) at 0000, 0500, 0700, 0900, 1100, 1200, 1300, 1500, 1700, 1800, 1900, and 2100, local time. We manually filtered GPS locations to eliminate points with reported errors, repetitive post-mortality points, and locations that were obvious errors, using a stepwise method described in Chapter 3. All retained points were presumed to be accurate for analyses, though we recognize that datasets may have contained additional errors that we failed to identify.

Doppler PTTs were programmed to report locations with a duty cycle of 10 hours on, attempting to contact a satellite every 60 seconds, and 24 hours off; locations were classed based on the number of satellites the PTT connected with to indicate estimated error (location class 3 = < 250 m error, 2 = 250 – 500 m, 1 = 500 – 1,500 m, 0 = > 1,500 m, A = unknown error, B = unknown error, and Z = invalid location; Douglas et al. 2012). We used the Douglas-Argos filter in Movebank (http://www.movebank.org) to reduce the dataset to locations that were most biologically reasonable (Douglas et al. 2012; Chapter 5). We additionally omitted portions of datasets where juvenile hawks were located significantly outside of known Swainson’s hawk migration routes (most presumably perished after going off course; Chapter 5), to keep analyses representative of the majority of the Swainson’s hawk population. All retained points were, again, presumed to be accurate locations for analyses.

Hawk data were divided into four seasons based on patterns of movements (Chapters 3 and 5): breeding range (primarily northern Texas for hawks in this study), fall (outbound) migration, nonbreeding range (Argentina and Uruguay), and spring (return) migration. Locations of migration and nonbreeding-range data in this study were representative of locations where most Swainson’s hawks might be found during those seasons (Bechard et al. 2010; see Airola et al. [2019] for exceptions from the unique California population). However, ‘breeding range’ data for hawks captured in this study represented only a small portion of the known Swainson’s hawk breeding range, which stretches across grasslands and deserts of most of western North America (Bechard et al. 2010).

Adult hawks tracked in this study flew an average of 25 kmh^{-1}, and 99% of data was < 53 kmh^{-1} (Chapter 3). The most common time gap between location estimations was 2 hours. We assumed the maximum distance a hawk might move between 2-hour locations was about 50 km, and therefore we created study areas for searching for wind turbines and modelling by adding a 50-km buffer to all transmitter points (Fig. 6.1 and 6.2) and for groups of points representing each season; for simplicity, we eliminated inner-gap spaces, connected closely-spaced buffers at the shortest distance, and connected disjunct polygons by creating additional 50-km-wide buffers around single transmitter trajectory lines as needed (i.e., gap connections followed likely hawk pathways) to end up with solid study-area polygons. We assumed hawks could occur anywhere within the study areas for analyses.

In addition to using all Swainson's hawk locations to understand areas for risk assessment, we used PTT-reported altitude data associated with each point to further understand the relationship hawks had with wind energy hazards; we were specifically interested in locations where hawks might be within the rotor-sweep zone of wind turbines. PTTs reported estimated altitude above ellipsoid (± 22 m; Microwave Telemetry, Inc.), which we converted to altitude above sea level by subtracting values from a geoid undulation map (Poessel et al. 2018, Earth Gravitational Model EGM2008; National Geospatial-Intelligence Agency, https://earth-info.nga.mil/GandG/wgs84/gravitymod/egm2008/egm08_gis.html). We then estimated height above ground by subtracting values from an ASTER digital elevation map (National Aeronautics and Space Administration, https://search.earthdata.nasa.gov); specifically, Movebank (http://www.movebank.org) estimated elevation for each hawk location using an inverse-distance weighted interpolation, which averages the nearest elevation values on a grid while giving greater weight to nearer values. Due to the error associated with original altitude estimates, conversions, DEMs, and interpolation, and the range of heights that a rotor-sweep zone might exist at, we focused on Swainson's hawk points with estimated above-ground heights between 0 and 200 m (i.e., we assumed locations > 200 m accurately placed hawks out of the zone of potentially contacting wind turbine blades).

Wind turbine locations

We obtained locations of wind turbines installed across the United States by July 2020 from the United States Geological Survey (USGS) Wind Turbine Database (https://eerscmap.usgs.gov/uswtdb). We were unable to locate a similar database for global wind energy locations, so created our own database of wind turbine locations by scanning satellite imagery.

We first used information provided by The Wind Power (https://www.thewindpower.net, last accessed 7 Aug 2020) to gather generalized locations of wind farms in North, Central, and South America; we did not know the accuracy of reported locations and could not obtain coordinates per turbine, so we used this information to focus our manual-search efforts to regions throughout the global Swainson’s hawk study area where wind turbines were most likely to be found. We downloaded Sentinel-2A imagery (spatial resolution = 10 m) from USGS (https://glovis.usgs.gov); we selected imagery from Jan 2019 to Aug 2020 that contained as few clouds as possible. We used imagery with known turbine locations from northern Texas to identify common patterns of wind farm design, such as repeating rows of turbines along straight roads, or more variable road designs but still with repeating distances and patterns of turbines along roadways, then we systematically searched images across the study area to identify suspected wind turbine locations. We cross-referenced high-spatial-resolution (as low as 15 cm) Google Earth imagery (https://www.google.com/earth/), Google Maps imagery (https://www.google.com/maps), and the World Imagery basemap in Arcmap 10.7 to confirm turbines and to locate additional turbines where possible. However, imagery dates vary in all programs (1969 to current), with older images especially common in remote and unpopulated regions. This constrained our ability to use high-resolution imagery to cross-check suspected turbine locations or to find additional turbines was variable. We marked points as ‘turbines’ when we could confirm their presence with high-resolution imagery, and as ‘suspected turbines’ when we identified patterns on Sentinel-2 images that were likely indicative of a wind farm, but we could not cross-reference the location.

We quantified the total number of turbines we detected within the study area buffer, the number of facilities (i.e., groups of turbines presumably managed as one unit), and turbines per facility. We grouped turbines within the United States by USGS-reported project name, assuming each project represented one turbine facility. We did not have enough information to differentiate international wind facilities, so we assumed all close-proximity turbines with similar spatial patterns belonged to a single facility.

We added buffers around confirmed and suspected turbine locations at 200 m (high risk of a bird encountering wind turbine blades; we assumed this buffer would include most rotor-sweep zones even with a 50-100 m difference between manual point placement and actual turbine location), 600 m (moderate risk of blade encounter), and 1,200 m (low risk). We then quantified hawk locations within buffers as an initial assessment of risk hawks in this study were likely subjected to while being monitored.

Modelling hawk occurrence and likelihood of turbine presence

We created resource selection functions (RSF) to estimate the relative probability of Swainson's hawks occurring throughout their global range, and then created resource selection probability functions (RSPF) to estimate the probability of wind energy occurrence (Manly et al. 2004), using methods inspired by Miller et al. (2014). We considered the hawk analysis to be a design II, first order site-selection estimation (Manly et al. 2004), because 'use' was measured from individual hawks and 'availability' was estimated from random locations across study areas. Our largest study area was approximately 10% of the breeding range, approximately 85% of the migratory pathway (lacking areas across Mexico), and 90 to 100% of the nonbreeding range in Argentina and Uruguay (but small numbers of hawks [vagrants and the California population] overwinter elsewhere; Browning 1974, Herzog 1996, Bechard et al. 2010, Airola et al. 2019). Because hawks may behave differently during different seasons, we modeled year-round hawk data together and seasons separately, to compare important variables and outcome of final models between pooled and season-specific datasets. We modeled wind energy as if probability of occurrence were based entirely on landscape variables, but we recognize that other factors, such as economics and land ownership, play a role in actual wind energy siting. A primary goal of this analysis was to identify where Swainson's hawks were most likely to overlap the industry if the wind energy market is saturated. Because siting wind energy facilities would not differ by season, we modeled wind turbines across the global hawk study area and clipped out seasonal subsets as needed. We additionally modelled wind energy within only the United States portion of the study area, because at the time of this research the vast majority of wind turbines were located in that country. We included elevation, slope, aspect, terrain ruggedness, land cover type, distance to water, distance to major road, and wind speed datasets. We created a-priori sets of candidate models with additive and interactive factors. We used Akaiki's information criterion (AIC; Manly et al. 2004) and subjective reasoning to select a single representative model for each dataset. Last, we used final models to create predictive hawk and wind energy maps and compared data to draw conclusions.

We downloaded ASTER digital elevation models (30-m spatial resolution; National Aeronautics and Space Administration, https://search.earthdata.nasa.gov; Fig. 6.3) with which we estimated slope, aspect, and a terrain ruggedness index (TRI; Riley et al. 1999) using ArcMap 10.7 ('Slope' and 'Aspect' tools) and Program R 3.6.2 (package 'spatialEco'; Evans et al. 2021). Slope represented the maximum rate of change (in degrees) between a cell and the immediate surrounding cells (a 3 x 3 grid), and aspect represented the cardinal direction of that maximum change (Fig. 6.3). TRI was estimated using the formula $TRI = Y[\Sigma(x_{ij} - x_{00})^2]^{1/2}$, which considers the difference in elevation between a raster cell and two layers of surrounding cells (a 5 x 5 grid); the TRI formula classifies each cell with integers from 0 to infinity (e.g., TRI < 80 = level terrain and TRI > 959 = cliffs and extremely rugged terrain; Riley et al. 1999; Fig. 6.3). We included a global land cover map (2009 GlobCover V2.3; 300-m spatial resolution; The European Space Agency, http://due.esrin.esa.int/page_globcover.php), which we simplified to a binary variable: raster cells were 'open land', which represented grasslands, agriculture, deserts, and shrublands, (i.e., all of which may be habitat for Swainson's hawks; Bechard et al. 2010) or cells were not 'open land' (i.e. forests, water, ice, urban areas, etc.; not typical habitat for Swainson's hawks; Fig. 6.3); we were not sure if wind energy required or heavily used open landscapes, so we also included this variable in wind energy models. Many raptors are attracted to roadways due to associated perching structures (e.g., powerline poles, signs, planted trees, etc.), and wind energy companies rely on major roadways for shipping materials; we therefore created a raster that estimated distance to major roads from the gROADS v1 file (major roads across North, Central, and South America in 2010; NASA Socioeconomic Data and Applications Center, https://sedac.ciesin.columbia.edu/data/set/groads-global-roads-open-access-v1) using the ‘Euclidean Distance’ tool in ArcMap 10.7 (using geodesic distance; 250-m spatial resolution; Fig. 6.3). We included a map of annual average wind speed at 100 m above ground (250-m spatial resolution; Global Wind Atlas, https://globalwindatlas.info/; Fig. 6.3), because wind speed is highly relevant to wind energy construction, and we assumed wind speed may be important to hawk landscape selection, especially during migration; wind direction is another likely important factor for hawks, but we found no way to incorporate this highly variable factor at the spatial and temporal resolution we dealt with in these models. Last, we wanted to include proximity to water in models, but chose different ways to incorporate water variables for wind energy and hawk modelling. Wind energy can be deliberately built near water bodies, such as the ocean or large lakes, to take advantage of the influence of water on wind patterns, but can also be built with no association to water; we therefore created a ‘distance to major water body’ variable by combining polygons of large water bodies (rivers, lakes, and oceans) from multiple sources (Table 6.1), then created the raster using the ‘Euclidean Distance’ tool (250-m spatial resolution; Fig. 6.3). Swainson’s hawks may associate with water for several reasons: hawks use fresh water for drinking and bathing, linear features, such as rivers and coastlines, may guide hawks during migration and exploratory travel, hawks may be attracted to riparian vegetation for roosting, prey availability may change with distance to water, and atmospheric influences, such as availability of thermals, wind direction, and wind strength, associated with water may attract or repel hawks. We were concerned that hawks may have different associations with fresh water sources than salt water (e.g., Swainson's hawks will cross rivers and lakes, but do not generally cross the ocean during migration [Chapter 3], and hawks do not associate with coastlines during breeding and nonbreeding seasons), so we chose to model those water types separately. We selected inland lakes and rivers to create a distance to major freshwater body raster (250-m spatial resolution; Fig. 6.3), and we created a binary raster (100-m spatial resolution) that represented ocean or not; we only included the ocean variable for migration and year-round hawk datasets (Fig. 6.3). Last, because raw environmental data had varying units and scales, we normalized non-binary raster data prior to extraction and modelling using the equation $x_{new} = \frac{x_i - x_{min}}{x_{max} - x_{min}}$; this ensured all data were scaled between 0 and 1, so differences among raw data would not bias model fitting.

When modelling hawk data, we excluded birds that did not complete a single season in the relevant dataset. For example, we excluded adults that never completed a winter season due to mid-season mortality or transmitter failure from winter-season modelling. For first-summer juveniles, we excluded birds that did not survive to the first migration. For modelling year-round hawk data, we restricted analysis to hawks that survived at least one year from capture, so all included birds had locations from every season. We pooled data from multiple seasons (including incomplete seasons after the first complete season) for each bird where applicable, to maximize data available for analysis. We only selected locations between 0 and 200 m above ground to use for RSF modelling, because these locations were the most relevant to assessing the risk of hawks encountering wind turbines. We then created random points to represent ‘available resources’ (ArcMap 10.7 ‘Create Random Points’ tool) equal to the number of relevant hawk locations across study area polygons (points were stratified across individuals), and we extracted all environmental data from real and random-point locations.

For wind energy datasets, we combined equally weighted sets of turbine data and ran candidate models on data for the entire study area or the portion of the study area within the United States. Similar to hawk models, we considered each wind energy facility to be an ‘individual’ with turbine locations within being repeated measures on each ‘individual’, because we assumed turbine locations within facilities would be spatially autocorrelated (Miller et al. 2014). For the RSPF, random points needed to only represent ‘unused space’, so we removed polygons around turbines that represented ‘used space’ from the study areas; we created minimum convex polygons (plus a 2-km buffer) around each facility, then removed facility polygons from the global hawk study area in ArcMap 10.7 (‘Erase’ tool) to create a new unused study area polygon for turbine modelling; we then clipped the unused study area polygon by a United States border polygon to represent our second modelling dataset. We selected all facilities with ≥ 50 turbines, then selected 50 random turbine locations within each facility to include in modelling datasets. We then created equal numbers of random points throughout the two unused study area polygons (stratified by facility name) and added environmental variables to the used and unused point files.

We created Pearson's and Spearman's correlation matrices (examining linear and monotonic relationships, respectively) for pooled datasets (i.e., all relevant birds or turbines and both real and random location data). When a correlation was more extreme than 0.50 (i.e., $r > 0.50$ or $r < -0.50$), we chose one of the two variables to exclude from the candidate models for that dataset. We selected which to exclude based on a priori reasoning, as to which term was more likely to influence Swainson's hawks or turbine construction and based on how excluding one or the other term affected AIC scores in preliminary global main-effects models (i.e., models with all other variables included).

We then considered pairs of environmental variables for including interaction terms in model sets. We assumed that with a large amount of data there would be interacting patterns that are not biologically relevant to birds or logically relevant to constructing turbines. We therefore considered every possible pair of variables and, based on a priori biological, behavioral, and logistical reasoning (e.g., reasonable constraints of turbine construction), excluded any pairs of terms where we could not come up with an explanation that would represent a logical hypothesis to test (Table 6.2). Prior to including interaction terms in model sets, we checked for interaction patterns in the data (i.e., does this interaction actually occur within the data of any one bird in each bird dataset, or within either of the combined-turbine datasets?) using the 'plotmodel' script in Program R (package 'sjPlot'; Lüdecke et al. 2021); we determined a selected interaction term should be included if regression lines crossed in plots, and excluded the term if regression lines were parallel or failed to cross.

We created a global model for each dataset, then selected variables to remove to create the model set using preliminary model results (i.e., examining p-values of a global-model analysis of variance, removing greatest p-value terms first) as well subjective biological and logical reasoning. We created additive and interactive versions of every model, and, for simplicity, more-complex models included all interactions relevant to terms in the model. We limited model sets to 20 candidate models that we felt might represent hawk occurrences and turbine placement (Tables 6.3 – 6.8). We ran mixed-effects models, blocking on bird name or facility number to account for repeated measures and the spatial and temporal autocorrelation of point data, using the 'glmer' script in Program R (package 'lme4'; Bates et al. 2020) with a binomial distribution. We recorded coefficients (i.e., beta values for each term) of top models (lowest AIC); no models were within 2 delta or of high enough weight to consider model averaging. We then used the 'Raster Calculator' tool in ArcMap 10.7 to create each predictive map (with spatial resolution equivalent to the largest-resolution input data) using the logistic equation: $\frac{1}{1 + e^{-(\beta_0 + \beta_1 x_1 + \dots + \beta_k x_k)}}$. We interpreted results of RSPF maps as true probabilities of turbines occurring in map cells when the market is saturated, and we interpreted results of RSF maps as cells ranked by relative importance to Swainson's hawks that are 0 to 200 m above ground, rather than probabilities, based on the input data (Manly et al. 2004).

We compared preliminary results between fall- and spring-migration datasets. There was > 75% overlap of study-area buffers, means and histograms of used and random environmental variables were extremely similar, and correlations and interactions were nearly identical. We therefore decided to merge the two into a single ‘migration’ dataset. We merged random points created in individual migration buffers with real migration data for modelling. To keep data as balanced as possible, we restricted modelling to hawks that completed both migratory seasons at least once. Our final map therefore represented a prediction of hawk occurrence during any migration season.

To compare final maps, we converted raster values into polygons that represented 3 or 4 categories that described how likely it might be to find a wind turbine facility or a Swainson’s hawk in each region. For models that estimated probabilities of current and future wind turbine presence, we classified < 33% as regions with low probability, 33 to 67% as regions with a moderate probability, and > 67% as regions with the highest probability. Because hawk RSF models produced relative ranking values rather than probabilities, we used the hawk data to guide our classification scheme, similar to Miller et al. (2014); we extracted model raster data onto hawk locations used in creating the models, then organized the data from smallest to largest values. We recorded which raster values represented the first 5% of data as regions of poor probability for finding hawks, the next 15% represented fair probability, the next 30% represented good probability, and the remaining 50% represented excellent probability. To categorize maps, we used the Reclassify tool in ArcMap 10.7 to turn raster values into categories, then converted maps using the Raster to Polygon tool. We used the Union tool to combine hawk and turbine model polygons, then classified as relative risk categories in terms of likelihoods that a Swainson’s hawk will occur and that wind energy exists now or might be built in the future (Table 6.9).

Results

We tracked 41 Swainson's hawks (24 adults and 17 juveniles) for 7 - 1887 days (mean = 529 ± 462 days) from May 2012 to August 2020. We collected data on 89 breeding seasons across 41 birds, 67 fall migrations across 35 birds, 61 nonbreeding seasons across 30 birds, and 53 spring migrations across 26 birds (including incomplete seasons); after filtering, we had 186,021 hawk locations to consider in analyses (84,013 breeding season, 45,507 nonbreeding season, 32,183 fall migration, and 24,318 spring migration; Fig. 6.1). Our estimates of PTT height were -2,059 to 9,818 m above ground (mean = 135 ± 363 m above ground), with 113,377 locations (61% of all data) occurring between 0 and 200 m above ground (mean = 47 ± 44 m above ground); heights between 0 and 200 m were spread evenly across the map (Fig. 6.1) and comprised 78% of breeding-season data (65,288 points), 49% of fall-migration data (15,758 points), 46% of winter-season data (20,903 points), and 47% of spring-migration data (11,428). Heights > 200 m above ground made up 20% of data, and heights < 0 m (likely errors stemming from altitude and/or elevation estimations) made up 19% of data.

USGS indicated 64,553 turbines had been constructed by July 2020 across the United States and territories; 22,754 turbines in 355 facilities (1 – 239 turbines per facility, mean = 65 ± 49 turbines) were located within the hawk search area (Fig. 6.2). We found 3,504 additional turbines throughout the global study area; we confirmed the locations of 3,059 with high-resolution imagery and found 445 locations we suspected to be turbines, based on patterns in Sentinel-2 imagery or that were construction locations that appeared to be building turbines (Fig. 6.2). Specifically, we found 2,162 suspected and confirmed turbines within the study area in Mexico, 31 in Guatemala, 15 in El Salvador, 104 in Honduras, 92 in Nicaragua, 302 in Costa Rica, 101 in Panama, 313 in Argentina, and 384 in Uruguay (Fig. 6.2). We grouped international turbines into 53 'facilities' (i.e., close-proximity turbines with similar spatial patterns), with 1 to 506 turbines per 'facility' (mean = 66 ± 91 turbines).

Most hawk locations between 0 and 200 m above ground had no risk for encountering known wind turbine hazards (i.e., 90% were outside of turbine risk buffers and 84% were also outside of facility boundaries; Table 6.10). Of those locations with some degree of risk, 99% were within the United States and 98% occurred during the breeding season (Fig. 6.4). Few hawk locations (< 1%) were within the highest-risk buffers at any time (Table 6.10).

We excluded slope from all models, because of correlation with TRI (r = 0.57 – 0.91), and because we felt TRI might be more descriptive of terrain than slope values. We excluded elevation, distance to roads, and open lands from the year-round hawk data models, because of correlation with wind speed (r = 0.54, r = -0.51, and r = 0.51 – 0.56, respectively), and because in preliminary models the more-parsimonious model appeared more influential on AIC scores. We excluded elevation from the breeding-range models, because of correlation with wind speed (r = 0.51 and 0.52), because we assumed wind speed might be a more important factor for a soaring hawk species, and because wind speed had a better effect on AIC in preliminary models. We excluded open lands from migration models, because of correlation with wind speed (r = 0.52 and 0.53), and for similar reasons as for breeding-range data. We also excluded open lands from the global turbine models, because of correlation with wind speed (r = 0.52 and 0.59), and because wind is one of the top factors for siting wind turbines. We also excluded distance to water from United States turbine models because of correlation with elevation (r = 0.52 and 0.56), and because in preliminary models, elevation appeared more influential on AIC scores.

Our sample size was 21 to 34 birds per modelling dataset (21 birds for 'year-round hawk data', 34 birds for 'breeding-range data', 24 birds for 'nonbreeding-range data', and 21 birds for 'migration data'). For RSFs, we created 98,603 random points across the entire study area (equal to the number of hawk locations used in modelling). Of these, 64,363 points were allocated across the breeding-range study area, 19,660 points across the winter-range study area, 15,376 points across the fall-migration study area, and 10,691 points across the spring-migration study area (25,783 total random migration points). For RSPFs, we created 11,900 random points across the entire unused study area and 10,800 random points for the portion of the unused study area within the United States, which were equal to the number of turbine locations used in modelling.

