SPATIAL ECOLOGY OF BLACK AND TURKEY VULTURES IN THE SOUTHEASTERN UNITED STATES

by

AMANDA E. HOLLAND

(Under the Direction of James C. Beasley and Robert J. Warren)

ABSTRACT

Knowledge of the spatial ecology of black (*Coragyps atratus*) and turkey vultures (*Cathartes aura*) is surprisingly limited, despite these species' importance in ecosystem function and considering economic costs associated with human-vulture conflicts. To build upon our understanding of the spatial ecology of sympatric black and turkey vultures in the southeastern United States, I collected >2.8-million GPS locations from 9 black and 9 turkey vultures from 2013-2015 using solar-powered GSM/GPS transmitters. From these data, I developed monthly home ranges and core areas using the dynamic Brownian Bridge Movement Model, and quantified and compared space use, activity patterns, roost reuse frequency, roost site fidelity, habitat characteristics of evening roosts, and aspects of resource selection based on utilization distributions by species and sex across multiple spatio-temporal scales. My results build upon understandings of vulture spatial ecology and provide insights into mechanisms underlying facilitation of niche differentiation between these sympatric species.

INDEX WORDS: Black Vulture, Turkey Vulture, Spatial Ecology, Home Range, Resource Selection, Habitat Characteristics, Utilization Distributions, GPS Tracking

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DEDICATION

I dedicate this to my best friend, Keith Holland.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Page

CHAPTER 1. INTRODUCTION AND LITERATURE REVIEW

Black (*Coragyps atratus*) and turkey vultures (*Cathartes aura*) are obligate scavengers that forage almost exclusively on carrion (Kirk and Mossman 1998, Buckley 1999). These broad-winged, large-bodied birds utilize both natural and anthropogenic thermals and wind energy to soar long distances with minimal energy expenditure (Mandel and Bildstein 2007, Mandel et al. 2008). Both species have adapted relatively well in the face of anthropogenic changes to the landscape and populations have increased over the last several decades (Kirk and Mossman 1998, Ogada et al. 2012a). Typically associated with road kill, agricultural areas, and landfills, black and turkey vultures commonly use anthropogenic sources for forage and roost sites (Kirk and Mossman 1998, Buckley 1999), often roosting on human-made structures (Buckley 1998, Avery et al. 2002, Evans and Sordahl 2009) and occasionally nesting in abandoned buildings (Kirk and Mossman 1998, Buckley 1999).

The regular association of vultures with human-dominated landscapes frequently results in conflict. Collisions with human structures (commonly known as “bird-strikes”), including airplanes, automobiles, wind turbines, buildings, communication towers, and electric infrastructure, are major reasons for a better understanding of the movement patterns of vultures and other birds (Marra et al. 2009, Avery et al. 2011, Dolbeer 2011, Martin et al. 2011, Loss et al. 2012, Walter et al. 2012). Considering substantial body sizes averaging 2.2 kg and 2 kg, respectively (Kirk and Mossman 1998, Buckley 1999) and propensity to kettling, or circling flights in groups, (Kirk and Mossman 1998, Buckley 1999), black and turkey vultures are some of the most hazardous species to aircraft (Blackwell and Wright 2006, DeVault et al. 2011, Dolbeer et al. 2012). These species are a major cause of damaging bird-strikes at airfields (Avery 2004, Dolbeer et al. 2012, Dolbeer et al. 2014). Between 1990 and 2013, in the United States alone, over 55% of reported civil aircraft strikes with vultures resulted in damages, the costs of which exceeded US$28 million and over 48,000 hours of aircraft down-time, although these reported costs are drastic underestimations (roughly 20%) of actual estimates because not all wildlife strikes are adequately reported (Blackwell and Wright 2006, Dolbeer et al. 2014). Adding to the hazards that vultures pose to aircraft is the observation that populations of black and turkey vultures are increasing (Avery 2004, Sauer et al. 2012). However, this trend is in dramatic contrast to the sudden and extreme declines that other vulture species have been experiencing in recent years.

Globally, 61% of vulture species are currently threatened with extinction (Ogada et al. 2012a) due to a variety of causes including direct persecution by humans (i.e., shootings, poisonings and harassment) and secondary effects resulting in unintentional harm. For example, Asian populations of *Gyps* vultures have declined by more than 95% due to renal failure caused by ingesting carcasses treated with the anti-inflammatory drug diclofenac (Ogada et al. 2012a). In addition, efforts to recover the critically-endangered California condor (*Gymnogyps californianus*) in western North America have been hampered by poisonings caused by accidental ingestion of lead ammunition fragments in unretrieved carcasses and gut piles (Walters et al. 2010). Moreover, vulture populations worldwide are detrimentally impacted when they consume carnivore carcasses of animals deliberately poisoned by humans (Ogada et al. 2012a, DeVault et al. *in press*).

Vultures play a critical role in ecosystems and the impact of global vulture declines are largely underestimated (Sekercioglu et al. 2004, Sekercioglu 2006, Moreno-Opo et al. 2012, Ogada et al. 2012a, Ogada et al. 2012b). Vultures are highly adapted for carcass location and consumption (Kirk and Mossman 1998, Buckley 1999) and are excellent competitors for carrion resources (Sebastián-González et al. 2013, DeVault et al. *in press*). Vultures have highly acidic stomachs effectively capable of removing pathogens within carcasses (Houston and Cooper 1975), thus, their presence in ecosystems help to reduce bacterial infection rates (Sekercioglu 2006, DeVault et al. *in press*). Undeniably, the detrimental effects of the ecological absence of vultures are considerable. For example, following the ecological extinction of vultures in India (Ogada et al. 2012b), competition at carrion resources declined and populations of rats and feral dogs increased, causing a significant human health concern (Ogada et al. 2012b). Indeed, the human health costs associated with the loss of vulture species in India were estimated to exceed US$34 billion between 1993 and 2006 due to elevated risks of rabies from feral dog bites (Markandya et al. 2008). The ecological implications of vulture declines in many other systems have yet to be fully described but are likely to be considerable (Sebastián-González et al. 2013, DeVault et al. *in press*).

Despite the ubiquity of vultures in the Americas and their association with human-dominated landscapes, black and turkey vultures are surprisingly understudied. A few studies have estimated home ranges using a variety of tracking techniques and home range estimator methods (Coleman and Fraser 1989, Arrington 2003, DeVault et al. 2004, Avery et al. 2011, Houston et al. 2011, Fischer et al. 2013, Hedlin et al. 2013). However, comparisons of vulture home ranges calculated using similar estimator methods reveal substantial variation both within and among species and across regions (DeVault et al. 2004, Fischer et al. 2013). For example, estimations of mean annual 95% fixed-kernel density (KDE) home ranges were over 20 and 38 times larger for black and turkey vultures on the southern coast of South Carolina than the heavily forested Savannah River Site in South Carolina (DeVault et al. 2004, Fischer et al. 2013). Variations may be explained in part by differences in sample size, accuracy of tracking techniques, and estimator methods, but also may be due to differences in habitat quality and resource availability between sites (DeVault et al. 2004, DeVault et al. 2005, Kelly et al. 2007, Rolando 2002). Additionally, differences in physiological condition (López-López et al. 2013), social status (Donázar et al. 1999, Wallace and Temple 1987), and competition (Buckley 1996, Buckley 1998, DeVault et al. 2005, Donázar et al. 1999, Kirk and Houston 1995, Wallace and Temple 1987) may result in home range size variation.