For global turbine data, the top model included elevation, TRI, aspect, distance to road, wind speed, and interactions between elevation and aspect, TRI and distance to road, and TRI and wind speed; the ratio of model weights implied the top model was 4.9 times more likely than the global model to best represent the data (Table 6.3). Factors within the final model that appeared to have the highest weight on model results (i.e., beta values were one to three orders of magnitude higher than other betas) were the interactions between TRI and distance to roads and between TRI and annual average wind speed; other higher-weight variables included TRI and wind speed, while aspect, distance to roads, elevation, and the interaction between elevation and aspect contributed the least to model results (Table 6.11).

Regions of the global-range turbine map with the highest probability of finding current and future wind energy facilities contained 79% of confirmed and suspected turbine locations. Regions with a moderate probability of finding wind turbines contained an additional 12% of turbine locations. High- and moderate-probability regions were mostly concentrated in the northern portion of the map, in the states of Texas, New Mexico, Oklahoma, Nebraska, Colorado, and Kansas in the United States. Additional locations included the Oaxaca region of southern Mexico, linear strips through Honduras, Nicaragua, Costa Rica, Panama, and Colombia, the bend in the Andes through Bolivia, and many areas throughout Uruguay and the Cordoba, La Rioja, San Luis, La Pampa, and Buenos Aires provinces of Argentina (Fig. 6.5). Regions with the lowest probability of finding wind turbines contained 9% of confirmed and suspected turbine locations. In most cases, low-probability turbines were on the outskirts of facilities that were mostly within moderate- and high-probability categories. The global turbine model failed to identify an important south Texas/northeast Mexico region where many wind facilities existed along the coastline and throughout inland areas, so 65% of wind turbines in that region were on low-probability map cells (Fig. 6.6). Additionally, the map classed an entire turbine facility in Panama as being low probability. However, overall, the model identified regions with existing wind facilities well.

For United States turbines within the study area, the top model included elevation, TRI, distance to road, wind speed, open landscapes, and interactions between elevation and distance to road, TRI and distance to road, and TRI and wind speed; the ratio of model weights implied the top model was 3.5 times more likely than the global model to best represent the data (Table 6.4). Factors within the final model that appeared to have the highest weight on model results were the interactions between elevation and distance to road, TRI and distance to road, and TRI and wind speed, while open lands and elevation were the least influential terms in this model (Table 6.11).

Regions of the United States portion of the hawk study area with the highest probability of finding wind energy facilities contained 53% of known wind turbines. Regions with a moderate probability of finding wind turbines contained an additional 32% of turbine locations (85% combined). This model predicted a smaller amount of area most suitable for building turbines than included in the global data, and it did not do as good a job at reflecting actual turbine locations (Fig. 6.7). This model missed large areas in the northernmost region (in Colorado, Kansas, Nebraska, and large areas in western Texas). This model predicted more suitable space in the south-Texas region that the previous model largely missed; however, this model still missed (i.e., classified as ‘low probability’) 50% of turbines built in that region (Fig. 6.6). Overall, this model did not predict wind energy locations as well as the global-study-area model, so we used the more-comprehensive model for comparing to Swainson’s hawk predictive maps.

To represent year-round hawk data, we selected the global model, which included TRI, aspect, distance to major freshwater bodies, annual average wind speed, ocean, and interactions between TRI and distance to water, TRI and wind speed, and distance to water and wind speed (Table 6.5); this model had a weight of 100%. TRI, wind speed, and all interactions were the most influential variables in this model, and aspect contributed the least to results (Table 6.11).

The year-round hawk predictive model highlighted the two ends of the global range, as well as the Oaxaca region of Mexico, a portion of migration pathway through Nicaragua and Costa Rica, and Bolivia (Fig. 6.8). This model accurately indicated our trapping study area (a region surrounding Amarillo and Lubbock, Texas) as being an excellent region to find Swainson's hawks (Fig. 6.8). The model also accurately labeled oceanic waters as poor regions to find hawks (Fig. 6.8).

To represent breeding-season hawk data, we selected the global model, which included terrain ruggedness, aspect, distance to major freshwater bodies, distance to major roadways, annual average wind speed, open lands, and interactions between TRI and distance to water, TRI and distance to roads, TRI and wind speed, distance to water and distance to roads, and distance to water and wind speed (Table 6.6); this model had a weight of 100%. TRI, distance to water, wind speed, and all interactions contributed most to model results. Aspect, open lands and distance to roads contributed the least to results (Table 6.11).

The breeding-range model (Fig. 6.9) was more selective than the year-round model (Fig. 6.8) in indicating regions of good and excellent likelihood of finding Swainson's hawks; 85% of breeding-range locational data used in modelling was centered on a relatively small area surrounding Amarillo and Lubbock, Texas (i.e., where we trapped hawks and most adults from this study bred; Fig. 6.10), which may have biased model results to environmental data in that region. The model accurately indicated southern Texas is an unlikely region to find breeding Swainson's hawks, but inaccurately indicated good and excellent regions in the eastern portion of the map, where Swainson's hawks would actually be rare (Fig. 6.9). The model largely missed that Swainson's hawks would be more likely to be found as you go north and west through this portion of the breeding range (Fig. 6.9).

For nonbreeding-season hawk data, we again selected the global model, which included elevation, TRI, aspect, distance to fresh water, distance to roads, wind speed, open lands, and interactions between elevation and wind, TRI and distance to water, TRI and distance to roads, TRI and wind, distance to water and distance to roads, and distance to water and wind speed (Table 6.7); the ratio of model weights implied this model was 11.5 times more likely than the next model to best represent the data. TRI and all interactions were the most significant variables in producing model results for the model selected to represent this dataset, and open lands, aspect, elevation, distance to roads, and wind speed were the least influential variables (Table 6.11).

The nonbreeding-season model accurately identified large swaths of eastern Argentina and western Uruguay as being regions of high likelihood of finding overwintering Swainson’s hawks (Fig. 6.11). In regions identified by the model as poor locations, Swainson’s hawks from this study were infrequent visitors (Fig. 6.11). The northern section of good and fair probabilities were regions used throughout the season by several juvenile Swainson’s hawks in this study (Chapter 5; Fig. 6.11).

For hawk migration data, we again selected the global model, which included elevation, TRI, aspect, distance to fresh water, distance to roads, wind speed, ocean, and interactions between elevation and wind, TRI and distance to water, TRI and distance to roads, TRI and wind speed, distance to water and distance to roads, and distance to water and wind speed (Table 6.8); the ratio of model weights implied this model was 10.4 times more likely than the next model to best represent the data. Beta coefficients among model variables were the most similar out of all models we selected to represent various datasets; TRI and the interactions between TRI and distance to water and TRI and distance to roads were the most influential terms on model results, and wind speed and aspect were the least influential terms (Table 6.11).

The migration hawk model accurately predicted land use and migration pathways (i.e., most hawk data fell on ‘excellent’ landscapes) from Texas to northern Colombia, though the model indicated more space through these regions than hawks actually use during migration (Fig. 6.12). The model accurately predicted a pathway through the Andes Mountains that hawks used in Colombia (i.e., hawks quickly cross one mountain range, then travel south though a valley, then quickly cross the next range; Fig. 6.12). The bubbles of hotspots through the Amazon Rainforest correspond somewhat with stopover locations (described in Chapter 3), but also indicate that hawks spend little time in that region, which lines up with our movement data well (Fig. 6.12). Last, the model predicts a large swath of Argentina as appropriate migration start and end locations, which is accurate (Fig. 6.12).

The year-round hawk risk model (i.e., the hawk predictive model results combined with the wind energy predictive model results) highlighted several regions of high to extreme risk for Swainson’s hawks: nearly the entire breeding range, southern Texas and northern Mexico (at the start or end of the migration pathway), the Oaxaca region of southern Mexico, linear strips through Nicaragua, Costa Rica, and Panama, central Bolivia, and several areas throughout Argentina and Uruguay (Fig. 6.13). We compared these regions to all available hawk data and found 60% of locations indicated hawks were at high to extreme risk of encountering wind turbine hazards overall (94%

were locations recorded during the breeding season). Trajectories indicated that hawks moved through most hazardous regions, except in Central America, where hawks mostly selected pathways that would avoid prime wind turbine areas, and throughout Argentina and Uruguay, where hawks spent little time in high-risk regions (Fig. 6.13).

Similar to the hawk predictive model, the breeding range model of risk (Fig. 6.14) was more selective than the year-round version (Fig. 6.13). Regardless, 88% of breeding-season hawk data fell within hazardous regions of this model. This model highlighted the known breeding areas of hawks in this study as being largely areas of extreme risk to Swainson’s hawks (Fig. 6.10).

The nonbreeding-range risk model (Fig. 6.15) indicated fewer hazardous regions for Swainson’s hawks than the year-round model (Fig. 6.13). We found 5% of nonbreeding hawk locations within hazardous areas (mostly concentrated in southern Buenos Aires province, Argentina, and throughout Uruguay), but most locations and trajectories indicated hawks spent most of their time in regions with a low risk of turbine construction (Fig. 6.15).

The migration risk model (Fig. 6.16) highlighted similar regions of high risk as the year-round model (Fig. 6.13). We found 10% of migration data fell within hazardous areas. Results were so similar, that we chose to use the year-round model for all further references to hazards during migration.

Discussion

Our estimates of PTT height had substantial variability with many extreme values (from 2,000 m below ground to 9,000 m above ground), causing us to exclude much data from modelling datasets. PTTs used in this study had an estimated vertical error of ± 22 m (Microwave Telemetry, Inc., Columbia, Maryland), however Poessel et al. (2018) explained that estimating altitude can be confounded by the reference surface used in the technology, location of satellites at the moment of data transmission, errors in latitude and longitude estimates, errors in the digital elevation maps used in calculating above-ground height, etc. We do not know the proportion of height data that might have been significant errors, but patterns in changes in height over time suggest substantial errors may occur frequently. Due to this, we chose not to analyze altitude data obtained by our PTTs beyond including heights of 0 to 200 m above ground for this wind energy analysis.

Risk of hawks encountering wind energy facilities

Swainson’s hawks encounter the most risk from wind energy facilities on their breeding range in western North America. Our assessment was limited to our study area at the southeastern edge of the Swainson’s hawk breeding range in the south-central United States. However, the findings apply to many other regions throughout the full breeding range, particularly the eastern half where landscapes are suitable for hawk presence and wind speeds are consistently high enough for wind energy production (> 6 m/s for turbines examined in this study; Fig. 6.17). At minimum, we conclude most Swainson’s hawks may enter zones of high risk as they travel through the region during migration (Fuller et al. 1998, Kochert et al. 2011). Our examination of the wind energy industry throughout North and South America found that the industry has heaviest presence in the United States and Canada; many countries throughout the remainder of the Swainson's hawk global range either have little or no wind energy facility construction to date or have invested most heavily in placing wind energy facilities throughout regions that are unlikely to affect many Swainson's hawks. For example, Brazil is one of the leaders of wind energy construction in South America, but most turbines have been built along eastern coastlines that Swainson's hawks do not visit (Filgueiras and Silva 2003).

The high presence of wind energy facilities occurring on the breeding range may have significant implications for Swainson's hawks and other avian species. Wind energy presence might affect reproduction by displacing hawks from previously successful nesting locations, by reducing survival of adults and therefore likelihood of nest success and population growth, and by reducing survivability of recently fledged juvenile hawks that already experience a lower survival rate during the first year of life (Carrete et al. 2009, Kolar and Bechard 2016, Naef-Daenzer and Grüebler 2016, Dohm et al. 2019, Chapter 5). Additionally, Swainson's hawks spend the longest proportion of the year on the breeding range (5 – 6 months compared to 2 – 4 months on the nonbreeding range and 1 – 3 months on each migration; Bechard et al. 2010). The length of the annual presence of Swainson's hawks combined with extensive wind energy developments across much of their breeding range among the great plains may place hawks at risk for a significant proportion of their life cycle. Importantly, collision with wind turbine blades (i.e., the focus of most hazard research) is not the only risk for hawks associated with the industry; power line electrocution, collision with wind energy construction and maintenance vehicles, effects to prey populations, etc., are additional hazards that can impact hawk populations and are increased when the wind energy industry is frequently encountered, such as on the High Plains of Texas.

Outside of the breeding range, Swainson's hawks are at a relatively lower risk of encountering wind energy hazards. We identified five regions beyond the primary breeding range that pose wind energy risks to Swainson's hawks. Southern Texas and northeastern Mexico (within the breeding range for some [Fig. 6.17], but, more importantly, a migration pathway for many Swainson's hawks; Bechard et al. 2010, Kochert et al. 2011) contain several large turbine facilities and multiple hotspots with high potential for future construction. The Oaxaca region of southern Mexico is a funneling point for Swainson's hawk migration; hawks appear to generally skirt around mountains and funnel through a valley just north of the turbine fields, then turn southeast to travel the Pacific coastline (Fig. 6.18). The primary pathway traveled may allow most hawks to avoid current wind energy hazards, but 46% of hawks in this study briefly travelled through known facilities at least once. Future wind energy construction in the region could place the majority of migrating hawks at risk in this region. Cabrera-Cruz and Villegas-Patraca (2016) monitored migrating raptors in this Oaxaca region, and similarly found that most birds adjusted flight paths and avoided entering wind farms. Hawks encounter small, linear regions of wind energy risk that correspond with turbine facilities built throughout Central America, however migration trajectories indicate hawks may avoid most of these regions (Fig. 6.13). Detailed migration analyses showed that hawks moved through Central America at a fast rate, making few stopovers or roosting stops (Fuller et al. 1998; Chapter 3), which reduces the chance of flying at a height that would place hawks at risk of wind turbine collision (e.g., most hawks traversing Panama flew > 350 m above ground, well above turbine rotor sweep zones; Smith 1985). Therefore, while some wind energy risk exists, Central America appears to be relatively safe for Swainson's hawks. The bend in the Andes Mountains in central Bolivia may pose a future risk to migrating hawks. To our knowledge no wind energy facilities have been built there yet, but modeled data suggests this as the only region for Bolivia to build a wind energy industry. All hawks in this study traveled through zones that, based on wind energy development potential, would be considered high to extreme risk zones in Bolivia during at least one, if not every, migration (Fig. 6.19). Last, several regions throughout Argentina and Uruguay were identified as zones of possible hawk risk. However, the region of highest concentration of hawk presence during the nonbreeding season in this and previous studies (e.g., Sarasola et al. 2008, Bechard et al. 2010, Kochert et al. 2011) lies across a generally safe zone.

Why have so few Swainson's hawk carcasses been reported at turbine fields?

Beston et al. (2016) suggested Swainson's hawks were at high risk of population decline from wind energy hazards. If all signs point towards the majority of wind energy risk existing on the breeding range, and published research on raptor mortality exists from breeding-range areas, a compelling question is why so few Swainson's hawk carcasses have been reported at wind farms? We located only 24 reports of Swainson's hawk fatality due to turbine collision, all within the United States (Howell 1997, Johnson and Erickson 2011, Loss et al. 2013, Graff et al. 2016, Watson et al. 2018*a*); additionally, one tagged hawk in this study died from collision with a turbine blade near its nesting territory (Chapter 3). In comparison, we found 358 red-tailed hawk (*Buteo jamaicensis*) fatalities, 232 American kestrels (*Falco sparverius*), 80 turkey vultures (*Cathartes aura*), 36 golden eagles, 14 ferruginous hawks (*Buteo regalis*), and 12 rough-legged hawks (*Buteo lagopus*) within those same publications plus one additional resource (Erickson et al. 2001), and further resources can easily be found for these and more species. Some wind facilities produce disproportionate risk to local species compared to others; for example, Katzner et al. (2017) identified 67 golden eagle fatalities at a single facility (Altamont Pass Wind Resource Area) over two years, while other facilities across the golden eagle range showed few or no fatalities (e.g., Erickson et al. 2001, Pagel et al. 2013). Internationally, raptor species are also at variable risk from local wind energy hazards; de Lucas et al. (2012) reported 221 griffon vulture fatalities in Spain, Bevanger et al. (2010) reported 39 white-tailed eagle fatalities in Norway, Bellebaum et al. (2013) reported 34 red kite fatalities in Germany, and Watson et al. (2018*b*) reported fatalities of ten raptor species from preliminary reports out of South Africa.

Perhaps behavioral differences might shed light on differential mortality risk. Smallwood et al. (2009) and Watson et al. (2018*a*) explained that observations of hawks using turbine fields indicated most birds were aware of hazards and generally paid attention to turbine activity to reduce fatality risk. Hunting requires focus and increases distraction and, thus, increases risk of failing to avoid hazards and causing a fatal collision (Smallwood et al. 2009). Many raptors and vultures hunt or search for carcasses from the wing, potentially spending much of the day in flight; turbine collision only occurs in flight, so the more time spent in the air raises risk. Some raptors will ‘kite’ (a behavior in which they search the ground for prey while strong winds passing across their set wings allows them to maintain flight with only occasional flapping); Watson et al. (2018*a*) noted ‘kiting’ may make raptors more vulnerable to blade strikes due to drifting while distracted. Most hawks will kite occasionally, but Swainson’s hawks rarely engage in this hunting behavior, which may reduce risk (Bechard et al. 2010). Swainson’s hawks often spend their hunting flights within a few meters of the ground (Palmer 1988), rather than high soaring. They will also hunt from perches and are well known for standing on the ground, catching insects with little effort or waiting for ground squirrels to emerge from burrows (Johnson et al. 1987, Canavelli 2000, Bechard et al. 2010, Littlefield and Johnson 2013). The difference with all these hunting behaviors is prey type; for their body size, Swainson’s hawks generally take smaller prey, such as insects, lizards, and small rodents (Canavelli 2000, Giovanni et al. 2007, Bechard et al. 2010), compared to other raptors (Fitch et al. 1946, Blair and Schitoskey 1982, Giovanni et al. 2007, Herzog et al. 2019). Staying closer to the ground to search for small prey may allow Swainson’s hawks to reduce risk of flying within rotor-swept zones in turbine fields.

Social interaction, such as pair bonding, playful interactions among juveniles, and antagonistic territorial behaviors, may also be distracting and increase chance for collision (Smallwood et al. 2009, Watson et al. 2018*a*). All raptors engage in these activities to varying degrees, and individual variation may place birds at higher or lower risk in turbine areas. Swainson’s hawks are territorial near nests, but generally tolerant of conspecifics in neutral hunting areas (Bechard et al. 2010), thus potentially lowering the risk of distraction due to interactions compared to more aggressive species. Outside of the breeding season, Swainson’s hawks are gregarious, tending to form huge flocks during migration and maintaining aggregations through the nonbreeding season (Canavelli 2000, Bechard et al. 2010, Cabrera-Cruz and Villegas-Patraca 2016). Flocking may increase risk if hawks are focused on following other birds and not on nearby hazards. However, this behavior may lower overall risk if flocks avoid hazards as birds respond to the avoidance behaviors of other individuals. For example, Cabrera-Cruz and Villegas-Patraca (2016) described an alteration of the primary migratory pathway used by Swainson’s hawks and other species in southern Mexico that was apparently in response to increasing wind farm construction; over time the pathway bent from a southeastern route to the coastline to more and more eastward along the mountains, allowing most hawks to avoid flying through the wind farms. This may be a response not only to the presence of hazards, but also may be anticipatory responses of hawks further behind in the flock shifting as they observe hawks ahead of them before they can even see the wind farms, and thus a case for social interaction lowering risk for most hawks.

Vigilance and avoidance behaviors may reduce risk for individual raptors in proximity to turbine facilities (Smallwood et al. 2009, Watson et al. 2018*a*). Displacement is the safest type of avoidance, as birds may select new areas to use rather than occupy areas with wind energy facilities. This, though, may have negative impacts, such as reducing use of areas with high prey density or previously successful nest locations (Madders and Whitfield 2006, Shaffer and Buhl 2016, Dohm et al. 2019). It is questionable how long displacement lasts, however, as studies have found most raptor species return to using wind farms as habitat within a few years post-construction, if they were displaced at all (Madders and Whitfield 2006, Dohm et al. 2019). Within facilities, raptors may show additional vigilance and avoidance behaviors that reduce risk. Watson et al. (2018*a*) described Swainson's hawks, red-tailed hawks, and ferruginous hawks employing evasive and reflexive escape maneuvers to avoid blade collision. Hawks also displayed awareness of increased hazards, flying through rotor-swept zones less when blades spun faster (i.e., in faster wind conditions; Watson et al. 2018*a*). However, the habituation displayed by hawks nesting near turbines, and their apparent comfort with frequent flights among spinning blades, increased their risk of fatality over the general hawk population using the area under observation (Watson et al. 2018*a*). Johnston et al. (2014) suggested migrating golden eagles detected wind energy hazards along ridgelines and adjusted to higher flight altitudes to avoid rotor-swept zones. Swainson's hawks may also use flight height to their advantage; Smith (1985) documented migrating Swainson's hawks typically flying at 375 to 2,650 m above ground in Panama. However, our transmitter data suggested only 20% of all locations and 37% of migratory locations were > 200 m above ground. This means a substantial proportion of observed hawk data may have been recorded within potential rotor-swept zones if hawks were in proximity to turbine facilities. While there is potential to avoid turbines by increasing flight height, the roosting and stopover behaviors of this species, as well as other moments near ground, contribute to risk (Kochert et al. 2011, Chapter 3). In another example, White-tailed eagles in Norway were subjected to an ecological trap within the wind farm under observation due to an apparent lack of avoidance behaviors; adult eagles were displaced to nesting territories outside of the wind farm, which pushed juvenile eagles out of those areas and into the wind farm as presumed unguarded habitat (Dahl et al. 2013). Juvenile eagles under observation engaged in distracting behaviors, such as social interaction and hunting, with no apparent avoidance of turbine hazards; this may suggest why this species suffers high wind-energy-related mortality compared to other species (Dahl et al. 2013).

In addition to the possibility of differences in risk among species, we have the issue of data transparency. In the United States, it is standard practice to monitor pre-construction bird populations and post-construction mortalities (Kuvlesky et al. 2007). However, those data are considered the intellectual property of wind farm owners, and thus are not required to be reported to the public (Kuvlesky et al. 2007). It is therefore difficult to get a full understanding of wind energy impacts to Swainson’s hawks and other species, because most data are not currently available for evaluation (Kuvlesky et al. 2007).

Modelling hawk and wind energy data

Overall, we consider the model results to have well reflected likely wind turbine and hawk occurrence, with some models being more realistic than others. The global-range wind turbine map did a better job of reflecting real wind energy locations than the USA-only map (Fig. 6.5 and 6.7), perhaps because the USA map was restricted to a small portion of the Swainson’s hawk range, rather than the extent of the continental United States. The inclusion of international turbine locations appeared to give a broader definition of landscape variables suitable for wind energy construction, which better encapsulated real locations in the resulting map. However, both maps missed an area of concentrated wind energy facilities in southern Texas and northeastern Mexico (Fig. 6.6); perhaps the environmental factors we selected failed to represent that region well. Alternatively, this may reflect that construction relies upon more than landscape features;

wind energy siting also depends upon economic forces, access to private and public lands, local laws and regulations, local public acceptance, etc. Modelling may never fully reflect siting of urban structures, like the wind energy industry, but at minimum, it gives us insights as to regions where sensitive fauna may be more likely to be impacted currently and into the future.

Modelling hawk locations produced mixed results. The year-round map accurately showed that hawks are most likely to be found at the extreme ends of their global range, where they spend most of their lives (Bechard et al. 2010). Within those regions, the model performed well in predicting areas we would most likely find Swainson's hawks, though the season-specific models may be a better representation of the data. The locations of 'good' and 'excellent' probability along the migration pathway represented areas where hawk data became highly concentrated through geographical bottlenecks in this and previous transmitter studies (Fuller et al. 1998, Kochert et al. 2011, Airola et al. 2019, Chapter 3).

The breeding-range map (Fig. 6.9) was highly accurate at predicting most of the specific breeding territories where hawks were captured and spent most of their breeding seasons (Fig. 6.10). However, the territorial nature of hawks caused significant bias in modelling, resulting in far less landscape being identified as 'good' and 'excellent' probability regions across the entire breeding-range map compared to the year-round model. One might question why our breeding-range study area was so large, if most breeding-season locations were highly concentrated in one small area (Fig. 6.10). An interesting finding of our overall hawk-tracking study was that after reaching the breeding range in April and May, about half of adults left their territories to wander hundreds of km, then returned to breed in the same territories as previous years (Fig. 6.20). We speculate that perhaps this is a time of searching for new mates or better territories. After breeding success or failure, hawks often spent time exploring, and we suspect non-breeding hawks were primarily nomadic the entire season. Prior to migration, Swainson’s hawks are known to leave territories to stage, where they gather in flocks and accumulate fat reserves for the journey (Johnson et al. 1987, Bechard et al. 2010, Kochert et al. 2011, Littlefield and Johnson 2013). However, our study area is a known staging region (Kochert et al. 2011, Littlefield and Johnson 2013); hawks from this study did not always move off territory until they made clear southward migratory movements with a lack of an obvious staging period, perhaps because hawks could find sufficient food and flocks to join with little effort (Chapter 3). Additionally, juvenile hawks were nomadic explorers throughout their boreal summer seasons and never established a territory during the years of observation (Chapter 5). Due to these behaviors, it was difficult to distinguish the beginning and end of the breeding season with this sample of birds, adding to the variability of hawk locations for this study, and to our understanding of the plasticity of seasonal behaviors in Swainson’s hawks. Although locations were highly concentrated during this season, resulting in possible model bias, the area surrounding breeding territories only reflected about 80% of total hawk locations, due to their ranging behaviors. Therefore, while this model was likely accurate for our data, the year-round model should be considered to better reflect breeding-season probabilities for the species overall, at least within this limited portion of the breeding range.

We believe the nonbreeding-range model accurately represented the expected locations of overwintering hawks described by previous research (e.g., Sarasola et al. 2008, Bechard et al. 2010, Kochert et al. 2011). Out of all hawk models, we considered this model to have performed best, in terms of representing the species, rather than solely the data we provided. The model was limited by our study-area boundary, however; a larger portion of Uruguay may be occasionally used by Swainson's hawks, and hawks have been observed as far south as Chubut province, Argentina (at least 260 km south of the study area; Jaramillo 1993). In addition, no hawks in this study overwintered in other regions, a behavior commonly observed in a California sub-population (Airola et al. 2019), and possibly by other vagrant hawks (Browning 1974, Hayes 1999).

The migration model produced patchy results that are not well reflective of the known linear migration pathways. From Texas through Colombia, the model does not perfectly predict migration corridors (i.e., the model reflects more 'good' and 'excellent' regions than should occur based on the hawk data), but most hawk data fell on 'good' and 'excellent' cells and avoided 'poor' locations. A region of especially good prediction is the valley between lines of Andes Mountains in Colombia, where hawks cross one set of mountains, then spend time travelling through the valley before crossing again, presumably taking the path of least resistance through this region (Chapter 3; Fig. 6.21). While the remainder of the pathway poorly describes migration corridors from the data, we believe the patches represent environmental variables at nightly roosting locations and stopovers (i.e., areas with concentrations of points; Chapter 3).

For all models, terrain ruggedness, and interactions involving this factor, were generally more influential on model results than other variables. Despite the TRI map reaching a maximum of 1,599 (extremely rugged terrain), the maximum TRI of a hawk location was 273 (moderately rugged), and 97% of locations were ≤ 80 (level terrain; Riley et al. 1999). This may reflect hawks' preference for open landscapes, which generally occur across relatively flat terrain, or regions with a high likelihood of thermal formation used for soaring flight (e.g., mountainous areas may have significant turbulence, horizontal wind, or heterogeneous surfaces that reduce chances of thermals forming). Orographic lift, produced when horizontal wind hits a vertical surface, may also be used by soaring hawks (Bildstein 2006, Duerr et al. 2015, Katzner et al. 2015), but we did not see much evidence for that based on the TRI numbers in this study. However, hourly data collection limited our ability to observe fine-scale behaviors and hampered an assessment of hawk avoidance of rugged terrain or use of orographic lift. Wind turbines were similarly located over generally flat terrain (TRI ranged from 0 – 141 [slightly rugged; Riley et al. 1999], mean = 20), which likely reflects an important limitation of turbine construction.

Annual average wind speed was a highly influential factor for wind turbine models and was retained in all hawk models with varying levels of influence on results. For wind turbine siting, wind speed is probably the most important factor to consider; the wind energy industry requires a minimal percentage of the year at appropriate wind speeds to make construction and maintenance of wind energy facilities profitable. In the sample of wind turbines examined in this study, annual average wind speed at 100 m above ground ranged from 6 to 16 m/s (mean = 9 m/s; Fig. 6.17).

Wind dynamics are also important for hawks, but on a scale that we were unable to describe in these model variables. Fine-resolution differences in moment-to-moment wind speed and direction would be far more important to an individual hawk than an average speed over time. Wind direction likely plays a far larger role during migration than speed as well, because winds can assist or hinder directional flight, and strong cross winds can blow hawks off course or out over water (a situation which can be deadly; Bildstein 2006). However, wind direction at heights relevant to hawks changes so frequently and seasonally, that we were unable to determine any reasonable way to incorporate that variable into models. We had a similar problem with finer scales of wind speeds, such as wind speed at the height a hawk was above ground at any given time (e.g., wind tends to be faster as you reach higher altitudes). All final hawk models suggested annual average wind speed plays a role in landscape selection, so we suggest even coarse measures of wind may be informative for understanding Swainson's hawk migration.

While proximity to water appeared unimportant for turbine data, water variables were consistently retained in high-ranking models for hawk data. Hawks may be attracted to or avoid water for a variety of reasons, including for drinking, wind dynamics, and risk of long over water passage (Bildstein 2006, Bechard et al. 2010, Vansteelant et al. 2015). The ocean variable is clearly important ecologically, as most soaring hawks do not generally cross large bodies of water (Bildstein 2006). We interpreted trajectories in this study as hawks making occasional 25-km crossings during migration (rarely up to 75 km; Chapter 3), but the hourly data collection limited our inferences (i.e., it is possible hawks never crossed water, but we received locations at either end of a water body that were interpreted as a crossing due to limited data). Coastlines may serve as important landmarks and migratory pathways (Bildstein 2006), particularly from southern Texas through Central America, where hawks tended to travel along coastlines, possibly to take advantage of wind dynamics and to avoid nearby mountains and rugged topography (Chapter 3). However, we do not understand the relationship of hawk data with distance to fresh water sources in this modelling study. Histograms suggested hawks spent the most time near water during migration and winter (i.e., histograms were skewed with peaks on or near 0 km), but distance to water may have been relatively unimportant during the breeding season (i.e., histograms showed two bell curves with peaks at 30 and 90 km, but few locations near 0 km). Hawks drink and bathe regularly but can do so at water sources of too fine a scale for our modelling efforts (e.g., puddles, leaks from irrigation structures, stock ponds, ephemeral wetlands, streams, etc.). We located a finer-resolution water body map for the United States (i.e., smaller lakes, ponds, wetlands, streams, channels, and tributaries), but were unable to find similar resources for most other countries throughout the study area. This limited our dataset to similarly large-scale data (major rivers and large lakes), which significantly restricted our ability to model water at a resolution that would realistically be used by hawks for activities such as drinking. Larger water bodies may be important as linear pathways, for associated habitat structures, such as availability of trees or abundance of prey, and for associated wind dynamics. Swainson’s hawks may travel along rivers for a limited navigational extent (Bildstein 2006), however rivers throughout the study area would generally be moving east or west as they travel to the ocean, while hawks mostly move north and south during migration, so navigation is unlikely to be important beyond simple landmarks. During breeding and nonbreeding seasons, trees associated with water bodies may be highly important, if the nearby landscape lacks trees to roost or nest in (Bechard et al. 2010).

Prey availability may vary with distance to water, but given Swainson's hawks' affinity for irrigated agriculture (e.g., Schmutz 1987, Smallwood 1995, Dechant et al. 2000, Mcconnell et al. 2008, Bechard et al. 2010) and the possibility of water sources too small to be included in our dataset, this issue may be of limited importance landscape-wide. Last, presence of water can change wind dynamics, influencing wind strength and directionality along large rivers, edges of lakes, and coastlines. This may affect thermal availability and may be advantageous enough to attract hawks or may repel hawks from large water sources. For example, Swainson's hawks in this study avoided crossing two large lakes in Nicaragua during migration (Chapter 3), possibly due to a lack of thermals and inappropriate wind dynamics. Ultimately, fresh water influenced data enough to show up consistently in top models, but we do not understand what the relationship might be for hawks. Indeed, the relationship could be spurious, due to the large number of data and large scale of inference and our limitation of only including large water sources.

Distance to roads was important for both wind energy siting and most hawk models. Similar to the water variable, distance to roadways was restricted to large-resolution data consisting of major highways and larger paved roads throughout the study area. Again, we found high-resolution and more-recent data for the United States but were limited by the resolution of available data for other countries; we therefore selected a resource with similar scale across the entire area for consistency. Hawks and turbines would both benefit from smaller road networks than we were able to include, which would likely influence model results. Additionally, roadways are dynamic; a wind energy company is not restricted by the availability of current roadways if new roads can be built as needed. We suggest that while this factor is an important consideration for modelling both wind energy and hawk presence, the dynamic nature of the presence of roads over time, and the scale at which data is included, present limitations on interpreting model results.

Elevation was included in many models, which suggests this may play some ecological or logistical role in these datasets. For hawks, elevation may be so closely tied to terrain ruggedness, that we generally interpret this landscape variable in a similar way; hawks are likely attracted to flat terrain, such as low-elevation coastlines and the 1,000-m-elevation plains used as nesting habitat in northern Texas (Chapter 2). For wind energy, elevations with suitably flat terrain for construction as well as suitable wind dynamics would be important considerations. For example, turbines may be constructed at higher elevations if the tops of ridges present the best wind resource, or low elevations if wind travelling through a canyon or along a coastline presents the best wind resource in the area.

Last, open land and aspect were included in many top models, but with such low beta coefficients that it is difficult to interpret any significant role of these variables compared to other model factors. Open landscapes play an obvious role as habitat availability for hawks, but when hawks migrate, they spend little time in any one location (Chapter 4). Further, they travel across forests, such as the Amazon Rainforest, which may have resulted in this factor not appearing to be necessary for migration and year-round datasets. There may be some relationship with constructing turbines in open versus forested landscapes, but because construction can easily manipulate the landscape as needed, we are not sure how important this factor may be if the wind resource is sufficient. Aspect may affect wind direction or land cover type, but, again, the models suggested such low importance to this variable that it is difficult to interpret anything important for either dataset.

Our assessment only gives a general impression of where, globally, Swainson's hawks might encounter wind turbine hazards, rather than any direct measure of risk at a specific turbine site. We did not incorporate turbine and farm designs (e.g., turbine height, length of blades, and type of pole, or how far apart turbines are placed throughout a landscape may affect likelihood of bird mortality; Erickson et al. 2001, Loss et al. 2013) or variable management strategies (e.g., wind turbines can be turned off during sensitive periods, such as migration, to reduce bird mortality; de Lucas et al. 2012, Smallwood and Bell 2020), which might alter risk at any given location. We additionally did not examine additional hazards, such as power lines or vehicular collisions (Erickson et al. 2001). This assessment should be considered one tool out of many for understanding risk to this and other species. For example, Before-After-Control-Impact surveys are frequently conducted at wind energy construction sites to assess prior risk and frequency of mortalities post-construction (e.g., Anderson et al. 1999, Kuvlesky et al. 2007, Shaffer and Buhl 2016, Smallwood and Bell 2020). However, the lack of transparency of data in the United States limits our current understanding of risk and mortality (Kuvlesky et al. 2007). Various other modelling types, such as collision risk models (e.g., Band et al. 2005, Carrete et al. 2009, Eichhorn et al. 2012, New et al. 2015) and spatial vulnerability indices (Noguera et al. 2010) can help us identify and understand fine-scale risk within a turbine facility, potentially incorporating details, such as bird behavior and wind farm design, that influence risk in any given area. Due to high risk on the breeding range, much potential exists for studying reproductive impacts from presence of wind energy (e.g., Usgaard et al. 1997, Anderson et al. 1999, Groen 2015, Kolar and Bechard 2016). Whether or not long-term displacement occurs, or its potential impact on population dynamics, is poorly understood and warrants further research (e.g., Madders and Whitfield 2006, Shaffer and Buhl 2016, Dohm et al. 2019).

Conclusion

Swainson's hawks appear to be at highest risk of encountering wind energy hazards on the breeding range. However, Swainson's hawks may be less vulnerable to collision with turbine blades than other raptor species (i.e., few mortality reports exist in the literature), due to various differences in behavior. Unfortunately, the lack of data transparency limits our ability to understand the full extent of this risk (Kuvlesky et al. 2007). Unlike more-sensitive species, the adaptability of the Swainson's hawk may allow it to thrive in the face of human-dominated landscapes, such as increasing wind farm presence, similar to this species' positive response to land conversion for agriculture (e.g., Schmutz 1987, Smallwood 1995, Dechant et al. 2000, Mcconnell et al. 2008, Bechard et al. 2010). Limited evaluations of reproductive potential within a wind farm landscape suggested no impact to nesting success (Groen 2015, Kolar and Bechard 2016), and we so-far see no strong evidence for significant displacement in northern Texas study areas (unpublished data). Therefore, while wind energy is a hazard to birds of prey, Swainson's hawks may be less likely than other raptor species to suffer significant population-level effects from collision mortality. In the face of gradual landscape change, Swainson's hawks may be an ecological winner across much of its range; time will tell.

Modelling techniques, such as methods we employed for this project, are useful for assessing potential risk from the wind energy industry and other human-related hazards for a variety of species. At the time, we could only find high-quality location data for wind energy in the United States, but if databases are created compiling global turbine information, this technique could be refined and expanded to raptors and other species of concern from around the world. Compiling published tracking and sighting records and collecting more locational data from raptors is valuable; this information will expand the ability to pinpoint hazardous locations, giving the growing wind energy industry better information for siting facilities and turbines that minimize avian mortality.

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Tables

Table 6.1. Sources for water body shapefiles we used to create ‘distance to major water bodies’ and ‘distance to major fresh water bodies’ rasters.

Type and location	Source
Hydrographic Features; United States	United States. Bureau of the Census. Geography Division. United States. Bureau of Transportation Statistics. (2014). Hydrographic Features (Polygons): United States and Territories, 2011. [Shapefile]. United States. Bureau of Transportation Statistics. Retrieved from https://earthworks.stanford.edu/catalog/stanford-jx308gf9049
Inland Waters; El Salvador	International Steering Committee for Global Mapping. Centro Nacional de Registros (El Salvador). (2013). Inland Waters, El Salvador, 2013. [Shapefile]. International Steering Committee for Global Mapping. Retrieved from https://earthworks.stanford.edu/catalog/stanford-jk252hs0406
Inland Waters; Honduras	International Steering Committee for Global Mapping. Instituto Nicaragüense de Estudios Territoriales. (2016). Inland Waters, Nicaragua, 2016. [Shapefile]. International Steering Committee for Global Mapping. Retrieved from https://earthworks.stanford.edu/catalog/stanford-qs779cw9995
Inland Waters; Nicaragua	International Steering Committee for Global Mapping. Instituto Nicaragüense de Estudios Territoriales. (2016). Inland Waters, Nicaragua, 2016. [Shapefile]. International Steering Committee for Global Mapping. Retrieved from https://earthworks.stanford.edu/catalog/stanford-qs779cw9995
Inland Waters; Uruguay	International Steering Committee for Global Mapping. Uruguay. Geographic Military Service. (2013). Inland Waters, Uruguay, 2013. [Shapefile]. International Steering Committee for Global Mapping. Retrieved from https://earthworks.stanford.edu/catalog/stanford-qf457gg7343

Table 6.1. Continued.

Type and location	Source
Inland Waters; Mexico, Belize, Costa Rica, Panama, Ecuador, Peru, Brazil, Bolivia, Paraguay, Argentina, Venezuela, and Chile	Hijmans, Robert. Nd. Country: Mexico, Belize, Costa Rica, Panama, Ecuador, Peru, Brazil, Bolivia, Paraguay, Argentina, Venezuela, Chile; Subject: Inland Water. [Shapefile]. DIVA-GIS. Retrieved from https://www.diva-gis.org/gdata
Lakes; Colombia	Lakes, Colombia, 2011. [Shapefile]. Instituto Geografico "Agustin Codazzi". Retrieved from https://earthworks.stanford.edu/catalog/tufts-colombia-lakes-11
Major Rivers; Colombia	Major Rivers, Colombia, 2011. [Shapefile]. Instituto Geografico "Agustin Codazzi". Retrieved from https://earthworks.stanford.edu/catalog/tufts-colombia-major-rivers-11
Water Bodies; Guatemala	The World Bank. 2017. Water Bodies in Guatemala. [Shapefile]. Retrieved from https://datacatalog.worldbank.org/dataset/water-bodies-guatemala
World Oceans	Patterson, Tom. Kelso, Nathaniel Vaughn. (2012). World Oceans, 1:10 million (2012). [Shapefile]. North American Cartographic Information Society. Retrieved from https://earthworks.stanford.edu/catalog/stanford-hs475jq1596

Table 6.2. Justifications for including or excluding interactions between pairs of factors in hawk and wind energy model sets.

Pairs of Factors	Justification for including or excluding interaction from models
Elevation and Aspect	Both aspect and elevation can impact wind speeds, so this interaction may be a consideration for turbine construction. However, we see no reason for this interaction to be important for hawks that are known to mostly rely upon rising air thermals to attain lift for soaring flight.
Elevation and Terrain Ruggedness Index	Turbines are generally constructed on flat landscapes. We can envision a situation where a higher or lower elevation location may be more likely to be selected when it contains flat terrain suitable for construction. However, we see no particular reason for this interaction to be interesting to investigate for hawks.
Elevation and Distance to Major Water Bodies	Swainson's hawks use fresh water, but we are unsure of their relationship with major water bodies; but, we see no reason for that relationship to interact with elevation values in a meaningful way, as in general, water will likely occur at only lower elevations. Turbines can be built deliberately near water due to the way water changes wind patterns, and thus turbines may be built in higher or lower elevation areas because water exists there. But turbines only require consistent winds, which can occur far from large water bodies, so we felt any patterns would likely wash out at the large scale we were examining. We therefore excluded this term from both datasets types.
Elevation and Distance to Major Roads	Turbines are more likely to be constructed near major roadways, to ease shipping materials. Therefore we can envision a situation where a high or low elevation location would be more likely to be selected when a major roadway is nearby, so we included this in turbine models. However, while hawks are attracted to roadways, the elevation term is only really relevant during migration when hawks are less likely to be influenced by distance to roadway, so we felt this interaction would likely not be important for hawks.
Elevation and Annual Average Wind Speed	Wind speed increases with elevation, which may impact landscape selection for both hawks (especially during migration) and constructing wind turbines. We considered this term for all model sets.

Table 6.2. Continued.

Pairs of Factors	Justification for including or excluding interaction from models
Elevation and Land Cover	The presence or absence of open landscapes (grasslands, shrublands, agriculture, and deserts) may occur at many elevations, depending on the geographic location. Swainson’s hawks are known to occupy open landscapes, but we see no reason for elevation to affect that. Turbines can be built in open and forested landscapes and even on water, so we didn’t feel this would interact in any meaningful way for turbines either.
Elevation and Ocean	Because ocean will only occur at 0 m elevation, we do not see why this term would interact for birds.
Aspect and Terrain Ruggedness Index	Turbines are known to select for flat landscapes, and hawks might also select flatter terrain, because steep terrain may be ineffective at producing the air thermals hawks seek out. At flat ruggedness values, aspect will be unimportant, therefore this interaction should not be a consideration for models.
Aspect and Distance to Major Water Bodies	We see no reason for these terms to interact in any meaningful way.
Aspect and Distance to Major Roads	We see no reason for these terms to interact in any meaningful way.
Aspect and Annual Average Wind Speed	Aspect can influence wind speed, therefore may be a consideration for wind turbine construction. However, we do not expect this to influence birds in any meaningful way at the geographic scales under consideration.
Aspect and Land Cover	We see no reason for these terms to interact in any meaningful way.
Aspect and Ocean	There will be no aspect over oceanic waters, so there is no reason for these terms to interact.

Table 6.2. Continued.