The need to assess underlying factors that influence patterns of vulture movement and resource selection are underscored by the variations in prior home range estimates across landscapes (Coleman and Fraser 1989, DeVault et al. 2005). A bird’s annual movement patterns are influenced not only by external factors, such as weather, climate and habitat, but also physiological factors (DeVault et al. 2005, Donázar et al. 1999, López-López et al. 2013, Mandel et al. 2008, Ramenofsky et al. 2012, Rolando 2002). Sex is one biological factor that has been found to play a role in explaining differences in movement and foraging patterns of Andean condors (*Vultur gryphus*) (Donázar et al. 1999) and other animals (Austin et al. 2004, Tracey et al. 2013). Because vultures are highly social, exhibiting hierarchical behavior between individuals and groups that forage and roost together (Kirk and Houston 1995, Kirk and Mossman 1998, Buckley 1999), sex may be an important factor to consider when determining variations in movement patterns and resource selection among vultures (Donázar et al. 1999, Evans and Sordahl 2009, Wallace and Temple 1987). Black and turkey vultures are sexually monomorphic (Kirk and Mossman 1998, Buckley 1999) making it difficult, if not impossible, to determine sex of individuals based on phenotype. For an assessment comparing home range sizes in breeding (*n*=6; Houston et al. 2011) and wintering (*n*=4; Hedlin et al. 2013) seasons for migratory turkey vultures, sex was determined in a single vulture based on observations of copulation events and two other vultures based on DNA sex determination from feather samples (Hedlin et al. 2013, Houston et al. 2011); no other studies have quantified movement behavior patterns based on sex for these species. Moreover, vulture movement patterns change over the course of an annual cycle (López-López et al. 2013). Coleman and Frasier (1989) found mean summer (15 March – 14 September) home ranges to be more than double the size of winter (15 September – 14 March) home ranges for black and turkey vultures in southern Pennsylvania and northern Maryland. Vulture movements are also expected to be centered on the nest location during breeding season (Houston et al. 2011), but may be more ephemeral during the non-breeding season. Home ranges have been estimated only once with consideration to breeding (Houston et al. 2011) and winter seasons (Hedlin et al. 2013) but these were estimated for migratory turkey vultures that breed and winter in entirely difference regions. No prior studies have estimated home ranges with consideration to the effects of sex and seasons for non-migratory black or turkey vultures.

Competition for and spatial arrangement of carrion resources can influence movement and foraging patterns of scavenging birds (Kirk and Currall 1994, Donázar et al. 1999, Austin et al. 2004, DeVault et al. 2004, Ramenofsky et al. 2012). Interspecific differences in resource selection and movement patterns likely exist as turkey vultures locate carrion by enhanced olfaction as well as vision, whereas black vultures locate carrion primarily by visual detection alone (Kirk and Mossman 1998, Buckley 1999). Interestingly, Coleman and Fraser (1989) found no evidence of territorial defense or differences in selection of roosting, nesting, and foraging sites for sympatric black and turkey vultures tracked by VHF radio telemetry in the Mid-Atlantic region. However, niche segregation by habitat was indeed evident in sympatric vultures wintering in Venezuela (Kirk and Currall 1994). Spatial differences in resource selection by species might be increasingly evident at finer scales.

Quantifying characteristics of spatial ecology and resource selection for roosting and foraging habitats of sympatric black and turkey vultures in the southeastern United States will provide benefits to vulture management and conservation. Prior assessments have described substantial variation in individual vulture movements; therefore, a critical need remains to elucidate potential factors contributing to such variations. Recent advancements in tracking device technologies allow the collection of fine-scale spatial data, information that has been unattainable in many previous studies of vulture spatial ecology. Utilization of GPS satellite transmitters to monitor fine-scale vulture movements and the potential differences in resource utilization among individuals and between species will enhance our understanding of spatial ecology of sympatric black and turkey vultures in the southeastern United States. This research seeks to fill these important gaps by quantifying the space use and resource selection patterns of sympatric black and turkey vultures with greater resolution than previous studies conducted on these species.

The goals of this research, therefore, are to improve understandings of vulture spatial ecology and resource selection by sympatric species at multiple spatial and temporal scales to help inform management and conservation of black and turkey vultures in the southeastern United States. In Chapter 2, home ranges and core areas are delineated using the dynamic Brownian Bridge Movement Model (Kranstauber et al. 2012), activity patterns quantified from flight and stationary fixes, and measures of roost reuse and roost site fidelity are quantified and compared among species, sexes, and seasons. In Chapter 3, habitat attributes associated with vulture evening roost sites are assessed seasonally, differences in seasonal reuse frequency and site fidelity of vultures to evening roost sites are quantified, and differences in monthly resource selection within home ranges are elucidated with consideration to species and sex.

To accomplish this research, 295 vultures were trapped using an air-propelled net-cannon at sites baited with wild pig (*Sus scrofa*) or similar carcasses at multiple sites interspersed throughout the Savannah River Site, South Carolina, USA (33.24º N, 81.67º W). I affixed one of 20 solar-powered 70-g Groupe Spécial Mobile/Global Positioning System (GSM/GPS) transmitters to a total of 27 adult vultures (13 black and 14 turkey) via backpack harness. Each of the 27 vultures carried one of 20 GSM/GPS transmitters over a range of durations. Five transmitters stopped reporting locations sometime after deployment and were never recovered (lost). One lost transmitter was affixed to a black vulture for which no locations were ever reported and was thus unrecoverable after the bird was released. The other four lost transmitters were affixed to three turkey vultures and one black vulture for which locations were reported over a range of durations before locations simply stopped reporting for no obvious reason. It is presumed that these transmitters were dropped from the birds in areas without adequate GSM cell coverage or the transmitters possibly failed due to mechanical issues. Transmitters dropped from vultures six times due to harness failures but were recoverable and redeployed. Two transmitters were removed from black vultures due to mortalities and redeployed. Of the 20 transmitters deployed, 11 were carried for over two years, five were carried for over one year, two were carried for five and eight months, respectively, and two were carried for over two months. The GSM/GPS transmitters recorded locations at variable intervals, with highest frequency of reported locations at times when solar availability (and thus peak battery power) was highest (Bryan et al. 2014). Vulture locations from the GSM/GPS transmitters were reported by e-mails sent via GSM cell tower signals (Microwave Telemetry, Inc. 2013). When vultures flew beyond range of a GSM cell tower, the transmitters stored locations for delivery at a later time when the vulture returned to within GSM cell tower range (Microwave Telemetry, Inc. 2013). Location data were downloaded and compiled on a regular basis over the course of the study.