Pairs of Factors	Justification for including or excluding interaction from models
Terrain Ruggedness Index and Distance to Major Water Bodies	We expect hawks to avoid rugged areas, and we are unsure of their relationship with fresh water bodies, so this interaction may be a consideration for hawks (e.g., hawks may fly closer to water when landscape is flat and produces good thermals, or hawks may use more-rugged landscapes when water is available). As stated above, turbines are most likely to be built near major roadways, and turbines may be deliberately built near water when wind conditions are suitable, so there may be an interaction for wind energy as well.
Terrain Ruggedness Index and Distance to Major Roads	As stated above, turbines are most likely to be built near major roadways, therefore we can envision a situation where a more rugged area might be selected for construction if it contains suitable micro-locations to build turbines and is near major roadways. Birds likely avoid rugged terrain, but are attracted to roadways for perches, so perhaps this interaction might occur in hawk datasets as well.
Terrain Ruggedness Index and Annual Average Wind Speed	Wind speeds can be affected by presence of rugged terrain, as well as the ability to move across flat terrain. Both hawks and wind energy producers are likely to select landscapes based on wind conditions, therefore there may be important considerations when wind is positively influence by the shape of terrain.
Terrain Ruggedness Index and Land Cover	These two terms likely correlate, because more-rugged terrain is more likely to be forested. However, we see no reason for that to influence hawk or turbine location in any significant way.
Terrain Ruggedness Index and Ocean	Like elevation and aspect, terrain will be flat over oceanic raster cells, so there is no reason for these terms to interact.

Table 6.2. Continued.

Pairs of Factors	Justification for including or excluding interaction from models
Distance to Major Water Bodies and Distance to Major Roads	Hawks are attracted to roadways, and we don't know if hawks will be attracted to or repelled by major fresh water bodies. We can envision a situation where they would be more likely to be near water when roadways with suitable perches and hunting grounds are present. Turbines can be built near or away from water, but are more likely to be built near major roads, so we also can envision some interactions occurring with those datasets.
Distance to Major Water Bodies and Annual Average Wind Speed	Wind conditions can change around sources of water, so this may be an important term to consider for hawks. We included this term for turbines for similar reasons.
Distance to Major Water Bodies and Land Cover	We see no reason for these terms to interact in any meaningful way.
Distance to Major Water Bodies and Ocean	For birds, these water variables measure different types of water that do not co-occur, so there is no reason for these variables to interact in the data.
Distance to Major Roads and Annual Average Wind Speed	Hawks are likely attracted to both roads and ideal wind conditions, but we don't see why those terms would interact for hawks in any meaningful way. There may be an important interaction for turbine construction, however, because shipping materials requires nearby roadways, so manufacturers would be more likely to select an ideal-wind area near major roads than one far from roadways.
Distance to Major Roads and Land Cover	We see no reason for these terms to interact in any meaningful way.
Distance to Major Roads and Ocean	Roads would not occur over ocean, so there is no reason for these terms to interact.

Table 6.2. Continued.

Pairs of Factors	Justification for including or excluding interaction from models
Annual Average Wind Speed and Land Cover	We see no reason for these terms to interact in any meaningful way.
Annual Average Wind Speed and Ocean	Wind conditions can change around sources of water, so this may be an important term to consider for hawks.
Land Cover and Ocean	Open lands will not co-occur with ocean, so there is no reason for these terms to interact.

Table 6.3. Results from modelling global-range wind turbine locations with various environmental variables. Factors included in models are elevation (E), terrain ruggedness index (T), aspect (A), distance to nearest major water body (ocean, lake, or large river; DW), distance to nearest major road (DR), and annual average wind speed at 100 m above ground (W). Interactions are denoted by * between terms. N refers to number of turbine facilities that were included as a random factor in models (1|Facility), n refers to number of real and random wind turbine location data that were evaluated, k refers to the number of parameters in each model (i.e., number factors plus an intercept), AIC refers to Akaike's Information Criterion, delta AIC refers to the difference between any model's AIC value and the top model (lowest AIC), model weight refers to the relative likelihood of each model being the best model for the data. Model sets were restricted to 20 possible models selected using various a-priori criteria.

Model	N	n	k	AIC	ΔAIC	Weight
(1|Facility) + E + T + A + DR + W + E*A + T*DR + T*W	238	23,800	10	11,480.23	0.00	0.83
(1|Facility) + E + T + A + DW + DR + W + E*A + T*DW + T*DR + T*W	238	23,800	12	11,483.41	3.18	0.17
(1|Facility) + E + T + A + W + E*A + T*W	238	23,800	8	11,511.93	31.70	0.00
(1|Facility) + E + T + A + DW + W + E*A + T*DW + T*W	238	23,800	10	11,514.62	34.40	0.00
(1|Facility) + E + T + DR + W + T*DR + T*W	238	23,800	8	11,520.21	39.98	0.00
(1|Facility) + E + T + DW + DR + W + T*DW + T*DR + T*W	238	23,800	10	11,522.24	42.02	0.00
(1|Facility) + E + T + W + T*W	238	23,800	6	11,552.85	72.63	0.00
(1|Facility) + E + T + DW + W + T*DW + T*W	238	23,800	8	11,554.50	74.28	0.00
(1|Facility) + E + T + A + DR + W	238	23,800	7	11,567.89	87.66	0.00
(1|Facility) + E + T + A + DW + DR + W	238	23,800	8	11,569.29	89.07	0.00
(1|Facility) + E + T + A + W	238	23,800	6	11,569.98	89.76	0.00
(1|Facility) + E + T + A + DW + W	238	23,800	7	11,571.19	90.97	0.00
(1|Facility) + T + A + DW + W + T*DW + T*W	238	23,800	8	11,583.48	103.25	0.00
(1|Facility) + E + T + DR + W	238	23,800	6	11,593.45	113.22	0.00
(1|Facility) + E + T + W	238	23,800	5	11,594.48	114.25	0.00
(1|Facility) + E + T + DW + DR + W	238	23,800	7	11,594.54	114.31	0.00
(1|Facility) + E + T + DW + W	238	23,800	6	11,595.38	115.15	0.00
(1|Facility) + T + A + W + T*W	238	23,800	6	11,612.61	132.38	0.00
(1|Facility) + T + A + DW + W	238	23,800	6	11,630.92	150.69	0.00
(1|Facility) + T + A + W	238	23,800	5	11,660.26	180.04	0.00

Table 6.4. Results from modelling the United States portion of hawk range wind turbine locations with various environmental variables. Factors included in models are elevation (E), terrain ruggedness index (T), aspect (A), distance to nearest major road (DR), annual average wind speed at 100 m above ground (W), and open landscapes (binary variable; either land cover is grassland, shrubland, desert, or agriculture, or it is not; O). Interactions are denoted by * between terms. N refers to number of turbine facilities that were included as a random factor in models (1|Facility), n refers to number of real and random wind turbine location data that were evaluated, k refers to the number of parameters in each model (i.e., number factors plus an intercept), AIC refers to Akaike's Information Criterion, delta AIC refers to the difference between any model's AIC value and the top model (lowest AIC), model weight refers to the relative likelihood of each model being the best model for the data. Model sets were restricted to 20 possible models selected using various a-priori criteria.

Model	N	n	k	AIC	ΔAIC	Weight
(1|Facility) + E + T + DR + W + O + E*DR + T*DR + T*W	216	21,600	10	21,201.16	0.00	0.76
(1|Facility) + E + T + A + DR + W + O + E*A + E*DR + T*DR + T*W	216	21,600	12	21,203.61	2.45	0.22
(1|Facility) + E + DR + W + O + E*DR	216	21,600	7	21,210.26	9.10	0.01
(1|Facility) + E + A + DR + W + O + E*A + E*DR	216	21,600	9	21,212.89	11.73	0.00
(1|Facility) + E + T + DR + W + E*DR + T*DR + T*W	216	21,600	9	21,219.09	17.93	0.00
(1|Facility) + E + T + A + DR + W + E*A + E*DR + T*DR + T*W	216	21,600	11	21,221.41	20.25	0.00
(1|Facility) + E + DR + W + E*DR	216	21,600	6	21,228.58	27.42	0.00
(1|Facility) + E + A + DR + W + E*A + E*DR	216	21,600	8	21,231.07	29.91	0.00
(1|Facility) + E + T + A + DR + W + O	216	21,600	8	21,450.17	249.01	0.00
(1|Facility) + E + T + DR + W + O	216	21,600	7	21,450.63	249.47	0.00
(1|Facility) + E + A + DR + W + O	216	21,600	7	21,457.90	256.74	0.00
(1|Facility) + E + DR + W + O	216	21,600	6	21,458.10	256.94	0.00
(1|Facility) + E + T + A + DR + W	216	21,600	7	21,464.26	263.10	0.00
(1|Facility) + E + T + DR + W	216	21,600	6	21,464.84	263.68	0.00
(1|Facility) + E + A + DR + W	216	21,600	6	21,472.35	271.19	0.00
(1|Facility) + E + DR + W	216	21,600	5	21,472.66	271.50	0.00
(1|Facility) + E + T + W + T*W	216	21,600	6	21,723.12	521.96	0.00
(1|Facility) + E + T + W	216	21,600	5	21,723.96	522.80	0.00
(1|Facility) + T + DR + W + O + T*DR + T*W	216	21,600	8	22,038.33	837.17	0.00
(1|Facility) + T + DR + W + O	216	21,600	6	22,039.51	838.35	0.00

Table 6.5. Results from modelling year-round Swainson's hawk locations with various environmental variables. Factors included in models are terrain ruggedness index (T), aspect (A), distance to nearest major fresh water body (lake or river; DFW), annual average wind speed at 100 m above ground (W), and ocean (binary variable; either land is ocean or it is not; OC). Interactions are denoted by * between terms. N refers to number of birds that were included as a random factor in models (1|Bird), n refers to number of real and random hawk location data that were evaluated, k refers to the number of parameters in each model (i.e., number factors plus an intercept), AIC refers to Akaike's Information Criterion, delta AIC refers to the difference between any model's AIC value and the top model (lowest AIC), and model weight refers to the relative likelihood of each model being the best model for the data. Model sets were restricted to 20 possible models selected using various a-priori criteria.

Model	N	n	k	AIC	ΔAIC	Weight
(1|Bird) + T + A + DFW + W + OC + T*DFW + T*W + DFW*W	21	197,206	10	214,129.4	0.0	1.00
(1|Bird) + T + DFW + W + OC + T*DFW + T*W + DFW*W	21	197,206	9	214,170.4	41.0	0.00
(1|Bird) + T + A + W + OC + T*W	21	197,206	7	215,478.4	1,349.1	0.00
(1|Bird) + T + W + OC + T*W	21	197,206	6	215,516.5	1,387.1	0.00
(1|Bird) + T + A + DFW + W + OC	21	197,206	7	215,765.0	1,635.6	0.00
(1|Bird) + T + DFW + W + OC	21	197,206	6	215,810.1	1,680.7	0.00
(1|Bird) + T + A + W + OC	21	197,206	6	216,137.8	2,008.4	0.00
(1|Bird) + T + W + OC	21	197,206	5	216,176.5	2,047.1	0.00
(1|Bird) + A + DFW + W + OC + DFW*W	21	197,206	7	216,724.2	2,594.8	0.00
(1|Bird) + DFW + W + OC + DFW*W	21	197,206	6	216,775.1	2,645.7	0.00
(1|Bird) + T + A + DFW + W + T*DFW + T*W + DFW*W	21	197,206	9	217,550.0	3,420.6	0.00
(1|Bird) + T + DFW + W + T*DFW + T*W + DFW*W	21	197,206	8	217,835.3	3,705.9	0.00
(1|Bird) + A + DFW + W + OC	21	197,206	6	217,873.4	3,744.0	0.00
(1|Bird) + DFW + W + OC	21	197,206	5	217,928.6	3,799.2	0.00
(1|Bird) + A + W + OC	21	197,206	5	218,185.9	4,056.5	0.00
(1|Bird) + W + OC	21	197,206	4	218,234.7	4,105.3	0.00
(1|Bird) + T + A + DFW + W	21	197,206	6	218,925.7	4,796.3	0.00
(1|Bird) + T + A + W + T*W	21	197,206	6	218,958.2	4,828.8	0.00
(1|Bird) + T + DFW + W	21	197,206	5	219,219.0	5,089.6	0.00
(1|Bird) + T + A + W	21	197,206	5	219,337.6	5,208.2	0.00

Table 6.6. Results from modelling Swainson's hawk breeding-season locations with various environmental variables. Factors included in models are terrain ruggedness index (T), aspect (A), distance to nearest major fresh water body (lake or river; DFW), distance to nearest major road (DR), annual average wind speed at 100 m above ground (W), and open landscapes (binary variable; either land cover is grassland, shrubland, desert, or agriculture, or it is not; O). Interactions are denoted by * between terms. N refers to number of birds that were included as a random factor in models (1|Bird), n refers to number of real and random hawk location data that were evaluated, k refers to the number of parameters in each model (i.e., number factors plus an intercept), AIC refers to Akaike's Information Criterion, delta AIC refers to the difference between any model's AIC value and the top model (lowest AIC), and model weight refers to the relative likelihood of each model being the best model for the data. Model sets were restricted to 20 possible models selected using various a-priori criteria.

Model	N	n	k	AIC	ΔAIC	Weight
(1|Bird) + T + A + DFW + DR + W + O + T*DFW + T*DR + T*W + DFW*DR + DFW*W	34	128,726	13	92,682.27	0.00	1.00
(1|Bird) + T + A + DFW + DR + W + T*DFW + T*DR + T*W + DFW*DR + DFW*W	34	128,726	12	92,737.66	55.39	0.00
(1|Bird) + T + DFW + DR + W + O + T*DFW + T*DR + T*W + DFW*DR + DFW*W	34	128,726	12	92,827.81	145.54	0.00
(1|Bird) + T + DFW + DR + W + T*DFW + T*DR + T*W + DFW*DR + DFW*W	34	128,726	11	92,879.22	196.95	0.00
(1|Bird) + A + DFW + DR + W + O + DFW*DR + DFW*W	34	128,726	9	95,073.77	2,391.50	0.00
(1|Bird) + A + DFW + DR + W + DFW*DR + DFW*W	34	128,726	8	95,117.39	2,435.12	0.00
(1|Bird) + T + A + DR + W + O + T*DR + T*W	34	128,726	9	95,185.28	2,503.01	0.00
(1|Bird) + DFW + DR + W + O + DFW*DR + DFW*W	34	128,726	8	95,199.05	2,516.78	0.00
(1|Bird) + DFW + DR + W + DFW*DR + DFW*W	34	128,726	7	95,238.62	2,556.35	0.00
(1|Bird) + T + DR + W + O + T*DR	34	128,726	7	95,592.09	2,909.82	0.00
(1|Bird) + T + A + DFW + DR + W + O	34	128,726	8	95,821.92	3,139.65	0.00
(1|Bird) + T + A + DFW + DR + W	34	128,726	7	95,852.37	3,170.10	0.00
(1|Bird) + T + DFW + DR + W + O	34	128,726	7	95,978.58	3,296.31	0.00
(1|Bird) + T + DFW + DR + W	34	128,726	6	96,005.95	3,323.68	0.00
(1|Bird) + T + A + DR + W + O	34	128,726	7	96,421.95	3,739.68	0.00
(1|Bird) + T + DR + W + O	34	128,726	6	96,588.73	3,906.46	0.00
(1|Bird) + A + DFW + DR + W + O	34	128,726	7	97,184.54	4,502.27	0.00
(1|Bird) + A + DFW + DR + W	34	128,726	6	97,208.94	4,526.67	0.00
(1|Bird) + DFW + DR + W + O	34	128,726	6	97,331.10	4,648.83	0.00
(1|Bird) + DFW + DR + W	34	128,726	5	97,352.07	4,669.80	0.00

Table 6.7. Results from modelling Swainson's hawk nonbreeding-season locations with various environmental variables. Factors included in models are elevation (E), terrain ruggedness index (T), aspect (A), distance to nearest major fresh water body (lake or river; DFW), distance to nearest major road (DR), annual average wind speed at 100 m above ground (W), and open landscapes (binary variable; either land cover is grassland, shrubland, desert, or agriculture, or it is not; O). Interactions are denoted by * between terms. N refers to number of birds that were included as a random factor in models (1|Bird), n refers to number of real and random hawk location data that were evaluated, k refers to the number of parameters in each model (i.e., number factors plus an intercept), AIC refers to Akaike's Information Criterion, delta AIC refers to the difference between any model's AIC value and the top model (lowest AIC), and model weight refers to the relative likelihood of each model being the best model for the data. Model sets were restricted to 20 possible models selected using various a-priori criteria.

Model	N	n	k	AIC	ΔAIC	Weight
(1|Bird) + E + T + A + DFW + DR + W + O + E*W + T*DFW + T*DR + T*W + DFW*DR + DFW*W	24	39,320	15	51,081.14	0.00	0.92
(1|Bird) + E + T + DFW + DR + W + O + E*W + T*DFW + T*DR + T*W + DFW*DR + DFW*W	24	39,320	14	51,086.00	4.88	0.08
(1|Bird) + E + T + A + DFW + W + O + E*W + T*DFW + T*W + DFW*W	24	39,320	12	51,202.58	121.44	0.00
(1|Bird) + E + T + DFW + W + O + E*W + T*DFW + T*W + DFW*W	24	39,320	11	51,209.84	128.70	0.00
(1|Bird) + E + T + A + DFW + W + O	24	39,320	8	51,860.80	779.66	0.00
(1|Bird) + E + T + A + DFW + DR + W + O	24	39,320	9	51,862.53	781.39	0.00
(1|Bird) + E + T + DFW + W + O	24	39,320	7	51,876.58	795.44	0.00
(1|Bird) + E + T + DFW + DR + W + O	24	39,320	8	51,878.45	797.31	0.00
(1|Bird) + E + A + DFW + DR + W + O + E*W + DFW*DR + DFW*W	24	39,320	11	52,063.76	982.62	0.00
(1|Bird) + E + DFW + DR + W + O + E*W + DFW*DR + DFW*W	24	39,320	10	52,088.56	1,007.42	0.00
(1|Bird) + E + T + A + DR + W + O + E*W + T*DR + T*W	24	39,320	11	52,249.07	1,167.93	0.00
(1|Bird) + E + T + DR + W + O + E*W + T*DR + T*W	24	39,320	10	52,255.48	1,174.34	0.00
(1|Bird) + E + A + DFW + DR + W + O	24	39,320	8	52,295.34	1,214.20	0.00
(1|Bird) + E + DFW + DR + W + O	24	39,320	7	52,323.07	1,241.93	0.00
(1|Bird) + E + T + A + W + O + E*W + T*W	24	39,320	9	52,324.69	1,243.55	0.00
(1|Bird) + E + T + W + O + E*W + T*W	24	39,320	8	52,332.59	1,251.45	0.00
(1|Bird) + E + T + A + DR + W + O	24	39,320	8	52,580.14	1,499.00	0.00
(1|Bird) + E + T + A + W + O	24	39,320	7	52,582.74	1,501.60	0.00
(1|Bird) + E + T + DR + W + O	24	39,320	7	52,594.57	1,513.43	0.00
(1|Bird) + E + T + W + O	24	39,320	6	52,596.51	1,515.37	0.00

Table 6.8. Results from modelling Swainson’s hawk migration locations with various environmental variables. Factors included in models are elevation (E), terrain ruggedness index (T), aspect (A), distance to nearest major fresh water body (lake or river; DFW), distance to nearest major road (DR), annual average wind speed at 100 m above ground (W), and ocean (binary variable; either land is ocean or it is not; OC). Interactions are denoted by * between terms. N refers to number of birds that were included as a random factor in models (1|Bird), n refers to number of real and random hawk location data that were evaluated, k refers to the number of parameters in each model (i.e., number factors plus an intercept), AIC refers to Akaike’s Information Criterion, delta AIC refers to the difference between any model’s AIC value and the top model (lowest AIC), and model weight refers to the relative likelihood of each model being the best model for the data. Model sets were restricted to 20 possible models selected using various a-priori criteria.

Model	N	n	k	AIC	ΔAIC	Weight
(1|Bird) + E + T + A + DFW + DR + W + OC + E*W + T*DFW + T*DR + T*W + DFW*DR + DFW*W	21	52,134	15	61,073.35	0.00	0.91
(1|Bird) + E + T + DFW + DR + W + OC + E*W + T*DFW + T*DR + T*W + DFW*DR + DFW*W	21	52,134	14	61,078.04	4.69	0.09
(1|Bird) + E + T + A + DFW + DR + OC + T*DFW + T*DR + DFW*DR	21	52,134	11	61,095.01	21.66	0.00
(1|Bird) + E + T + DFW + DR + OC + T*DFW + T*DR + DFW*DR	21	52,134	10	61,099.53	26.18	0.00
(1|Bird) + E + T + A + DFW + DR + W + OC	21	52,134	9	61,177.57	104.22	0.00
(1|Bird) + E + T + DFW + DR + W + OC	21	52,134	8	61,181.94	108.59	0.00
(1|Bird) + E + T + A + DFW + DR + OC	21	52,134	8	61,191.38	118.03	0.00
(1|Bird) + E + T + DFW + DR + OC	21	52,134	7	61,195.73	122.38	0.00
(1|Bird) + E + T + A + DFW + W + OC + E*W + T*DFW + T*W + DFW*W	21	52,134	12	61,374.17	300.82	0.00
(1|Bird) + E + T + A + DR + W + OC + E*W + T*DR + T*W	21	52,134	11	61,375.95	302.60	0.00
(1|Bird) + E + T + DFW + W + OC + E*W + T*DFW + T*W + DFW*W	21	52,134	11	61,379.29	305.94	0.00
(1|Bird) + E + T + DR + W + OC + E*W + T*DR + T*W	21	52,134	10	61,382.31	308.96	0.00
(1|Bird) + E + T + A + DR + W + OC	21	52,134	8	61,385.45	312.10	0.00
(1|Bird) + E + T + DR + W + OC	21	52,134	7	61,391.92	318.57	0.00
(1|Bird) + E + T + A + DR + OC + T*DR	21	52,134	8	61,399.76	326.41	0.00
(1|Bird) + E + T + DR + OC + T*DR	21	52,134	7	61,406.24	332.89	0.00
(1|Bird) + E + T + A + DFW + W + OC	21	52,134	8	61,408.34	334.99	0.00
(1|Bird) + E + T + A + DR + OC	21	52,134	7	61,410.92	337.57	0.00
(1|Bird) + E + T + DFW + W + OC	21	52,134	7	61,413.10	339.75	0.00
(1|Bird) + E + T + DR + OC	21	52,134	6	61,417.42	344.07	0.00

Table 6.9. Risk categories (i.e., categories that landscapes were classified as in terms of risk of Swainson's hawks encountering wind turbine hazards) and corresponding categories from hawk and wind energy predictive models.