Using these data, objectives of this research were to (1) estimate and compare monthly home range and core area sizes for resident black and turkey vultures in the southeastern United States using the dynamic Brownian Bridge Movement Model; (2) describe differences in monthly, seasonal (breeding, summer, and winter), and annual activity rates by quantifying proportions of time spent in transit (flying), stationary (roosting, resting, and foraging), and switch (transitions between movement and stationary) states; (3) quantify and compare seasonal (breeding, summer and winter) roost site fidelity and roost reuse frequency by species; and (4) assess monthly resource selection within home ranges for habitat types including distances to landfills (0-500m and 500-1000m), distances to roads (0-500m), wetland, forest, developed/urban, developed/open, and undeveloped/open. This research seeks to fill important gaps by quantifying the space use and resource selection patterns of sympatric black and turkey vultures with greater spatial and temporal resolution than previous studies conducted on these species.

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CHAPTER 2

FINE-SCALE ASSESSMENT OF MONTHLY HOME RANGES AND ACTIVITY PATTERNS FOR RESIDENT BLACK AND TURKEY VULTURES IN THE SOUTHEASTERN UNITED STATES[1]

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ABSTRACT

Knowledge of the spatial ecology of black (*Coragyps atratus*) and turkey vultures (*Cathartes aura*) is surprisingly limited despite the role of these species in ecosystem function and considering the economic costs associated with human-vulture conflicts. Fine-scale assessments of space use patterns and resource use are particularly lacking for vultures, although development of new tracking technologies has allowed collection of data at finer temporal and spatial resolution than ever before. The objectives of this study, therefore, were to conduct the first assessment of monthly home range and core area sizes with consideration to sex, as well as to elucidate differences monthly, seasonal, and annual activity patterns for resident vultures in the southeastern United States based on analyses of fine-scale movement data. I gathered > 2.8-million GPS locations from 9 black and 9 turkey vultures from June 2013 – August 2015 using solar-powered GSM/GPS transmitters. From these data, I quantified home ranges and core areas using the dynamic Brownian Bridge Movement Model and evaluated differences as a function of species, sex, and month. Mean monthly home ranges for turkey vultures (60.94 ± 4.24 km^2) were significantly larger than those of black vultures (30.51 ± 2.57 km^2; $P=0.008$), although mean core area sizes did not differ between species (0.424 ± 0.027 km^2, 0.45 ± 0.062 km^2, respectively). Comparisons of space use between male and female vultures were only possible for black vultures, for which monthly space use differed nominally being larger for females in March-April. Vulture activity patterns revealed turkey vultures spend more time in flight and switch motion states (between flight and stationary) more frequently than black vultures across all temporal scales (monthly, seasonally, and annually). This study reveals immense variability in black and turkey vulture space use and activity rates across the annual cycle and provides a vital component for habitat selection analyses.

INTRODUCTION

Vultures, as obligate scavengers, provide invaluable ecosystem services by enhancing the flow of nutrients within food webs and reducing transmission of infectious disease rates through the removal of carrion (DeVault et al. 2003, Markandya et al. 2008, Wilson and Wolkovich 2011, Ogada et al. 2012b, Beasley et al. 2015). Specializing in carcass consumption (Kirk and Mossman 1998, Buckley 1999), vultures are adapted to detect and remove carcasses from landscapes more efficiently than any other terrestrial scavenger (Houston 1979, Sebastián-González et al. 2013). Because carrion is ephemeral and often randomly distributed (DeVault et al. 2003), vultures have evolved unique adaptations to exploit this spatially unpredictable resource (Kirk and Mossman 1998, Buckley 1999). Unfortunately, vulture populations have experienced drastic declines over the last few decades (Ogada et al. 2012a), making them among the most threatened groups of birds today, with 70% of species exhibiting population declines, 39% of which are considered either endangered or critically endangered, and 26% considered near threatened or vulnerable by the IUCN (2015). Consequences of reduced vulture populations are not trivial, as evidenced in India where populations of rats (*Rattus spp.*) and feral dogs (*Canis spp.*) increased following the ecological extinction of vultures, causing significant human health concerns and associated costs due to increased incidence of rabies (Ogada et al. 2012b).

Conversely, in North America, populations of black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*) are abundant throughout their ranges (Avery 2004, Sauer et al. 2012). These species have increased over the last several decades following the ban of DDT in the early 1970’s and continue to increase, likely due to many factors such as reductions in pesticide use and human persecution, increases in deer populations and roadkill, a greater number of landfills, and a warming climate (Kiff 2000). In addition, although timber practices are generally considered a limiting factor on vulture reproductive output due to removal of large, hollow trees (Kiff 2000), increases in abandoned buildings throughout North America may be providing compensatory nesting sites. These increases in black and turkey vulture populations have led to rises in conflicts between humans and vultures, including the substantial safety risk vultures in flight pose to aircraft personnel due to potential for air collisions known as "bird-strikes" (Blackwell and Wright 2006, DeVault et al. 2011, Dolbeer et al. 2012). Bird-strikes are a major justification for a better understanding of the movement patterns of vultures and other birds (Marra et al. 2009, Avery et al. 2011, Dolbeer 2011, Martin et al. 2011, Loss et al. 2012, Walter et al. 2012).

Despite their relative ubiquity, importance in ecosystem function, and concerns associated with increased populations, fine-scale analyses of the spatial ecology of black and turkey vultures are surprisingly limited. Previous home range estimates for black and turkey vultures have revealed considerable differences within and among species, as well as among different regions within their respective ranges. Space use variation is likely due to differences in individual physiology (López-López et al. 2013), social status (Donázar et al. 1999, Wallace and Temple 1987), and competition (Buckley 1998, Donázar et al. 1999, Kirk and Houston 1995, Wallace and Temple 1987). Differences in sample size and accuracy of tracking techniques also have contributed to the substantive differences in home range size reported among studies (Fischer et al. 2013). Fortunately, recent advancements in tracking technologies now allow researchers to gather high-resolution location data on vultures and other wide-ranging organisms in greater detail and with superior accuracy than ever before (Fischer et al. 2013). Fine-scale analysis of movement behavior is essential to improve understandings of the mechanisms underlying movement, interactions with environments, and other basic concepts of animal ecology (Cagnacci et al. 2010).

Spatio-temporal variation in the distribution and availability of resources undoubtedly plays an important role in home range size differences among studies (DeVault et al. 2004, DeVault et al. 2005, Kelly et al. 2007, Rolando 2002). In southern Pennsylvania and northern Maryland, mean winter home range sizes for black and turkey vultures were nearly half the size of summer home ranges (Coleman and Frasier 1989). Fluctuations in home range sizes may be in response to changes in spatial or temporal resource availability, but they may also demonstrate changes in animal behavior due to physiological vicissitude. For example, home range sizes of California condors (*Gymnogyps californianus*) were substantially smaller (5-6 times) during breeding season in November-March as compared to July-October, presumably because movements were limited and central to nest sites during nesting activities (Rivers et al. 2014).

An understanding of vulture movement activity patterns can lead to recognition of mechanisms underlying habitat selection within a home range. For example, measurements of activity patterns (i.e., time spent in flight vs. time spent roosting) can reveal the amount of search effort required by an individual to obtain important resources within its home range. For vultures, it is reasonable to assume that when a vulture is in flight, it is searching for some resource, be it carrion, a nesting location, or roost site. Vultures have shown immense behavioral plasticity in relation to local habitat structure and resource availability. For example, black and turkey vultures spent substantially more time in flight, presumably in search of carrion, at the heavily forested Savannah River Site than in areas where forage opportunities were more predictable, such as the agriculturally-dominated landscapes of Pennsylvania and Maryland (Coleman and Fraser 1989, DeVault et al. 2004). Additionally, vultures in coastal South Carolina spent more time in flight during winter than summer, likely due to the need for increased foraging efforts given reduced ability to detect carrion in colder months and reduced daylight hours (Avery et al. 2011).

To date, few prior studies have quantified home range sizes and activity patterns for resident, non-migratory black and turkey vultures, and none have examined variation in space use by month or sex. Thus, use of global positioning system (GPS) satellite tracking devices and fine-scale sampling regimes coupled with sex determination will greatly improve our understanding of the factors that underlie variations in movement patterns and space use by black and turkey vultures across an annual cycle, further developing our understandings of vulture ecology, benefitting wildlife managers concerned with reducing vulture-related conflicts (DeVault et al. 2005, Marra et al. 2009, Avery et al. 2011, Martin et al. 2011, Loss et al. 2012, Walter et al. 2012) and conservation of these ecologically invaluable species.

The objectives of this study, therefore, are to strengthen inferences on the spatial ecology of black and turkey vultures by comparing home range and core area size estimates between species and sexes at a finer temporal scale (monthly) than previous studies for these species, and to determine the proportion of time spent in transit (flying) versus stationary (roosting, resting, and foraging) to elucidate differences in monthly, seasonal (breeding, summer, and winter), and annual activity rates for resident black and turkey vultures in the southeastern United States. I hypothesize turkey vultures will range across larger areas and spend a greater proportion of time in flight than black vultures considering turkey vultures’ higher wing loading capacity, enhanced sense of smell, and higher likelihood of avoiding competitive interactions (Kirk and Mossman 1998). I further expect that turkey vultures will switch between flight (movement states) and roosting/resting (stationary states) more frequently than black vultures, considering turkey vultures typically forage either in pairs or solitarily (Kirk and Mossman 1998) and are thus more likely to flush from an area when disturbed or challenged at a feeding site. Both black and turkey vultures are monomorphic and both sexes contribute similarly to parental care (Kirk and Mossman 1998, Buckley 1999). Thus, I expect space use patterns will not differ as a function of sex, although differences may be evident at finer temporal and spatial scales. Additionally, I hypothesize monthly space use for each species will vary over an annual cycle with smaller ranges in winter and breeding season months due to reductions in daylight hours and propensity to restrict movements central to nesting locations in breeding seasons (Houston et al. 2011).

METHODS

Study Area

This research was conducted at the Savannah River Site (SRS) which is located along the border of Georgia and South Carolina in the southeastern United States. The SRS is a 780-km^2, limited-access, nuclear research facility owned and operated by the U.S. Department of Energy (DOE; White et al. 2000). Elevations range from <30 m to 115 m above sea level (White et al. 2000). Much of the SRS is relatively undisturbed by DOE activities and is primarily forested (White et al. 2000). The SRS is composed of planted pine forests managed by the U.S. Forest Service (DeVault et al. 2004), bottomland hardwood, wetland, and various industrial areas including five decommissioned nuclear reactors, radioactive materials processing plants, and landfills (White et al. 2000). The composition of largely undisturbed natural areas makes this site an ideal location in which to study resident vulture space use. Black and turkey vultures are abundant on the SRS as it provides important roosting, nesting, and foraging habitat for both species (DeVault et al. 2004, DeVault et al. 2005).

Vulture Trapping & Handling

In summer 2013 and spring 2014, I captured a total of 295 vultures using an air-propelled net-cannon at sites baited with wild pig (*Sus scrofa*) or similar carcasses at multiple sites interspersed throughout the SRS. Of these, 27 adult vultures (13 black and 14 turkey) were randomly selected to receive solar-powered 70-g Groupe Spécial Mobile/Global Positioning System (GSM/GPS) transmitters (Microwave Telemetry, Inc. 2013) attached via backpack harness. In an effort to target resident (i.e., non-migratory) individuals, trapping occurred outside the migration seasons for each species (Kirk and Mossman 1998, Buckley 1999). However, after all locations were collected, classification of each individual as either resident/non-migratory or migratory was verified by assessing each vulture's net squared displacement (NSD; see below) from evening roost locations. All vultures were affixed with numbered patagial tags for individual identification and handled in accordance with the University of Georgia Animal Care and Use Protocol No. A2013 02-004-Y2-A2. For all captured vultures, I collected standard morphological measurements and estimated age-class (adult or juvenile) based on coloration and wrinkling of the head (Kirk and Mossman 1998, Buckley 1999). Given that black and turkey vultures are sexually monomorphic (Kirk and Mossman 1998, Buckley 1999), it was not possible to control for balanced ratios of male and female black and turkey vultures from among those randomly selected to receive GPS tracking devices. However, I collected feather and blood samples from captured individuals to aid in sex determination via molecular methods.

Sex Determination

Sex was determined for transmittered vultures via sex-specific DNA markers amplified by polymerase chain reaction (PCR). Genomic DNA was extracted from whole blood (stored at -20ºC) or breast feathers using a bead beater protocol. Specifically, 50µl of blood was lysed using a combination of chemical (350µl of lysis buffer consisting of 4M guandidine thiocyanate, 0.01M Tris-HCl Ph 7.5, and 20µl/mL β-mercaptoethanol) and mechanical disruption using a 3.5 mm stainless steel bead for 30 sec at 1,500 oscillations per minute on a Mini-Beadbeater 24 (BioSpec Products Inc., Bartlesville, OK, USA). The lysed solution was then centrifuged and the supernatant was applied to a spin column with a silica gel membrane (EconoSpin, Epoch Life Science, Sugar Land, TX, USA). The column was then centrifuged to bind the nucleic acid and the membrane was washed twice with a buffer consisting of 1mM Tris HCl pH 7.5 and 162.8g potassium acetate before eluting with 75µl of ultra-pure water. DNA extraction from breast feathers was conducted following Qiagen DNeasy blood and tissue kit (Qiagen, USA) with a final elution volume of 100ul.

Following the methods of Ito et al. (2003), primers P2 and NP were used to amplify a part of the CHD1 gene of the W chromosome which distinguishes female birds from male birds. The PCR reaction occurred in 25µl volume using 1X PCR buffer (10mM Tris ph 8.4, 50mM KCl), 1.5m $MMgCl_2$, 0.2 mM deoxyribonucleotide triphosphate (dNTP), 0.4µM of each primer, 0.625 U Ampli Taq Gold polymerase (Thermo Fisher), 0.025µl 0.01% Tween 20 (Sigma-Aldrich, Missouri, USA), and 2µl DNA, initially denatured at 94ºC for 4 mins, followed by 43 cycles of 94ºC (30 secs), 48ºC (45 secs), and 72ºC (45 secs), and a final extension at 72ºC for 5 mins. PCR products were run on an ABI 3130/3100XL sequencer (Applied Biosystems, USA) for sex determination. All genetic analyses were conducted at the Savannah River Ecology Laboratory in Aiken, South Carolina.