Level of risk to Swainson's hawks	Relative likelihood of finding a Swainson's hawk in a region	Likelihood of finding a wind energy facility constructed in a region
Very Low	Poor to Fair	Low
Low	Good to Excellent	Low
Moderate	Poor to Fair	Moderate
High	Poor to Fair	High
Very High	Good to Excellent	Moderate
Extreme	Good to Excellent	High

Table 6.10. Number of Swainson’s hawk locations between 0 and 200 m above ground that fell within buffers indicating a high risk of colliding with wind turbine blades (≤ 200 m from known or suspected turbine location), moderate risk (200 – 600 m), and low risk (600 – 1,200 m); we additionally described locations within facilities (i.e., 2-km minimum convex polygons surrounding turbine groups), but not within risk buffers. Data obtained from 41 Swainson’s hawks breeding (caught as adult near breeding territories) or hatched (caught as juvenile) in northern Texas that were trapped from 2012 – 2018 and tracked with GPS and Doppler transmitters until 2020. Breeding season took place in the central-southern United States and nonbreeding season was in central Argentina and eastern Uruguay. ‘Fall’ refers to outbound or southward migration, and ‘spring’ refers to return or northward migration.

Season	High Risk	Moderate Risk	Low Risk	Within Facilities	No Known Risk	Total
Breeding	454	2,676	7,771	6,483	47,904	65,288
Nonbreeding	0	1	1	0	20,901	20,903
Fall migration	13	58	129	69	15,489	15,758
Spring migration	5	16	32	44	11,331	11,428
Overall	472	2,751	7,933	6,596	95,625	113,377

Table 6.11. Final models used in logistic equations to create maps. Factors included are elevation (E), terrain ruggedness index (T), aspect (A), distance to nearest major water body (ocean, lake, or large river; DW), distance to nearest major fresh water body (lake or river; DFW), distance to nearest major road (DR), annual average wind speed at 100 m above ground (W), open landscapes (binary variable; either land cover is grassland, shrubland, desert, or agriculture, or it is not; O), and ocean (binary variable; either land is ocean or it is not; OC). Interactions are denoted by * between terms.

Type of Data	Final Model Used to Create Predictive Maps
Year-round hawk data	-3.44 + 34.18(T) + 0.12(A) – 6.80(DFW) + 10.52(W) – 4.26(OC) + 27.26(T*DFW) – 90.65(T*W) + 17.80(DFW*W)
Breeding-season data	-37.96 + 138.26(T) + 0.36(A) + 45.05(DFW) + 4.06(DR) + 92.84(W) – 0.20(O) + 136.57(T*DFW) – 2,664.12(T*DR) – 223.59(T*W) – 49.60(DFW*DR) – 112.45(DFW*W)
Nonbreeding-season data	2.93 – 2.04(E) – 128.77(T) + 0.10 (A) – 13.72(DFW) – 5.24(DR) – 9.73(W) + 0.48(O) – 30.27(E*W) – 280.54(T*DFW) + 891.34(T*DR) + 519.85(T*W) – 34.87(DFW*DR) + 45.77(DFW*W)
Migration data	0.27 – 5.20(E) + 25.48(T) – 0.09(A) – 1.77(DFW) – 2.35(DR) – 0.15(W) – 2.57(OC) + 2.14(E*W) – 24.27(T*DFW) – 20.02(T*DR) – 0.89(T*W) + 5.95(DFW*DR) + 2.72(DFW*W)
Global-range turbine data	-26.64 + 6.67(E) + 85.22(T) + 0.94(A) – 3.11(DR) + 68.74(W) – 4.73(E*A) + 438.49(T*DR) – 332.65(T*W)
USA-range turbine data	-20.72 – 2.54(E) + 40.84(T) + 42.27(DR) + 51.78(W) + 0.24(O) – 181.58(E*DR) – 206.23(T*DR) – 111.31(T*W)

Figures

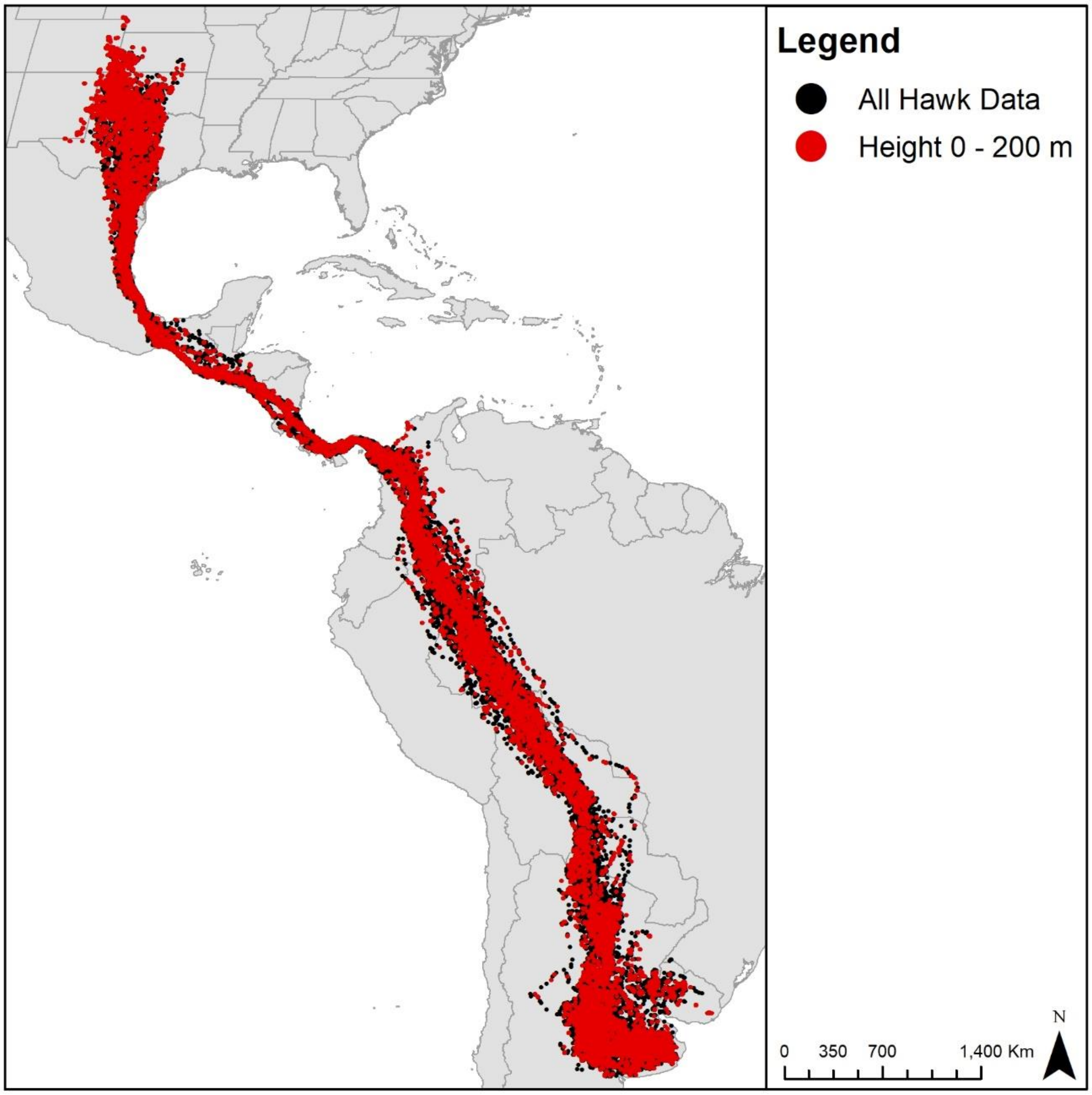

Figure 6.1. Swainson’s hawk transmitter data considered in wind-energy-risk analyses. ‘Height’ refers to height above ground, estimated from transmitters and elevation maps. Adult and juvenile hawks were trapped on breeding territories in northern Texas from 2012 – 2018 and were tracked from 2012 – 2020.

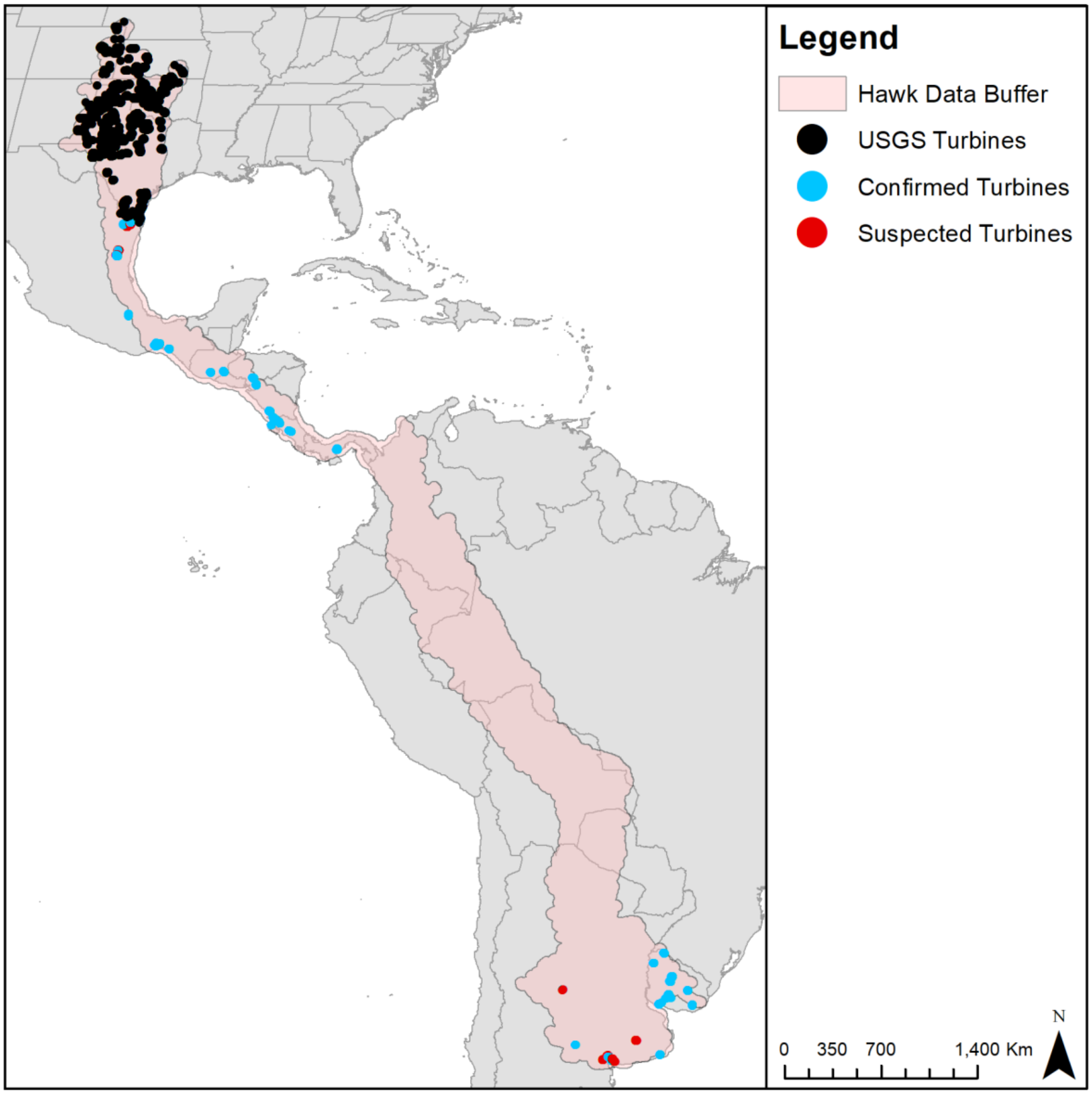

Figure 6.2. Wind turbine locations across the global range for Swainson’s hawks. Turbine locations were obtained from the United States Geological Survey (USGS) and by visual surveys of Sentinel-2 satellite imagery; we confirmed turbine locations and found additional turbines using high-resolution imagery where possible and marked locations as ‘suspected turbines’ when we could not locate recent high-resolution imagery with which to cross-reference. The polygon represents a 50-km buffer around Swainson’s hawk transmitter data collected from 2012 – 2020.
Adapted from: USGS Wind Turbine Database (https://eerscmap.usgs.gov/uswtdb), Sentinel-2 satellite imagery (https://glovis.usgs.gov), ArcMap 10.7 World Imagery, Google Earth (https://www.google.com/earth/), and Google Maps (https://www.google.com/maps).

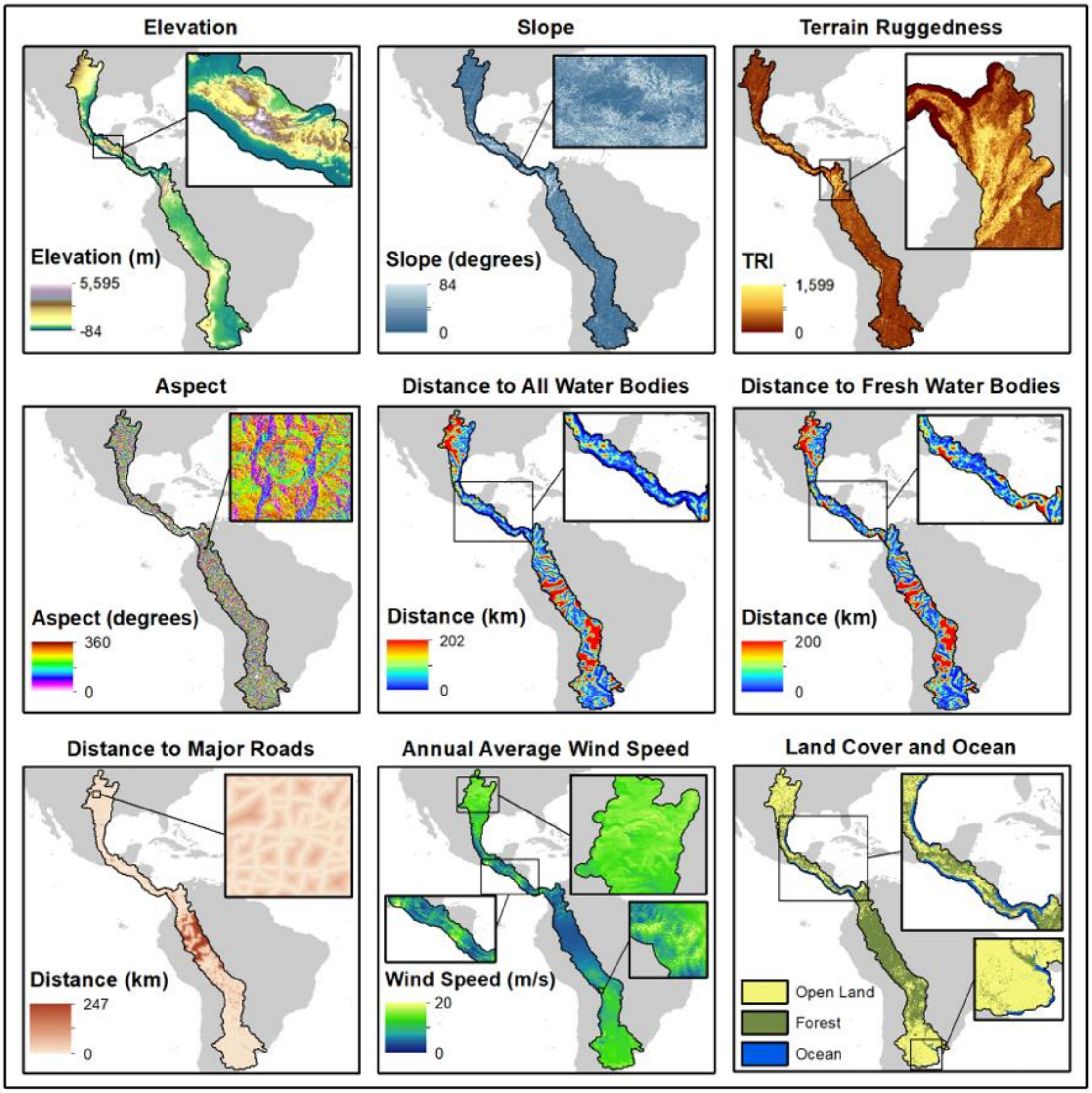

Figure 6.3. Raster datasets we used in modelling likelihood of finding Swainson's hawks or wind energy facilities throughout the global range of Swainson's hawks tracked with satellite transmitters. Inset maps show areas of interesting detail in each dataset. TRI refers to the Terrain Ruggedness Index. 'Water bodies' only refers to large lakes, rivers, and oceans.
Adapted from: Riley et al. 1999, Global Wind Atlas (https://globalwindatlas.info/), National Aeronautics and Space Administration (https://search.earthdata.nasa.gov), NASA Socioeconomic Data and Applications Center (https://sedac.ciesin.columbia.edu/data/set/groads-global-roads-open-access-v1), The European Space Agency (http://due.esrin.esa.int/page_globcover.php), and more references provided in Table 1.

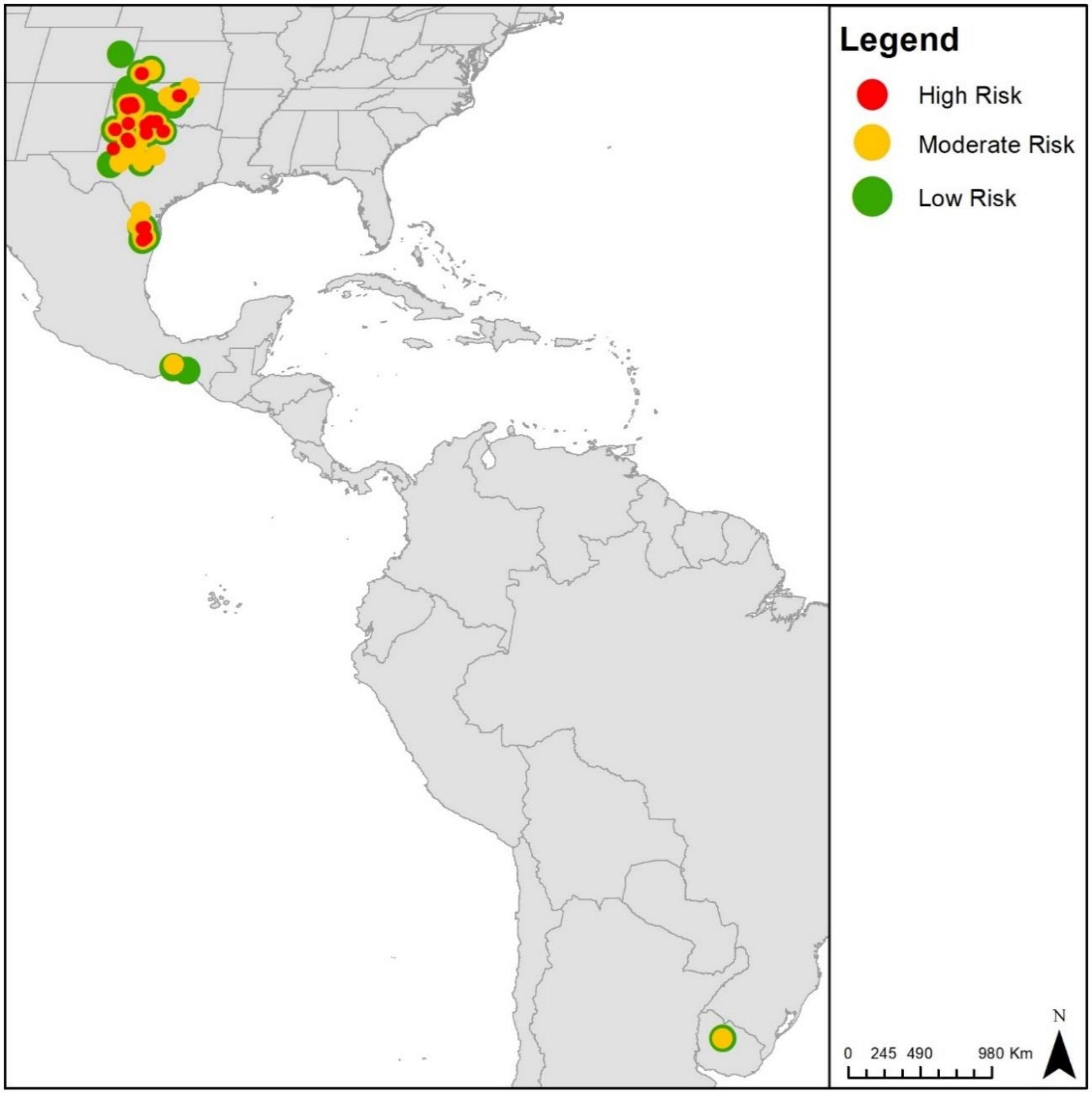

Figure 6.4. Swainson's hawk transmitter data that overlapped buffers indicating high (0 – 200 m), moderate (200 – 600 m), and low (600 – 1,200 m) risk of encountering wind turbine blades, a known hazard for raptors. Data obtained from 41 Swainson's hawks breeding (caught as adult) or hatched (caught as juvenile) in northern Texas that were trapped from 2012 – 2018 and tracked with GPS and Doppler transmitters until 2020.