Data Preparation

Solar-powered GSM/GPS transmitters reported location (lat/long coordinates), speed (knots), course, altitude (m), horizontal and vertical dilution of precision (HDOP, VDOP), and number of satellites used to obtain each fix. Fixes were recorded at variable intervals, with the highest frequency of fixes reported at times when solar availability (and thus peak battery power) was greatest (Bryan et al. 2014; Byrne et al., *in prep*). The frequency of fixes obtained was exceptionally high, with 25% of all locations collected at intervals of <1 minute, 51% with intervals of 1-3 minutes, 9% with intervals of 3-10 minutes, 7% with intervals of 10-30 minutes, and only 8% with intervals >30 minutes. Fixes received during the first two weeks post transmitter deployment were excluded from analyses to allow vultures to become accustomed to transmitters and return to normal movement patterns in the event of post-handling effects.

To avoid temporal bias in comparisons of space use (i.e., home range and core area) estimations and activity patterns, data for all vultures were subset and standardized to include only fixes received within equal timeframes (i.e., monthly, seasonal, or annual). Specifically, for monthly space use and activity patterns comparisons, data from September 2013 to August 2015 were sorted by month based on calendar definitions (e.g., June contained fixes from 1 June 2015 00:00:00 EST to 30 June 2015 23:59:59 EST). For comparisons of activity patterns by season, seasonal datasets were defined for three seasons (breeding, summer and winter), and included all fixes received within equal durations of 121 days and eight hours, with the exception of the first summer. The first summer only included data from the final 53 days and 16 hours of the season because GPS transmitters were deployed in mid-summer. Breeding season durations are similar for black and turkey vultures (Jackson 1983, Kirk and Mossman 1998, Buckley 1999), although in areas of sympatry, black vultures typically nest two weeks earlier than turkey vultures (1 February - 10 June for black vultures and 15 February - 24 June for turkey vultures; Jackson 1983, Kirk and Mossman 1998, Buckley 1999). Therefore, breeding seasons in this analysis included fixes from 8 Feb 00:00:00 to 9 June 07:59:59, which represent the median dates of those described for vultures breeding at 32°-33° latitudes (Jackson 1983), and encompassed the range of dates wherein adult black and turkey vultures are both influenced by breeding phenology, and standardized for ease of comparison. Fixes received within the tertiles preceding and following the breeding season were defined as winter (8 October 16:00:00 - 7 February 23:59:59) and summer (9 June 08:00:00 - 8 October 15:59:59), respectively. Seasonal data were collected for one and a half summer seasons, two full breeding seasons, and two full winter seasons. For comparisons of annual activity patterns, annual data include locations collected between 1 September 2013 to 31 August 2014 for the first year and 1 September 2014 to 31 August 2015 for the second year.

Home Range and Core Area Estimations

Location data were filtered to remove fixes with altitudes above 12,000 m, inconclusive data (“NegAlt”, “No Fix”, “2D”, “Batt Drain”, and “Low Voltage”), as well as any outliers (McConnell et al. 1992). Specifically, I used the McConnell (1992) algorithm to calculate the root mean square (rms) for each location based on reported transmitter speed. This algorithm compares the speed of each location against the previous and subsequent two locations, removes peaks in rms above a user-defined maximum speed (25 m/s), and recalculates rms until all locations are below the defined speed threshold.

From the filtered data, I assessed each vulture’s net squared displacement (NSD; Bunnefeld et al. 2011) from evening roost locations in order to verify that the vultures in this analysis were indeed resident, non-migratory individuals. Specifically, I identified evening roosts by extracting the average location from among fixes received between 20:00-00:00 hours for each vulture. For nights where no fixes were received between 20:00-00:00 hours, evening roosts were determined manually by examining location data for series of fixes within nighttime hours where the bird clearly did not move for several hours throughout the evening and into the following morning (00:00-04:00), reporting the evening roost as the average of those locations. NSD for each vulture was measured as the straight line distance between the starting roost location and the subsequent roost locations for the trajectory path of all roost locations (Bunnefeld et al. 2011). NSDs were plotted and migration movements identified by peaks in NSD within winter months (Figures 2-1, 2-2).

Filtered locational data were used to delineate monthly home ranges and core areas for individual vultures using the dynamic Brownian Bridge Movement Model (dBBMM; Kranstauber et al. 2012) with the ‘move’ package (Kranstauber and Smolla 2014) in the R program (R Core Team 2014). An advantage of the dBBMM method is that it accounts for both temporal autocorrelation and variation in trajectories between points (Kranstauber et al. 2012). To fit the dBBMM to vulture movement paths and allow for comparisons across each model, parameters were standardized (window size=47, margin=11, raster=30) with a location error of ±23 m based on the manufacturer’s estimate (Microwave Telemetry, Inc. 2013). To verify location error, I validated vertical and horizontal accuracy of the GSM/GPS transmitters with a series of static tests by placing the units in a range of environmental conditions with simulations of bird behavior, and determined accuracy to be greater than the manufacturer’s estimate (Table 2-1). Thus, I am confident dBBMMs produced with ±23 m location error delineate reliable boundaries of actual space use.

Using R (R Core Team 2014) and ArcMap GIS software (Esri 2012), I quantified monthly core areas and home ranges based on the 50% and 95% isopleths of the utilization distributions (UD), respectively. Shapiro-Wilk tests revealed that home range and core area sizes were not normally distributed; therefore, I log-transformed the data and used unbalanced repeated-measures linear mixed effects models to assess differences in space use across spatial scales. Specifically, at each spatial extent (home range and core area) I developed linear mixed-effects models with unstructured covariance structure using the ‘lme4’ package (Bates et al. 2015) in R (R Core Team 2014). In both mixed effects models, species, sex, and month were included as fixed effects and individual was incorporated as a random effect.

Activity Patterns

For 9 black and 9 turkey vultures, activity patterns were quantified from movement states (transit vs. stationary) ultimately determined after a series of data refinement procedures. Fixes were initially characterized as “transit” or “stationary” by assessing distance traveled between points and with consideration to the visual limitations of black and turkey vultures. For both species, a 2-meter object becomes indiscernible at 1.79 km (Lisney et al. 2013). Assuming that most movements are motivated by the need to search for feeding opportunities, and given that vultures forage on items smaller than 2-meters in size, 1.5 km is a conservative estimate to define distances between potential search areas. Therefore, transitional speeds over 1.5 km/hr (0.42 m/s) were manually characterized as “transit” and all others were characterized as “stationary” with consideration to altitudinal data such that locations were not mischaracterized as “stationary” when vultures were flying/circling at high altitudes. Although top flight speeds for vultures in the southeastern U.S. have not yet been reported, Mandel et al. (2008) observed a top speed for a single turkey vulture of 68 km/hr (18.9 m/s) in a migration study. Therefore, I assumed a reasonable max flight speed of a non-migratory vulture to be 90 km/hr (25 m/s). Locational data with flight speeds >90 km/hr between locations were removed immediately as outliers, as well as any locations without reasonable altitude readings (e.g., “NoFix” and negative altitudes), resulting in the removal of 0.77% of original locations.

My field-based accuracy test of the GSM/GPS transmitters revealed that the units were reliable indicators of activity state, with less than 1% of all locations reported as false movements (Byrne et al., *in prep*). Therefore, remaining fixes with speeds ≥1 knot were then characterized as “transit” and all others “stationary”. However, if the movement state of an individual fix was preceded and followed by a series fixes characterized by the contrasting movement state (i.e., a single “transit” fix in-between “stationary” fixes), the single fix was re-characterized as “solitary”. Fixes characterized as “solitary” were assumed to be false movements and removed from analysis. The proportion of “solitary” fixes (i.e. false movements) was similar for black (n=9, 0.90 ± 0.06%) and turkey vultures (n=9, 1.07 ± 0.07%), and coincided with results from the field-based accuracy test of the GSM/GPS transmitters. Fixes at the end or beginning of a series of “transit” or “stationary” fixes were re-characterized as “switch” states when preceded or followed by a series of fixes in the contrasting state. I used proportions of “switch” states to compare differences in transitions between flight and stationary behaviors by species.

The proportion of locations in transit or stationary states included in subsequent analyses are reported only from the total number of locations unambiguously classified in each state (i.e., excluding “switch” states). Thus, regardless of the number of locations classified as “switch” states, the proportion of “stationary” and “transit” locations summed to 100% for each individual. I used two-sample t-tests to determine whether differences in activity rates existed among species across monthly, seasonal, and annual timescales. Hereafter, “transit” states will be termed as “in flight” or “flying”.

RESULTS

From June 2013 to August 2015, I collected 2,823,627 GPS locations from 26 vultures (13 black and 14 turkey; Table 2-2). After removing birds with partial data and months with migratory movements (see Table 2-3), a total of 321 monthly 95% home ranges and 50% core areas were developed for 9 black vultures and 8 turkey vultures. Post-hoc molecular sex determination of transmittered vultures revealed my sampling included 5 male and 4 female black vultures, and 6 male and 2 female turkey vultures.

The two female turkey vultures (TUVU #03 and TUVU #01) monitored in this study exhibited migratory behaviors in at least one winter (Figure 2-1), despite my attempts to trap only non-migratory individuals. Therefore, analyses to elucidate differences in space use and activity rates between sexes were only possible for black vultures. In addition, home ranges and core areas estimated for these individuals during their winter migration months were excluded from comparisons with space use by resident vultures in this study. TUVU #03 migrated south into Florida during both winters, departing 13 November 2013 and returning 14 March 2014 in the first winter, and departing 15 November 2014 and returning 2 February 2015 in the second winter. The farthest distance travelled during migration for this individual was 757 and 774 km in year 1 and year 2, respectively. TUVU #01, migrated 514 km south into Florida during winter 2013, departing 19 October 2013 and returning 9 February 2014, wherein she remained through end of the study, 31 August 2015. Average maximum speed recorded during migration was 50.24 km/hr (min=43.56 km/hr, max=56.11 km/hr).

Monthly 95% Home Ranges and 50% Core Area Sizes

Monthly home ranges for turkey vultures (60.94 ± 4.24 km^2) were significantly larger than those of black vultures (30.51 ± 2.57 km^2; $F_{1,319}$=9.1646, *P*=0.008; Figure 2-3), although I found no difference between core area sizes of turkey vultures (0.424 ± 0.027 km^2) and black vultures (0.45 ± 0.062 km^2; $F_{1,319}=2.3198$, $P=0.1485$; Figure 2-4). Monthly space use by black vultures differed significantly over the course of the annual cycle for both home ranges ($F_{11,150}=5.4214$, $P<0.001$; Figure 2-3) and core areas ($F_{11,150}=6.385$, $P<0.001$; Figure 2-4). For turkey vultures, differences in monthly space use within the annual cycle was evident only for core area sizes ($F_{11,167}=7.607$, $P<0.001$; Figure 2-4) but not home ranges ($F_{11,167}=0.976$, $P=0.469$; Figure 2-3). Finally, although average monthly home ranges and core areas were notably larger for female black vultures than those of males in March-May, differences were not statistically significant across the annual cycle for either monthly home ranges ($F_{1,167}=0.523$, $P=0.493$; Figure 2-5) or core areas ($F_{1,167}=0.111$, $P=0.749$; Figure 2-6). I also found no evidence for an interactive effect of month and sex for black vulture monthly home ranges ($F_{1,167}=1.205$, $P=0.291$), however a significant interactive effect of month and sex existed for core areas ($F_{1,167}=2.5095$, $P=0.007$).

Activity Rates

Turkey vultures switched between stationary and movement states (7.35 ± 0.29%) significantly more than black vultures (4.46 ± 0.24%; $P<0.001$; Figure 2-6). Additionally, turkey vultures spent significantly more time in flight than black vultures across months ($F_{1,340}=13.48$, $P=0.002$; Figure 2-7), seasons ($F_{1,82}=12.25$, $P=0.004$; Figure 2-8), and years ($F_{1,82}=12.715$, $P=0.005$; Figure 2-9). Average monthly proportion of time spent in flight was 52.1 ± 1% for turkey vultures and 33.9 ± 1.7% for black vultures. Average seasonal proportion of time spent in flight was 51.2 ± 1.7% for turkey vultures and 34.6 ± 2.8% for black vultures. Average annual proportion of time spent in flight was 53.4 ± 1.8% for turkey vultures and 36.6 ± 5.1% for black vultures.

DISCUSSION

This study strengthens inferences on the spatial ecology of black and turkey vultures by providing information on the movement behavior of these species at a finer spatio-temporal resolution than any previous study to date. Although both species are obligate scavengers with substantial range overlap, my results reveal that substantive differences in home range size and movement behavior exist between these species. These data undoubtedly reflect differences in physiology, behavior, and social structure and thus represent underlying mechanisms of niche differentiation between species.

Comparisons of Home Ranges and Core Area Sizes

When compared with estimations of space use in prior studies, my results (derived from finer sampling frequencies than previous studies) agree with prior observations that turkey vulture home ranges are larger than those of black vultures, and as expected, mean monthly home ranges of turkey vultures were indeed larger than those of black vultures across nearly all months. Prior estimations using the dBBMM to quantify space use by these species on the coast of South Carolina found black vulture space use (50% UD: 38 ± 12 km^2; 95% UD: 467 ± 183 km^2) to be six times smaller than that observed for turkey vultures (50% UD: 227 ± 104 km^2; 95% UD: 2,854 ± 990 km^2; Fisher et al. 2014), but an earlier study of black and turkey vulture home ranges based on VHF telemetry and using fixed-kernel density (KDE) to quantify space use at the Savannah River Site found mean turkey vulture home ranges to be only twice the size of black vulture home ranges (DeVault et al. 2004). My results similarly show turkey vulture home ranges to be only about twice the size of home ranges of black vultures but only during the months of June through December, as similar home range sizes were observed throughout the rest of the year (January-May).