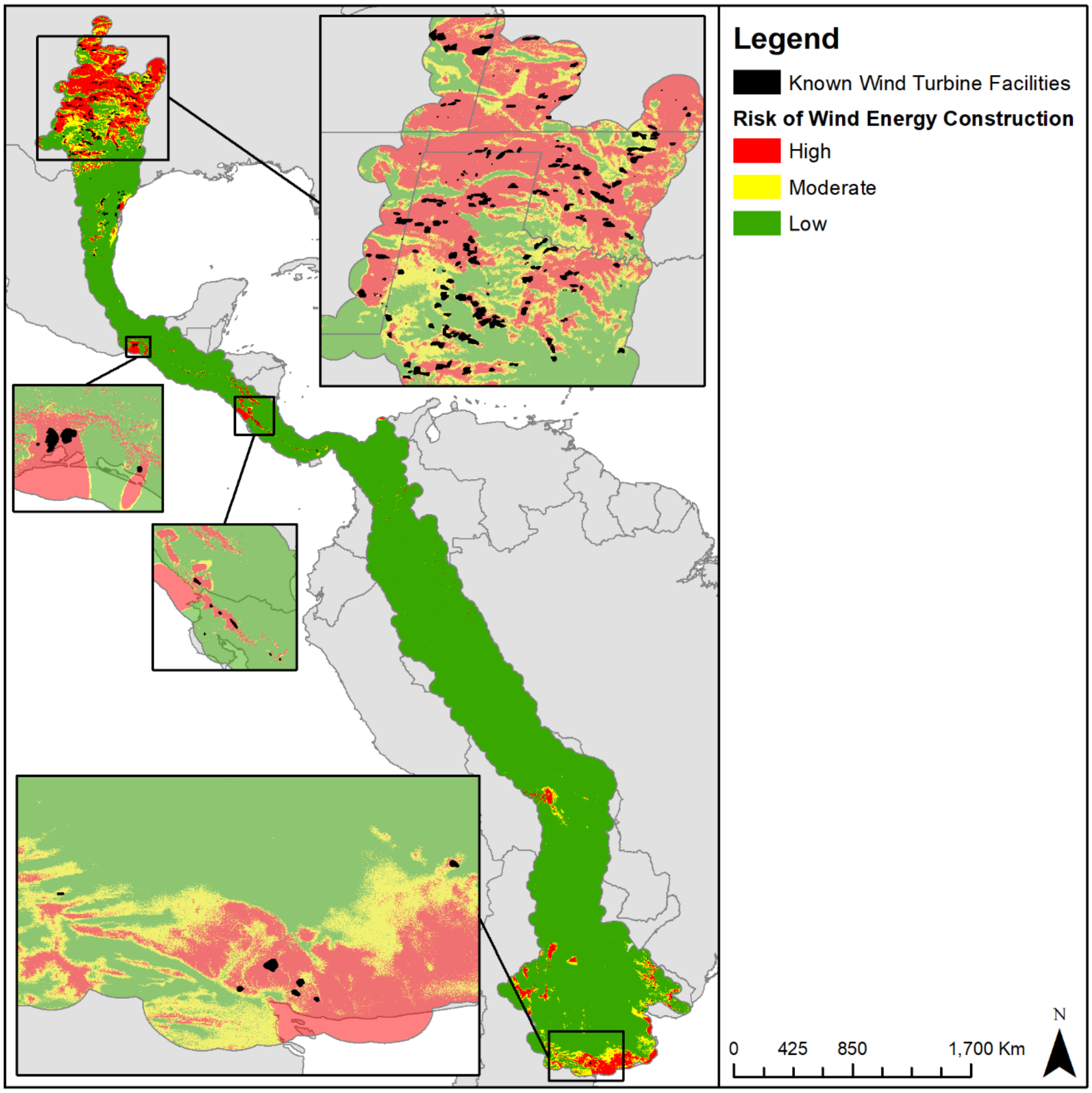

Figure 6.5. Risk of wind energy being constructed across the global range for Swainson's hawks tracked with satellite transmitters. Inset maps highlight several areas of high risk to show details of risk areas and locations of known wind energy facilities.
Adapted from: USGS Wind Turbine Database (https://eerscmap.usgs.gov/uswtdb), Sentinel-2 satellite imagery (https://glovis.usgs.gov), ArcMap 10.7 World Imagery, Google Earth (https://www.google.com/earth/), and Google Maps (https://www.google.com/maps).

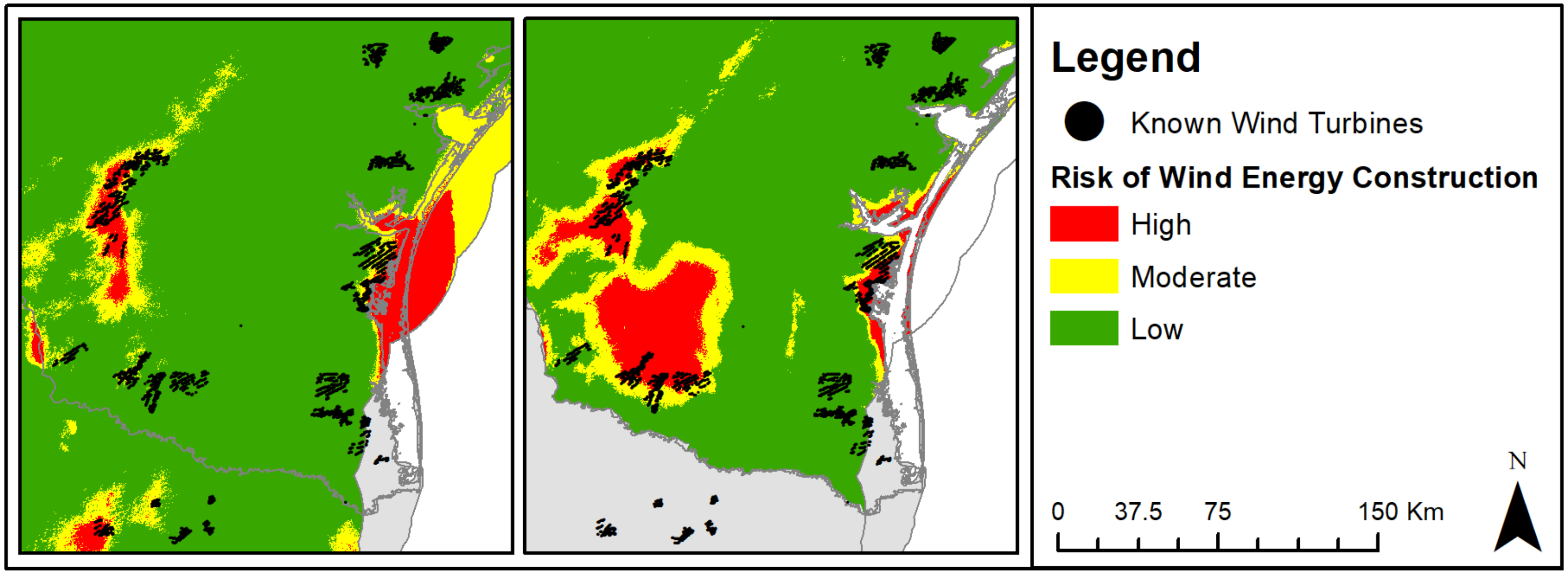

Figure 6.6. Both the global-range wind turbine model (left) and the United States turbine model (right) misidentified many wind turbine facilities in South Texas as being located in regions of low suitability for wind energy construction. *Adapted from*: USGS Wind Turbine Database (https://eerscmap.usgs.gov/uswtdb), Sentinel-2 satellite imagery (https://glovis.usgs.gov), ArcMap 10.7 World Imagery, Google Earth (https://www.google.com/earth/), and Google Maps (https://www.google.com/maps).

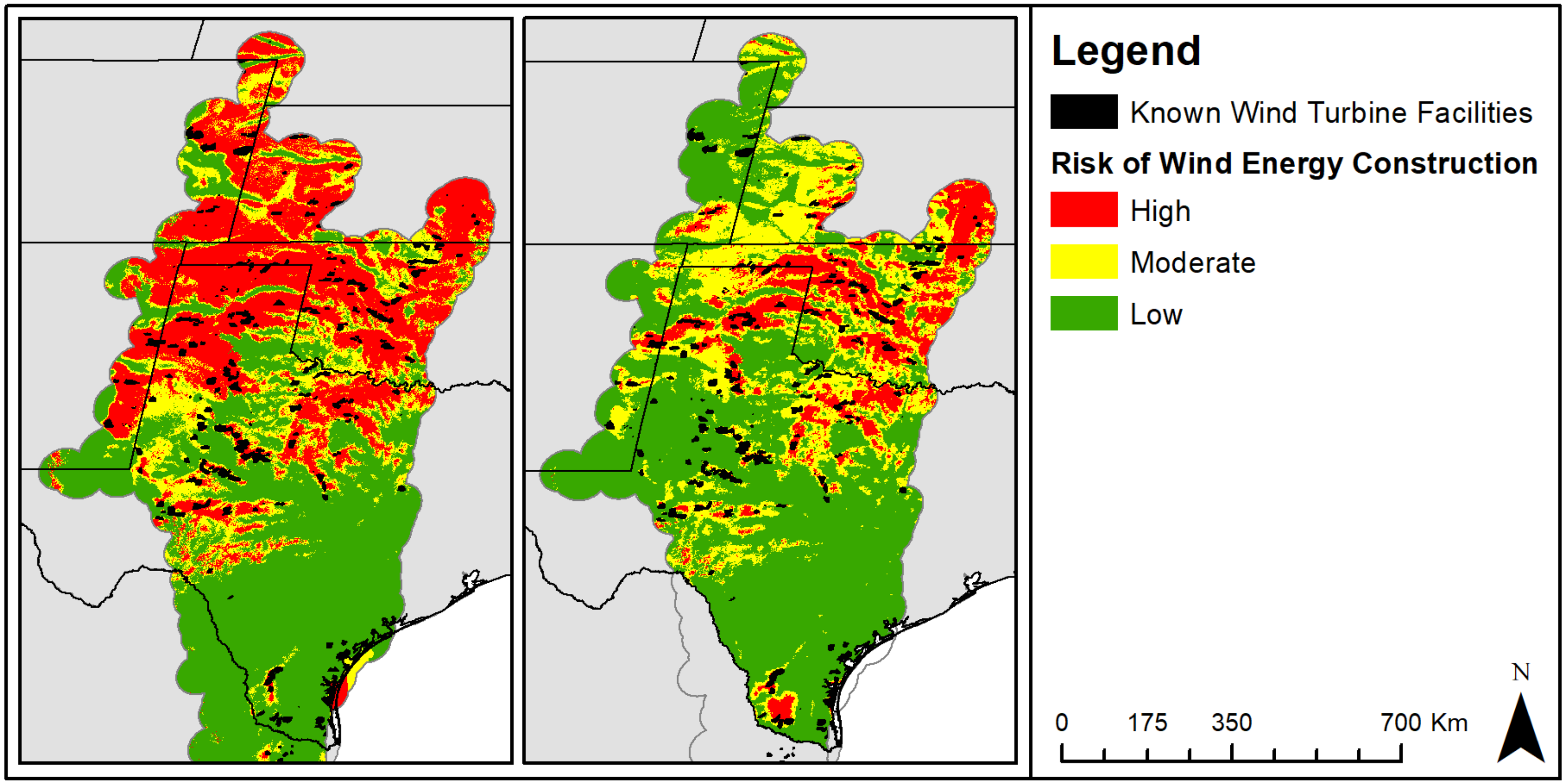

Figure 6.7. Comparing results of the global wind energy model (left) to the model based only on United States wind data (right).

Adapted from: USGS Wind Turbine Database (https://eerscmap.usgs.gov/uswtdb), Sentinel-2 satellite imagery (https://glovis.usgs.gov), ArcMap 10.7 World Imagery, Google Earth (https://www.google.com/earth/), and Google Maps (https://www.google.com/maps).

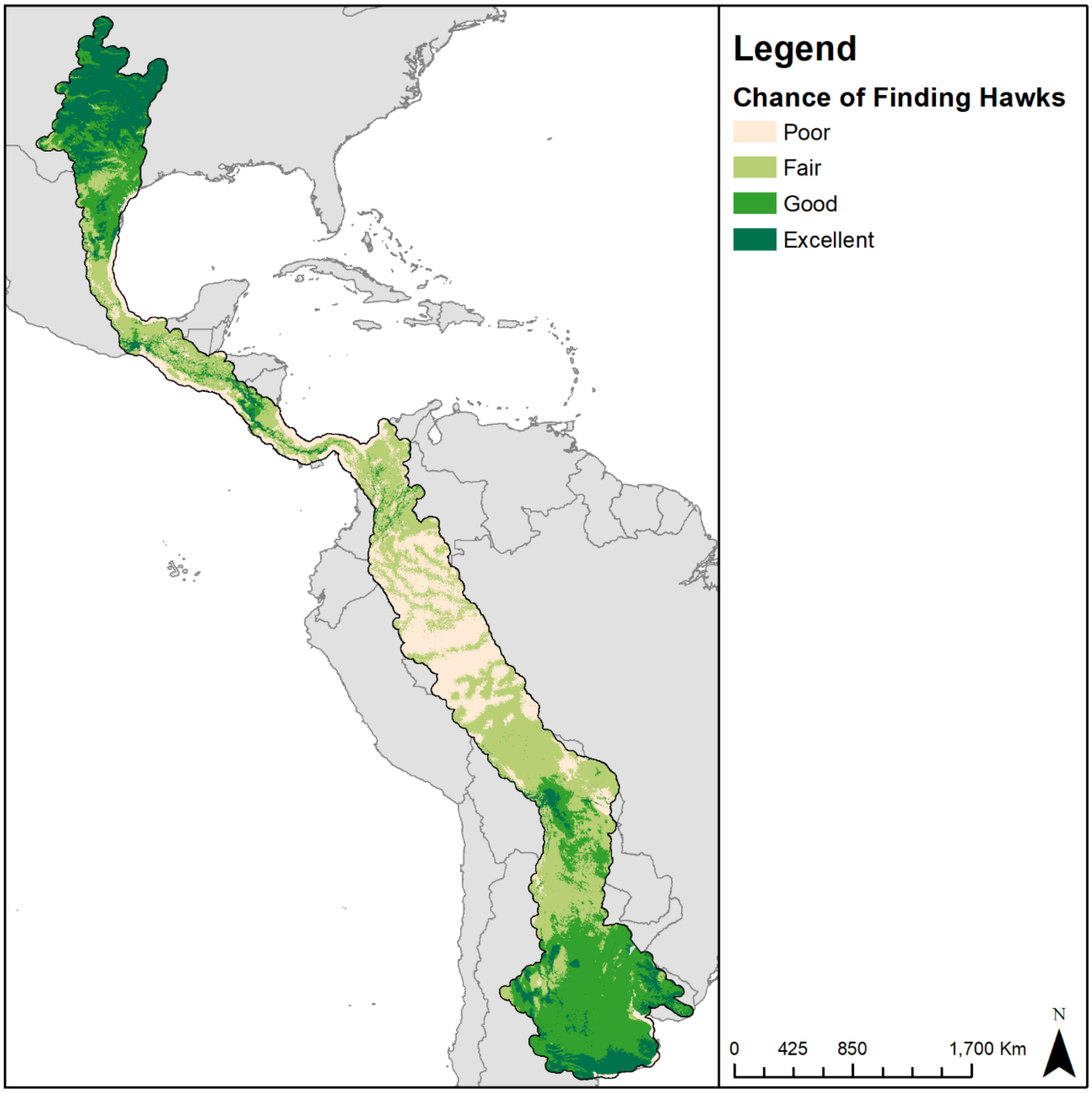

Figure 6.8. Results of a model meant to predict the likelihood of finding Swainson's hawks across their global range (based on a Northern Texas population of hawks followed over nine years using satellite transmitters).

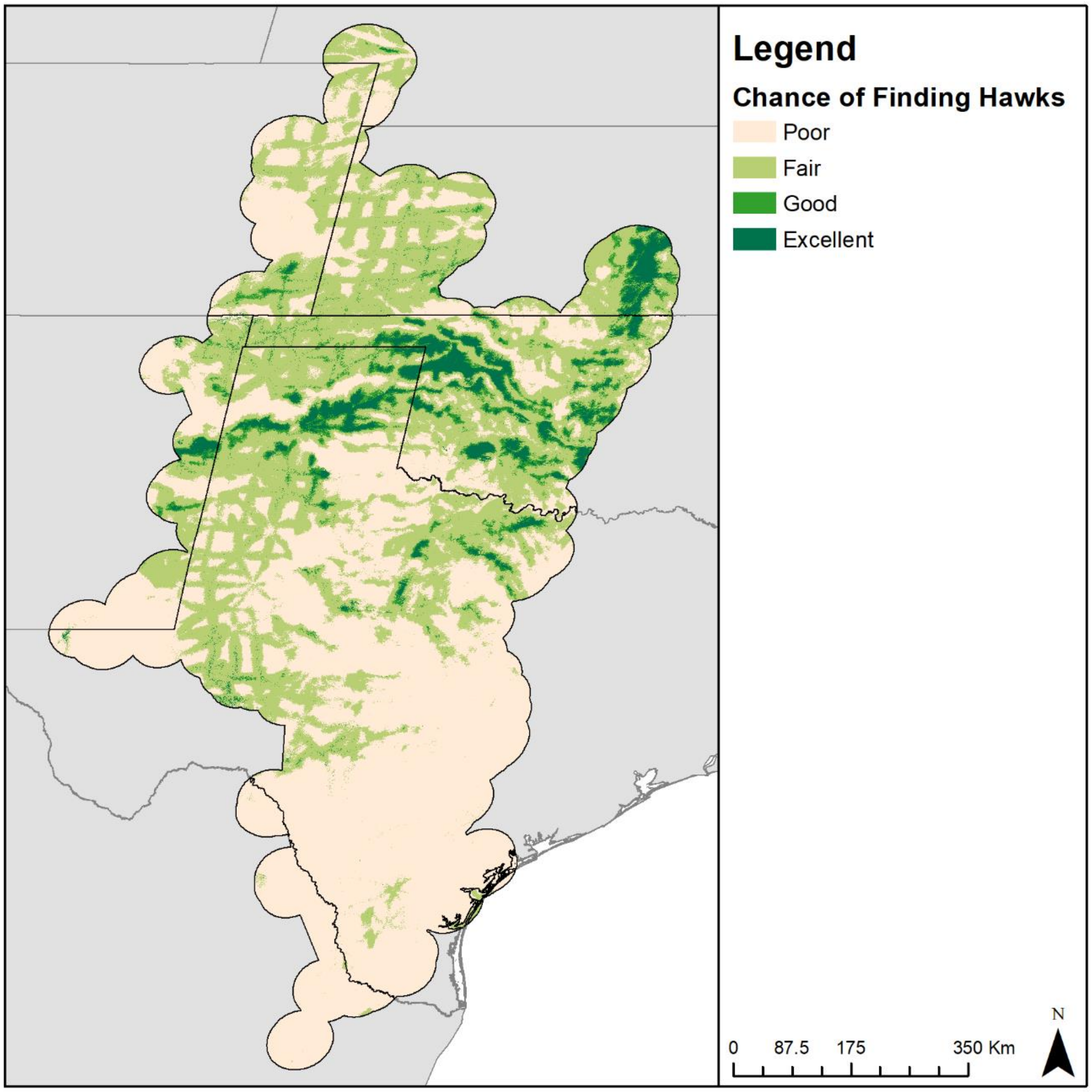

Figure 6.9. Results of a model meant to predict the likelihood of finding Swainson's hawks across the southeastern portion of their breeding range (based on a Northern Texas population of hawks followed over nine years using satellite transmitters). We included state borders in the United States for reference.

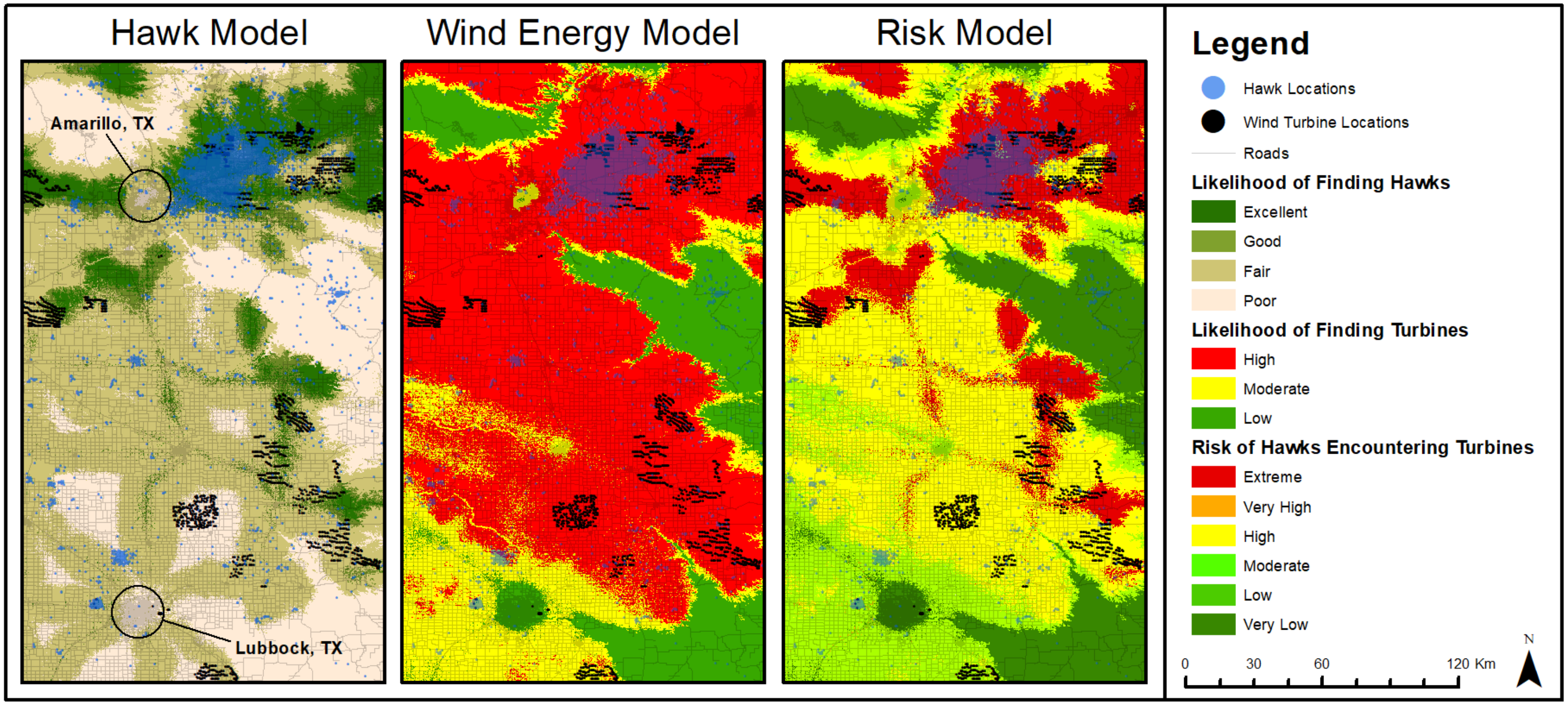

Figure 6.10. Three models (predicting presence of Swainson’s hawks, presence of wind energy hazards, and risk of hawks encountering wind energy) focused on the northern Texas study area where we captured adult and juvenile Swainson’s hawks for a satellite transmitter study (2012 – 2020). Maps highlight all known hawk locations and wind turbines. Roads and city names are provided for reference.
Adapted from: USGS Wind Turbine Database (https://eerscmap.usgs.gov/uswtdb).