DeVault et al. (2004) previously reported home range sizes that were nearly four (95% UD: 124 ± 51.2 km^2) and six (95% UD: 340.5 ± 85.7 km^2) times larger, and core areas nearly 50 (50% UD: 20.3 ± 3.3 km^2) and 90 (50% UD: 41.6 ± 13 km^2) times larger for black and turkey vultures, respectively, than I observed in my study. Furthermore, core areas sizes differed significantly between black and turkey vultures previously (DeVault et al. 2004), whereas I surprisingly found no significant difference between core area sizes of black and turkey vultures over the course of the year. Furthermore, in contrast to my expectation, turkey vulture home ranges did not vary over the annual cycle. This lack of variation in turkey vulture home range sizes may reflect the reliability of large (i.e., wild pig) carrion available throughout the Savannah River Site during all months of the year. Wild pig populations have increased on the Savannah River Site over the last several years and management efforts to control wild their abundance have resulted in a steady supply of carcasses distributed throughout the landscape that may be supplementing vulture populations with relatively reliable foraging opportunities (Beasley et al. 2013). However, accuracy of space use estimations increase with sampling frequency and this study includes significantly more locations than DeVault et al. (2004) owing to differences in tracking technologies used. Therefore, differences in estimates of space use may simply be due to differences in sampling frequency as well as home range estimation between methods.

Although I was not able to verify breeding status for each vulture in this study, all were adults presumably capable of breeding, and thus potentially influenced by breeding phenology during the months of February through June. If space use is influenced by centralized movements around nest locations, then I did not see evidence for this in my sampled population. Rather, mean monthly core areas and home ranges of black vultures actually increased during the breeding months versus months throughout the rest of the year. Similarly, turkey vulture core areas increased significantly during the breeding season. These increases in space use during the breeding season months were in contrast to my expectations and likely suggest individuals were roaming more widely, potentially in search of mates and/or nest locations. Black and turkey vultures are both known to participate in follow-flights or courtship flights (Kirk and Mossman 1998, Buckley 1999). Although my study did not address population dynamics, of the roughly 300 vultures marked for this study, only three (~1%) were recaptured and only a small number of tagged vultures were recorded by remote cameras placed over carrion bait as part of additional studies conducted during the time of my research. It may be possible that the vulture population in the southeastern United States is so abundant that competition for nest sites in high-quality areas is exceptionally high, making it difficult for sexually-mature vultures to establish and maintain successful nesting sites from among limited options. Interestingly, only one black vulture (BLVU #22) in this study appeared to possibly have a nest, which was in the same abandoned building in both years of the study, although this could not be confirmed and was based on centralized locations during months of the breeding seasons.

Comparisons of space use between male and female vultures were only possible for black vultures in this study due to low numbers of monitored female turkey vultures. Female black vultures generally had larger home ranges than male black vultures in March and April, and although these differences were not significant, these months coincide with chick-hatching dates and may be associated with an increase in energetic requirements following egg production by females. Otherwise, body sizes of male and female black and turkey vultures do not differ (Kirk and Mossman 1998, Buckley 1999), thus, their energetic requirements may be similar, and these results support my original hypothesis as well as prior understandings of space use by sexually monomorphic species (Kirk and Mossman 1998, Buckley 1999). However, larger sample sizes may reveal differences in male and female space use during the breeding seasons due to increased energetic demands by females associated with egg-production.

Comparisons of Monthly, Seasonal, and Annual Activity Patterns

Similar to prior studies of vulture activity patterns (Coleman and Fraser 1989, DeVault et al. 2004), and in accordance with my expectation, my results suggest that turkey vultures spend significantly more time in flight than black vultures across all temporal scales measured (monthly, seasonally, and annually). Higher activity patterns in turkey vultures are to be expected considering the amount of searching required by their solitary foraging strategy of detecting carcasses by scent (Kirk and Mossman 1998). Similarly, reduced activity patterns in black vultures would be expected as they spend substantial time in communal roosts for information-exchange, increasing foraging efficiency by following other vultures to carrion sites (Buckley 1997). Among turkey vultures, individuals were more active in the breeding season than the summer and winter seasons, and they transitioned between flight/movement and stationary states (roosting, foraging, and resting) more frequently than black vultures. Because black vultures are highly social and forage in groups, their movements may be more deliberate than those of turkey vultures. Group foraging provides benefits by “safety through numbers” as vigilance is shared among multiple members within the group. It is less likely that an entire group of black vultures will be flushed from an area than a solitary turkey vulture which is at greater risk for predation. Therefore, the higher proportion of “switch” state behaviors exhibited by turkey vultures may reveal their movements to be hastier and individuals are more reactive to disturbances at solitary roosts or forage sites than black vultures.

In conclusion, results of this study show that black and turkey vultures exhibit immense variability in space use and activity rates vary across the annual cycle. Evaluations based on broader-scale sampling regimes may fail to identify important patterns evidencing distinctions, and at these finer scales, this study reveals interesting and informative details regarding distinctions in space use and activity patterns by these sympatric species. Quantification of space use by black and turkey vultures through the development of monthly home range and core areas with the dBBMM provides a vital component for habitat selection analyses.

Table 2-1. Mean positional error (m) of GPS locations collected by 3 Microwave Telemetry solar-powered GPS/GSM avian transmitters in the horizontal and vertical dimensions across three test treatments; 1: transmitters on ground under open canopy, 2: transmitters on ground under forest canopy, and 3: transmitters suspended 11 m off the ground under open canopy. Number of GPS locations for each treatment=672.

	Mean Error (SD)	
Treatment	**Horizontal**	**Vertical**
1	5.5 (3.5)	7.4 (13.3)
2	12.4 (11.8)	12.6 (12.2)
3	8.1 (6.3)	8.9 (10.4)

Table 2-2. Number of locations received and range of dates over which GPS transmitters were carried for each adult vulture. Species: BLVU=black vulture (*Coragyps atratus*), TUVU=turkey vulture (*Cathartes aura*); ID: patagial tag identification number; Sex: F=female, M=male, U=unknown. Transmitter Deployment Start/End Date/Time: year/month/day hour:minute:second, Greenwich Mean Time (GMT).

					Transmitter Deployment Date/Time		
Species	**ID**	**Sex**	**No. Locations**	**Analysis Inclusion**	**Start**	**End**	**Status**
TUVU	00	Unk	225	N	2013/06/13 12:19:53	2013/07/10 17:43:38	Transmission ceased; fate of bird unknown
TUVU	01	F	257,753	Y	2013/06/26 14:00:42	2015/09/01 04:28:52	Active at end of study.
TUVU	02	U	143	N	2013/06/17 11:34:53	2013/06/17 17:00:01	Transmission ceased; fate of bird unknown
TUVU	03	F	258,859	Y	2013/06/26 14:32:23	2015/09/01 04:52:35	Active at end of study.
BLVU	04	Unk	0	N	2013/06/17 00:00:00	2013/06/17 00:00:00	Transmission ceased; fate of bird unknown
TUVU	06	M	215,442	Y	2013/06/17 13:15:54	2015/08/27 16:32:17	Active at end of study.
BLVU	08	M	102,537	Y	2013/06/18 18:07:12	2014/06/18 22:02:41	Transmission ceased; fate of bird unknown
TUVU	10	Unk	280	N	2013/06/18 18:18:17	2013/06/19 18:56:52	Transmitter dropped, redeployed onto new bird; fate of bird unknown
BLVU	12	M	178,571	Y	2013/06/20 11:38:11	2015/09/01 04:52:41	Active at end of study.
TUVU	13	F	41,625	Y	2013/06/27 13:24:20	2013/12/21 15:16:23	Transmission ceased; fate of bird unknown
TUVU	19	Unk	268	N	2013/06/27 13:30:56	2013/06/27 23:58:53	Transmitter dropped, redeployed onto new bird; fate of bird unknown
BLVU	22	F	121,498	Y	2013/06/20 12:34:26	2015/09/01 03:07:07	Deceased
BLVU	44	Unk	8,489	N	2013/07/03 12:57:26	2013/08/26 23:27:53	Transmitter dropped, redeployed onto new bird; fate of bird unknown
BLVU	46	Unk	20,560	N	2013/07/03 13:32:20	2013/09/21 12:51:13	Transmitter dropped, redeployed onto new bird; fate of bird unknown
BLVU	47	F	121,046	Y	2013/07/03 13:37:33	2015/09/01 04:31:54	Active at end of study.