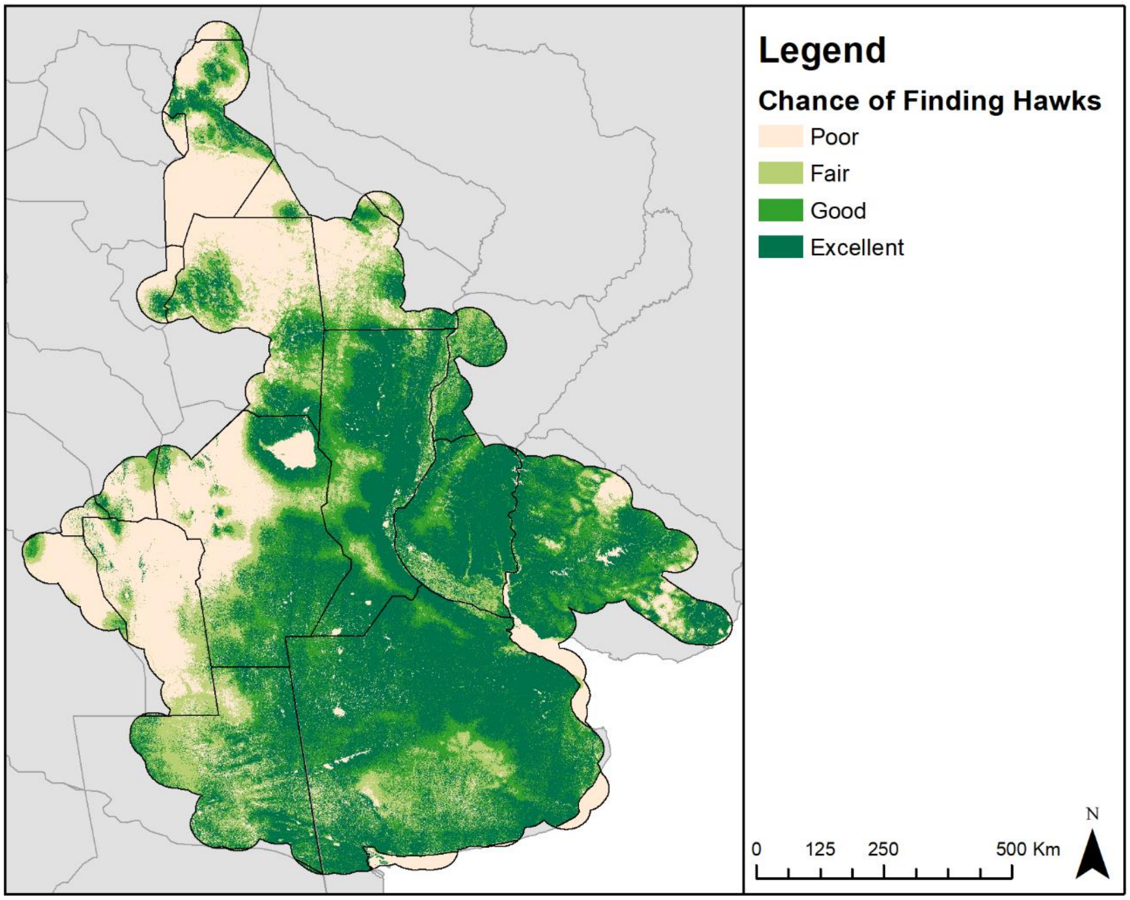

Figure 6.11. Results of a model meant to predict the likelihood of finding Swainson's hawks across their nonbreeding range (based on a Northern Texas population of hawks followed over nine years using satellite transmitters). We included provincial borders in Argentina for reference.

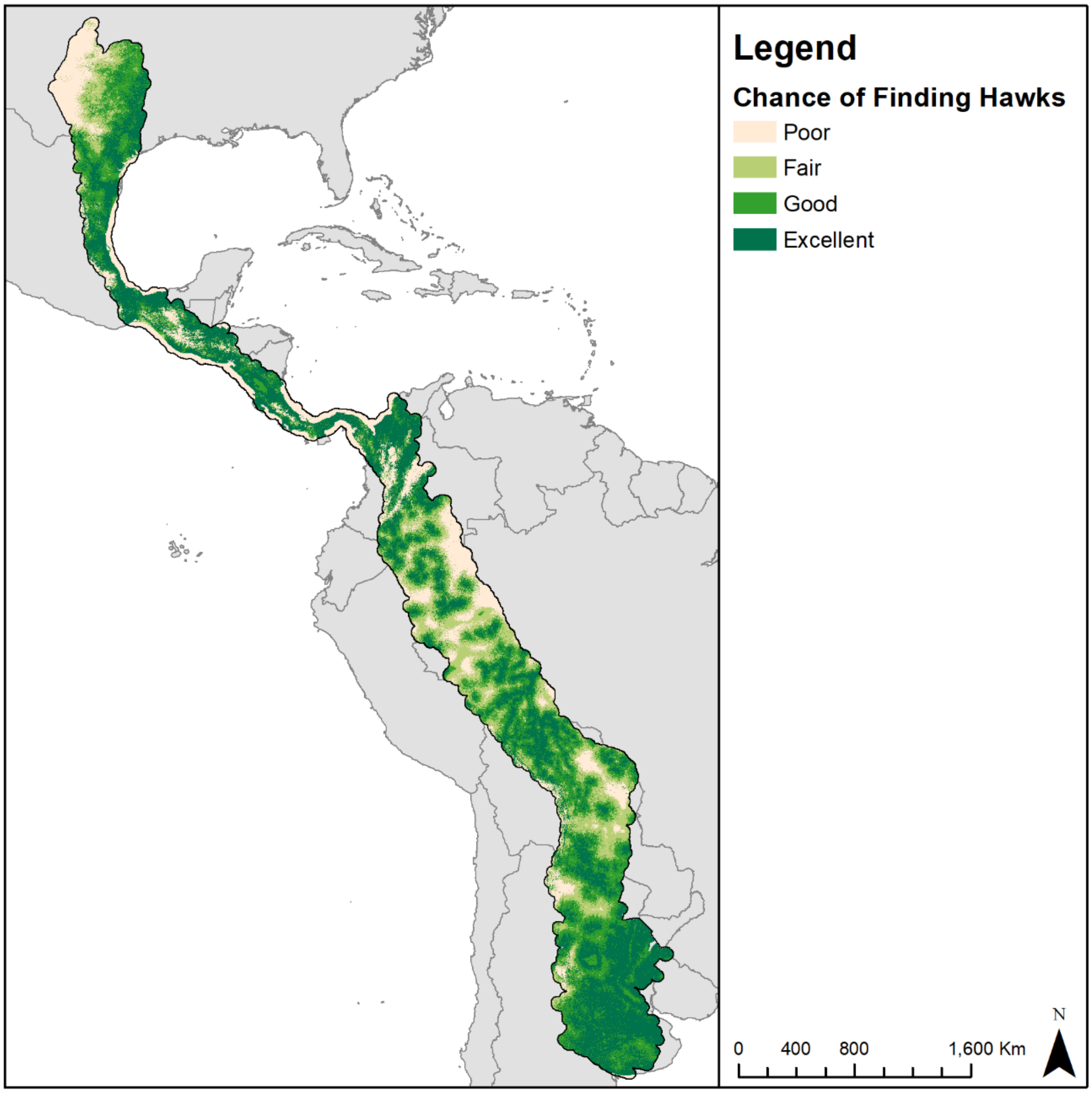

Figure 6.12. Results of a model meant to predict the likelihood of finding Swainson's hawks across their migration range (based on a Northern Texas population of hawks followed over nine years using satellite transmitters).

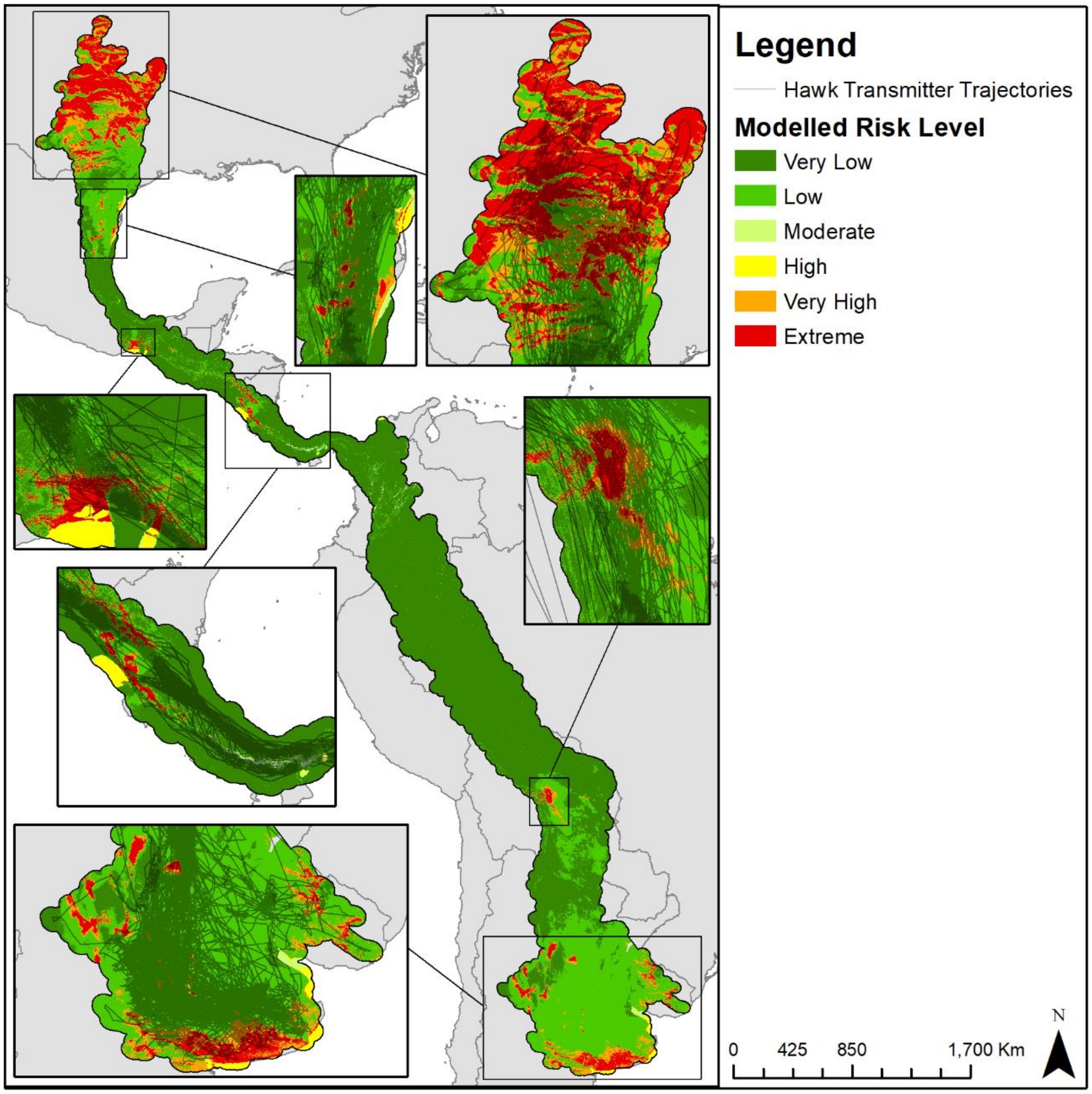

Figure 6.13. Risk of Swainson’s hawks encountering wind turbine hazards throughout their global range (based on a Northern Texas population of hawks followed over nine years using satellite transmitters). Inset maps highlight areas of high risk for hawks, overlaid with transmitter trajectories (lines connecting locational data) to show hawk movement through regions.

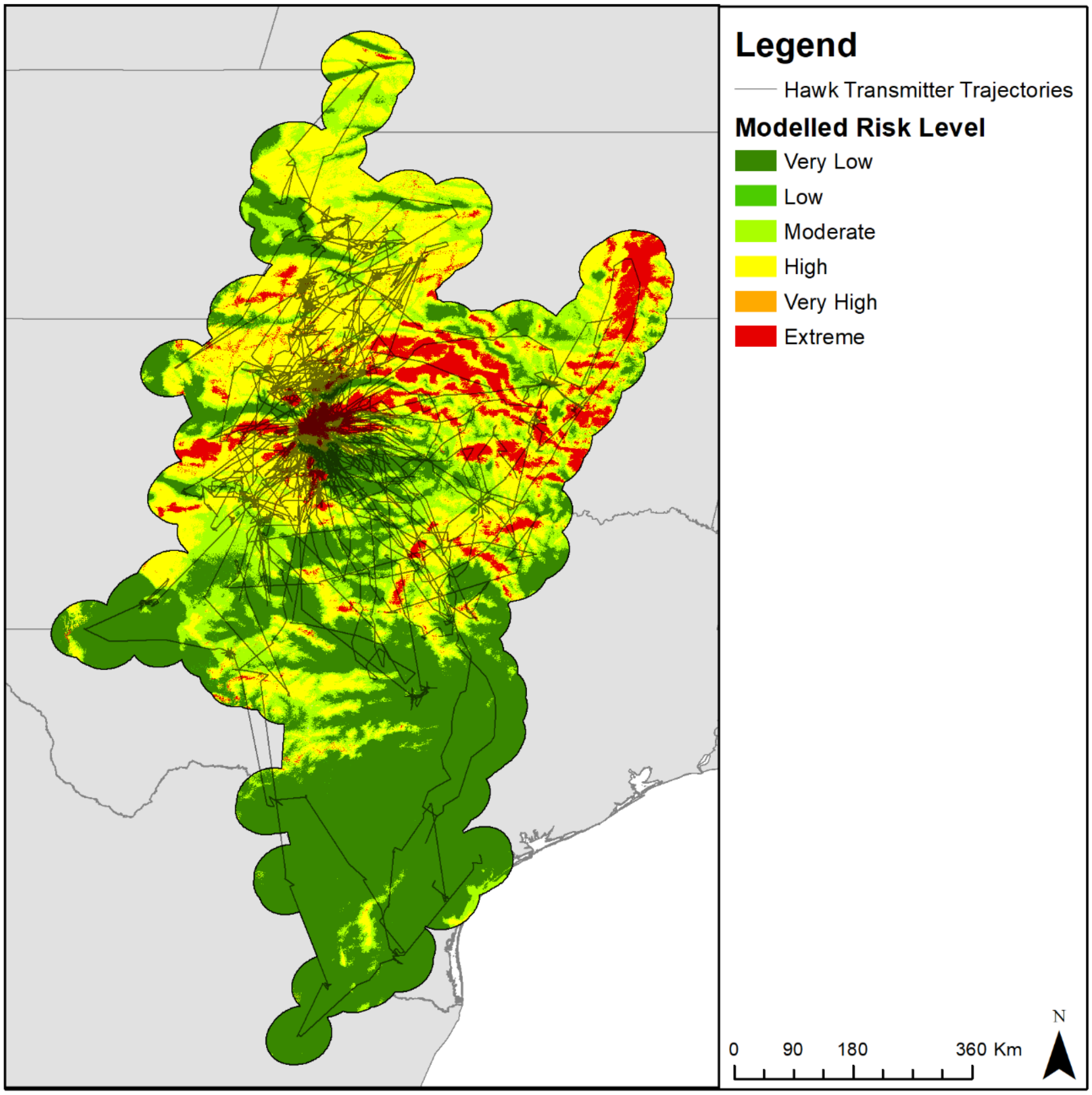

Figure 6.14. Risk of Swainson’s hawks encountering wind turbine hazards throughout their breeding range (based on a Northern Texas population of hawks followed over nine years using satellite transmitters), overlaid with transmitter trajectories (lines connecting locational data) to show hawk movement through regions.

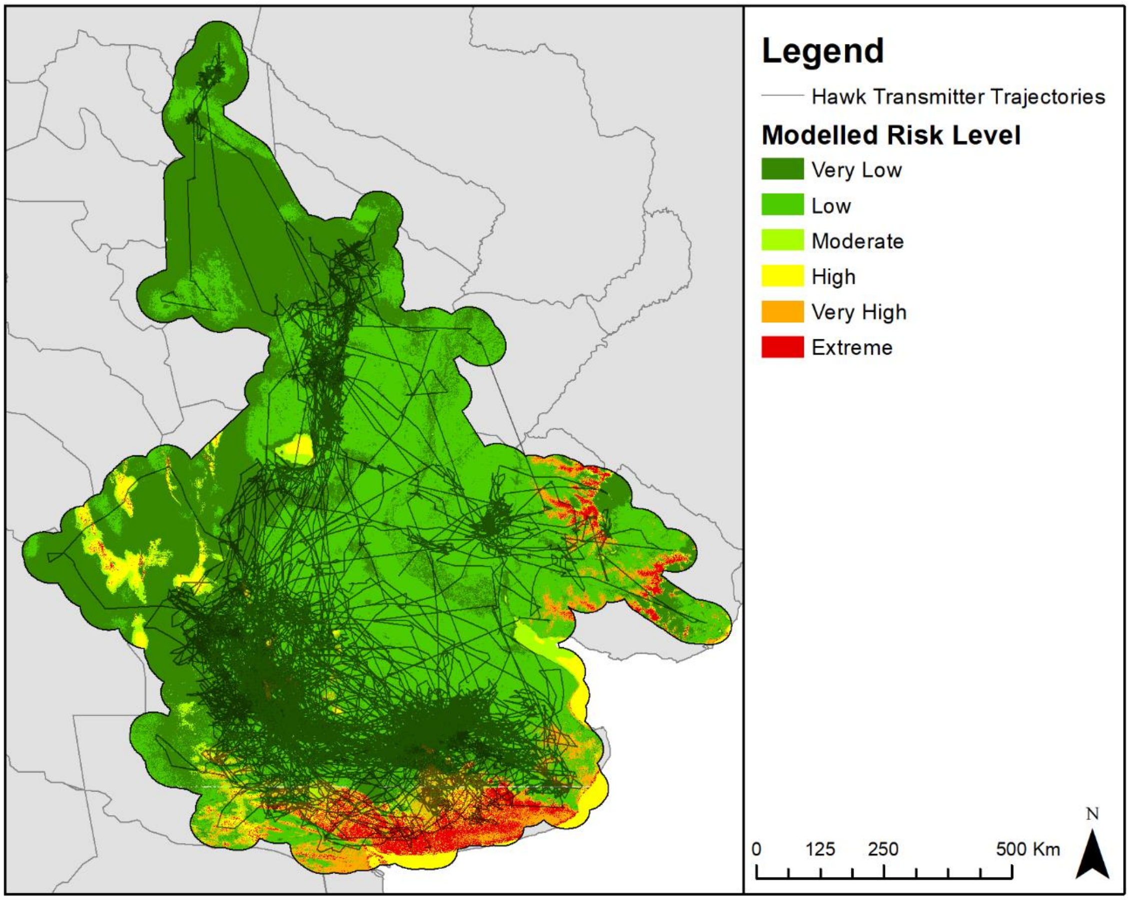

Figure 6.15. Risk of Swainson's hawks encountering wind turbine hazards throughout their nonbreeding range (based on a Northern Texas population of hawks followed over nine years using satellite transmitters), overlaid with transmitter trajectories (lines connecting locational data) to show hawk movement through regions.

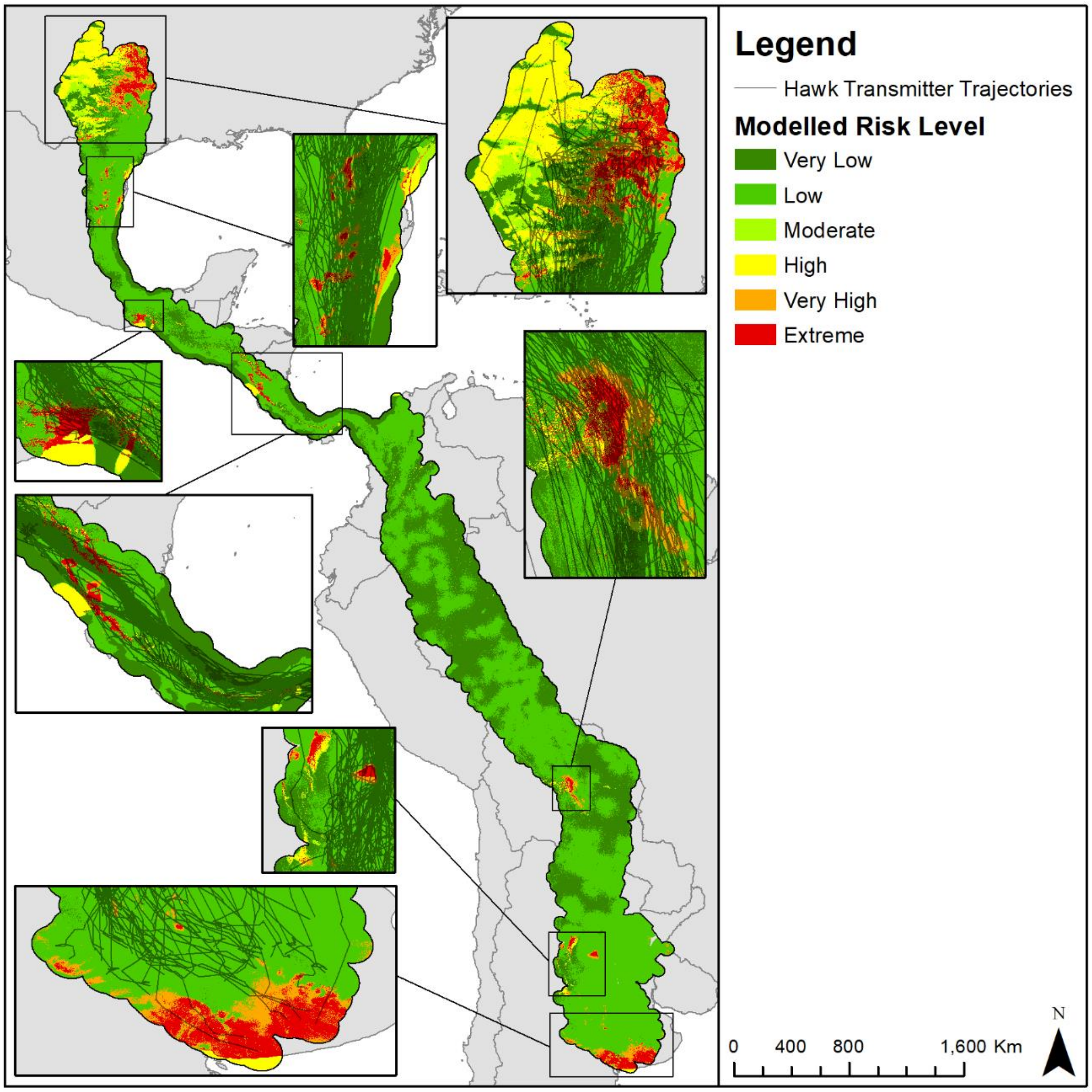

Figure 6.16. Risk of Swainson’s hawks encountering wind turbine hazards throughout their migration range (based on a Northern Texas population of hawks followed over nine years using satellite transmitters). Inset maps highlight areas of high risk for hawks, overlaid with transmitter trajectories (lines connecting locational data) to show hawk movement through regions.

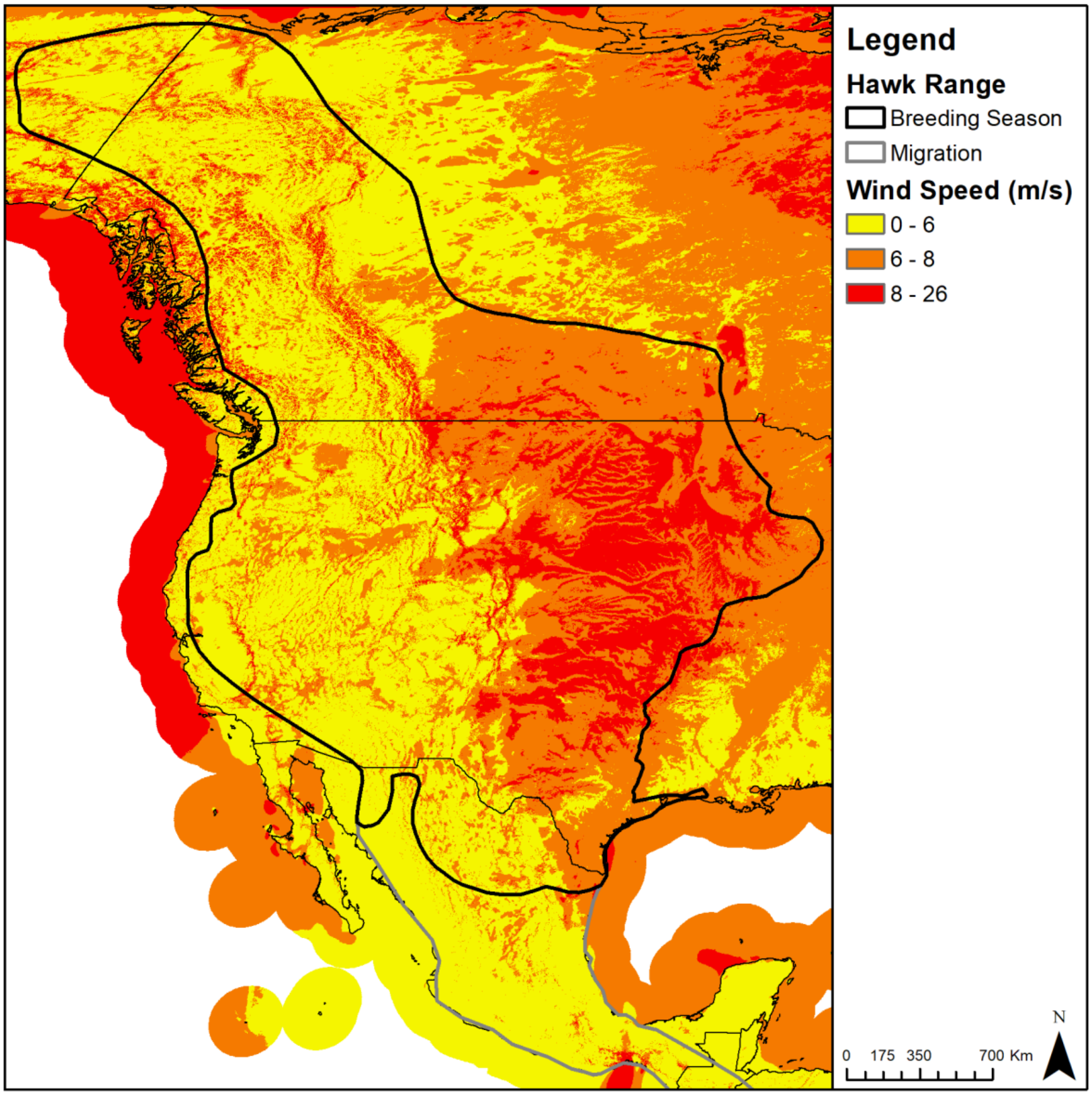

Figure 6.17. Estimated Swainson's hawks breeding and migration ranges over a map of annual average wind speeds at 100 m above ground in North America. Current wind turbine technology is unlikely to be placed in regions with average wind speed < 6 m/s. *Adapted from*: Bechard et al. (2010), eBird (https://ebird.org/science/status-and-trends/swahaw/range-map), Global Wind Atlas (https://globalwindatlas.info/).

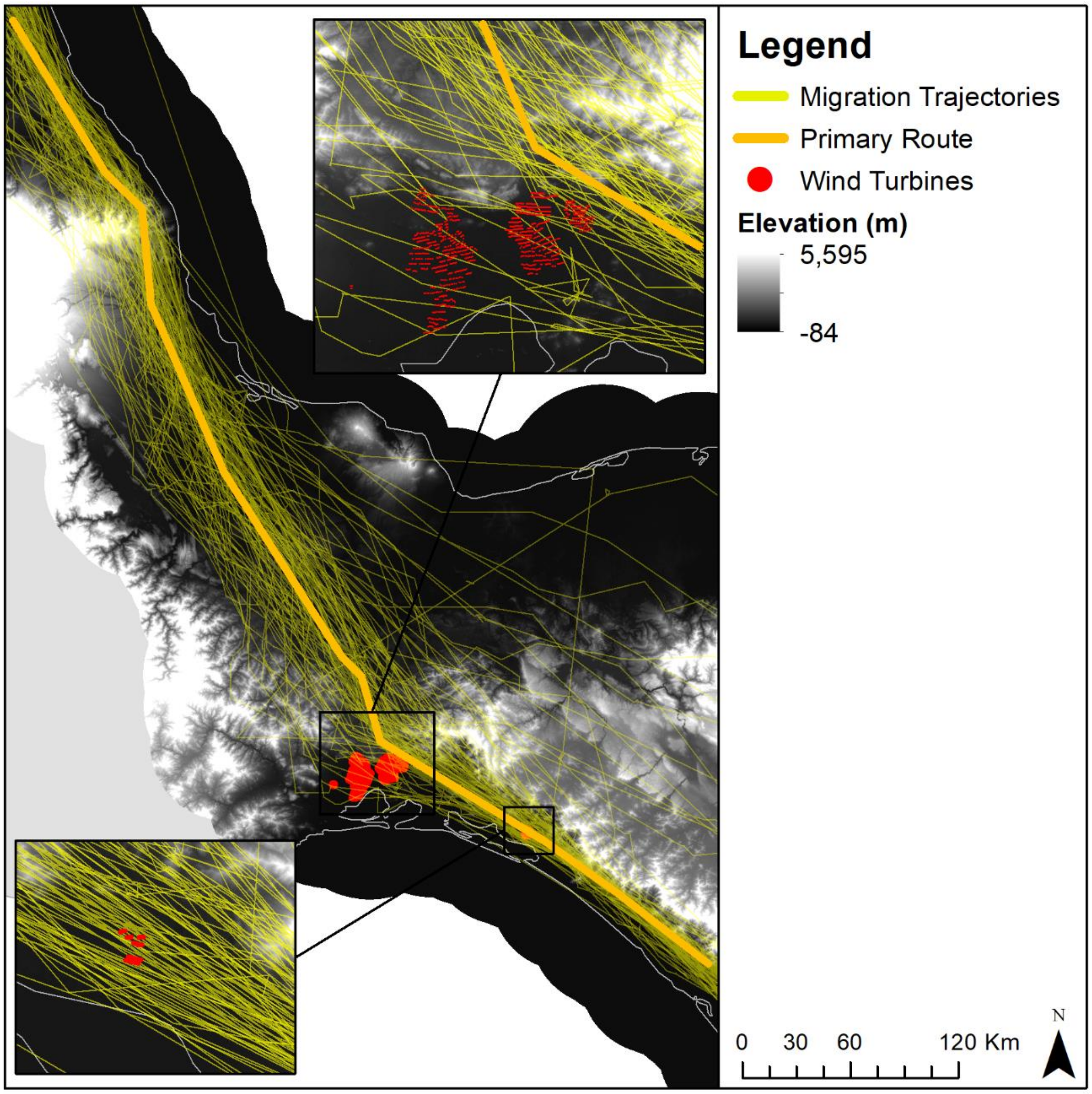

Figure 6.18. Swainson’s hawk migration through southern Mexico. Elevation, location of wind turbine hazards, and a general migration route are provided for reference. *Adapted from:* National Aeronautics and Space Administration (https://search.earthdata.nasa.gov), Sentinel-2 satellite imagery (https://glovis.usgs.gov), ArcMap 10.7 World Imagery, Google Earth (https://www.google.com/earth/), and Google Maps (https://www.google.com/maps).

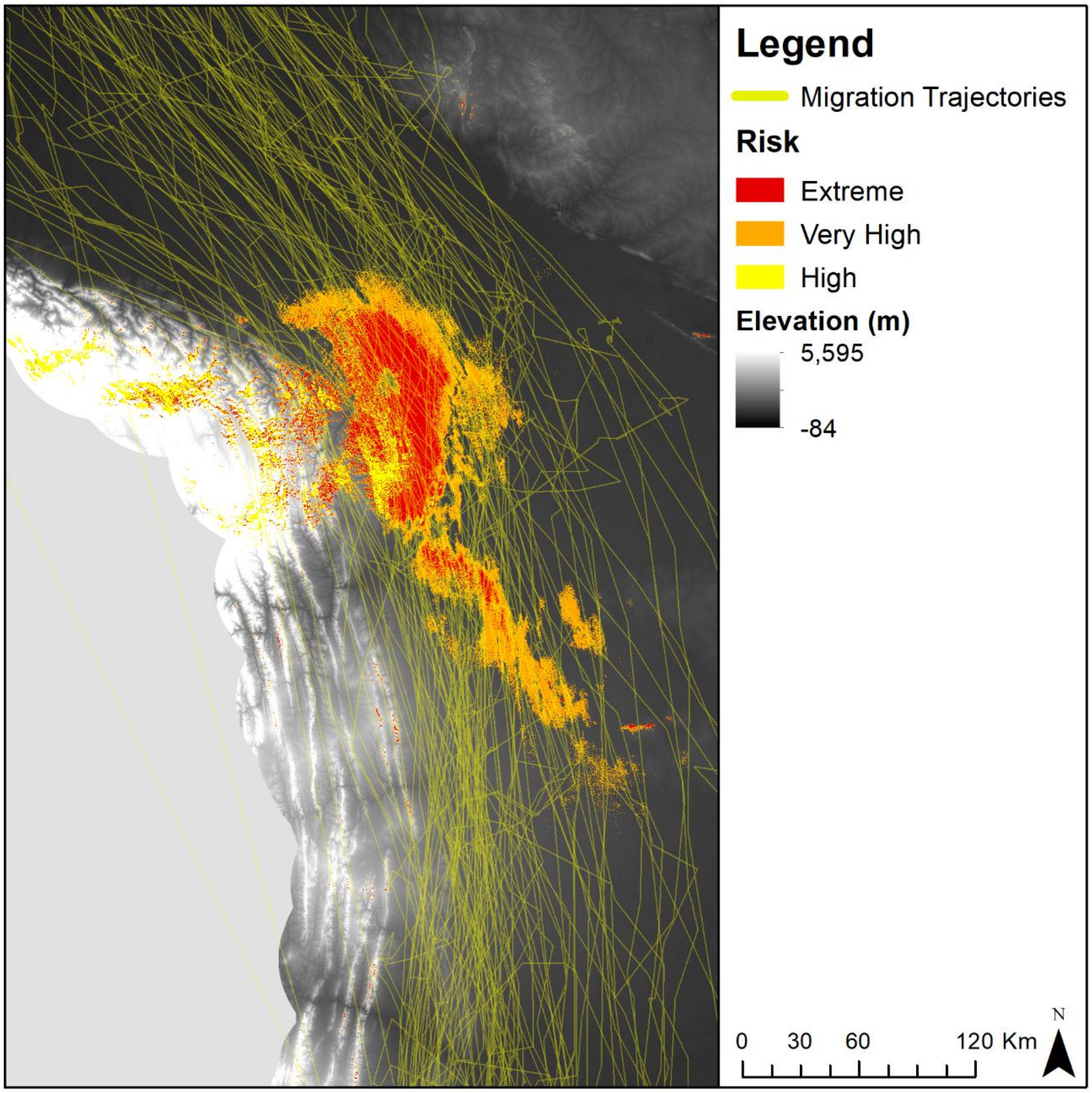

Figure 6.19. Swainson’s hawk migration through regions of high to extreme risk of hawks encountering wind energy hazards in central Bolivia. Elevation is provided for reference.
Source: National Aeronautics and Space Administration (https://search.earthdata.nasa.gov).

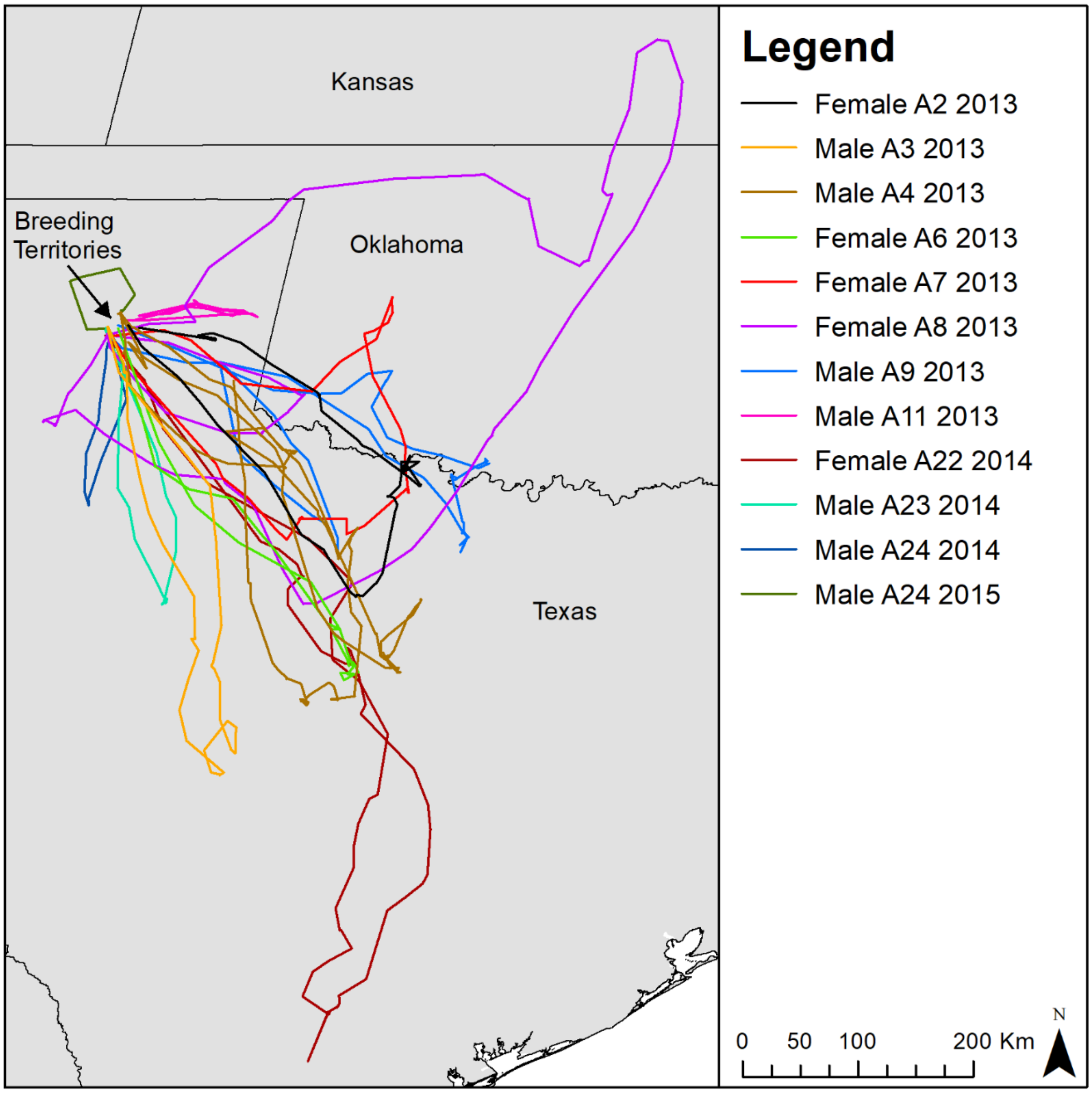

Figure 6.20. Pre-breeding movements, where some adult Swainson's hawks ended migration at their breeding territories, then immediately left the area for 2 to 27 days (mean = 10 days), moving at least 150 to 2,238 km (mean = at least 1,030 km), only to return and attempt to breed on previously used territories. We captured 24 adult hawks on breeding territories in northern Texas in 2012 – 2014 and equipped them with solar-powered GPS transmitters on backpack-style harnesses. Hawks are identified here by their sex, alphanumeric code, and the year this behavior occurred. Hawks did not make these movements every year of observation, and although we tracked many hawks over consecutive years, only one hawk (A24) made these movements twice.

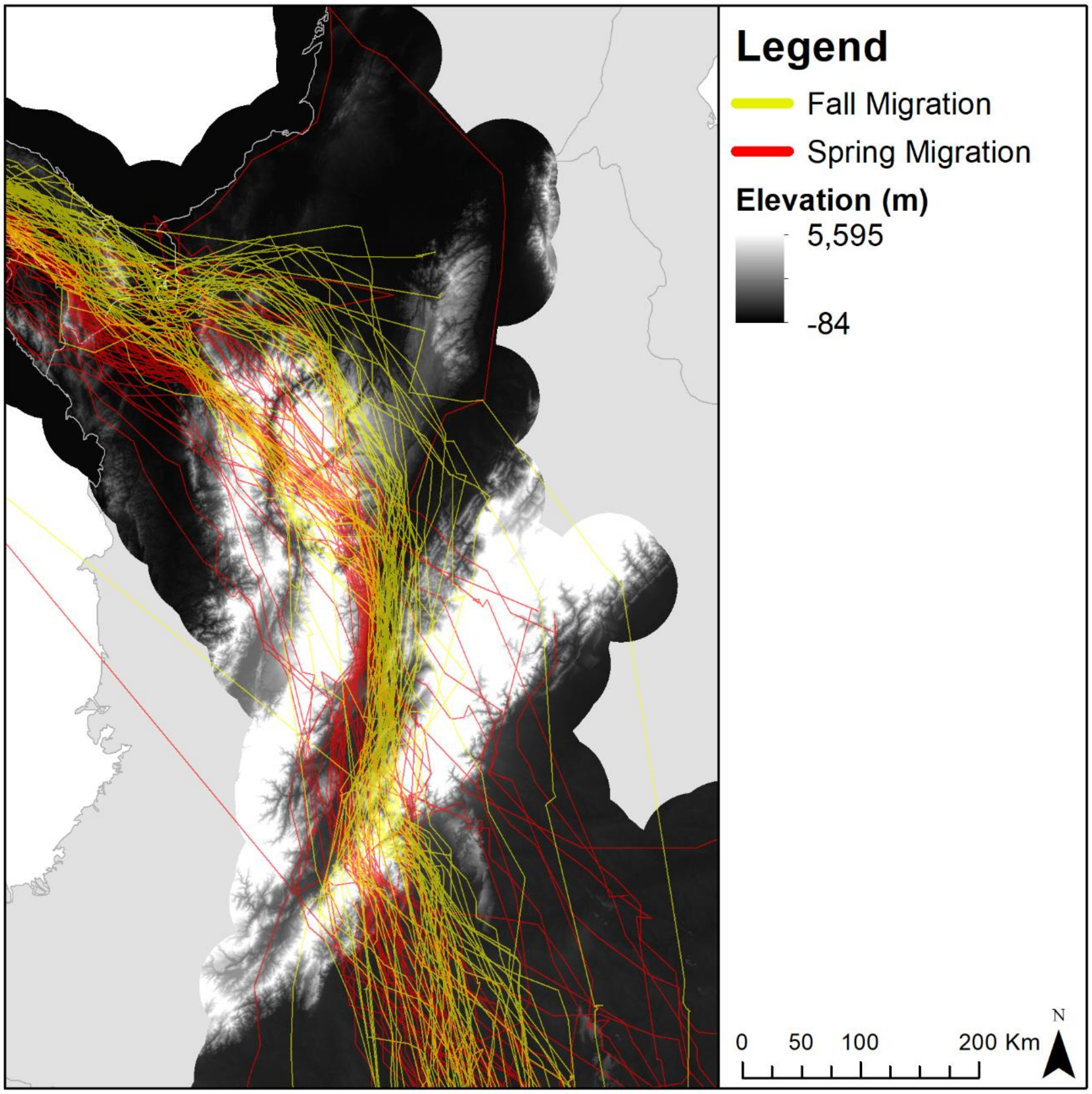

Figure 6.21. Swainson's hawk traverse the Andes Mountains while migrating through Colombia.
Adapted from: National Aeronautics and Space Administration (https://search.earthdata.nasa.gov).