Species	ID	Sex	No. Locations	Analysis Inclusion	Transmitter Deployment Date/Time		Status
					Start	End	
BLVU	48	M	96,043	Y	2013/07/03 13:44:23	2014/09/22 16:37:22	Transmitter dropped, redeployed onto new bird; fate of bird unknown
BLVU	57	F	31,931	Y	2013/07/05 11:32:24	2014/03/21 19:47:00	Dead, shot; redeployed onto new bird
TUVU	60	M	225,904	Y	2013/07/05 12:46:25	2015/09/01 04:58:46	Active at end of study.
BLVU	65	Unk	2,833	N	2013/07/08 12:16:11	2013/07/25 23:57:55	Dead, unknown cause; redeployed onto new bird
TUVU	75	M	201,902	Y	2013/07/09 15:29:50	2015/09/01 04:46:12	Active at end of study.
TUVU	76	Unk	25	N	2013/07/09 18:58:34	2013/07/10 20:48:07	Transmitter dropped, redeployed onto new bird; fate of bird unknown
TUVU	90	M	185,527	Y	2013/07/30 14:03:23	2015/09/01 02:56:53	Active at end of study.
TUVU	91	M	202,737	Y	2013/07/31 15:46:32	2015/09/01 04:55:41	Active at end of study.
BLVU	92	F	181,466	Y	2013/08/02 12:47:23	2015/09/01 04:21:36	Active at end of study.
BLVU	108	M	91,654	Y	2014/04/21 17:58:09	2015/09/01 04:20:15	Active at end of study.
TUVU	123	M	147,388	Y	2014/04/23 19:43:13	2015/09/01 04:48:56	Active at end of study.
BLVU	126	M	128,921	Y	2014/05/01 13:00:53	2015/09/01 04:54:57	Active at end of study.

Table 2-3. Individual vultures included in monthly space use and activity pattern analyses. Grey fields indicate inclusion in analyses; crossed grey fields indicate exclusion from space use analysis due to migratory movements for that month; white fields indicate exclusion due to partial data for that month; black fields indicate no data and thus exclusion from space use analysis. BLVU=black vulture (*Coragyps atratus*), TUVU=turkey vulture (*Cathartes aura*). ID: Patagial tag identification number. Sex: F=female, M=male. Year 1=1 September 2013 – 31 August 2014; Year 2=1 September 2014 – 31 August 2015.

			Year 1												Year 2											
Species	ID	Sex	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
TUVU	01	F	▒	☒	☒	☒	☒	☒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
TUVU	03	F	▒	▒	☒	☒	☒	☒	☒	▒	▒	▒	▒	▒	▒	▒	☒	☒	☒	☒	▒	▒	▒	▒	▒	▒
TUVU	06	M	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
TUVU	13	F	▒	▒	▒	□	□	□	□	□	□	□	□	□	□	□	□	□	□	□	□	□	□	□	□	□
TUVU	60	M	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	■	▒	▒	▒
TUVU	75	M	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	■	▒	▒
TUVU	90	M	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
TUVU	91	M	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
TUVU	123	M	□	□	□	□	□	□	□	□	□	▒	▒	■	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
BLVU	08	M	▒	▒	▒	▒	▒	▒	▒	▒	▒	□	□	□	□	□	□	□	□	□	□	□	□	□	□	□
BLVU	12	M	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
BLVU	22	F	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	■	▒
BLVU	47	F	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
BLVU	48	M	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	□	□	□	□	□	□	□	□	□	□	□	□
BLVU	57	F	▒	▒	▒	▒	▒	▒	□	□	□	□	□	□	□	□	□	□	□	□	□	□	□	□	□	□
BLVU	92	F	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
BLVU	108	M	□	□	□	□	□	□	□	□	□	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
BLVU	126	M	□	□	□	□	□	□	□	□	□	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒

Table 2-4. Individual vultures included in seasonal activity pattern analyses. Grey fields indicate inclusion in analyses; white fields indicate exclusion due to partial data for that month. BLVU=black vulture (*Coragyps atratus*), TUVU=turkey vulture (*Cathartes aura*). ID: Patagial tag identification number. Sex: F=female, M=male. Year 1=16 August 2013 00:00:00 EST – 9 June 2014 07:59:59 EST; Year 2=9 June 2014 08:00:00 EST – 9 June 2015 07:59:59 EST.

			Year 1			Year 2		
Species	ID	Sex	Summer	Winter	Breeding	Summer	Winter	Breeding
TUVU	01	F	▨	▨	▨	▨	▨	▨
TUVU	03	F	▨	▨	▨	▨	▨	▨
TUVU	06	M	▨	▨	▨	▨	▨	▨
TUVU	13	F	▨					
TUVU	60	M	▨	▨	▨	▨	▨	▨
TUVU	75	M	▨	▨	▨	▨	▨	▨
TUVU	90	M	▨	▨	▨	▨	▨	▨
TUVU	91	M	▨	▨	▨	▨	▨	▨
TUVU	123	M				▨	▨	▨
BLVU	08	M	▨	▨	▨			
BLVU	12	M	▨	▨	▨	▨	▨	▨
BLVU	22	F	▨	▨	▨	▨	▨	▨
BLVU	47	F	▨	▨	▨	▨	▨	▨
BLVU	48	M	▨	▨	▨			
BLVU	57	F	▨	▨				
BLVU	92	F	▨	▨	▨	▨	▨	▨
BLVU	108	M				▨	▨	▨
BLVU	126	M				▨	▨	▨

Table 2-5. Individual vultures included in annual activity pattern analyses. Grey fields indicate inclusion in analyses; white fields indicate exclusion due to partial data for that month. BLVU=black vulture (*Coragyps atratus*), TUVU=turkey vulture (*Cathartes aura*). ID: Patagial tag identification number. Sex: F=female, M=male. Year 1=1 September 2013 – 31 August 2014; Year 2=1 September 2014 – 31 August 2015.

Species	ID	Sex	Year 1	Year 2
TUVU	01	F	▨	▨
TUVU	03	F	▨	▨
TUVU	06	M	▨	▨
TUVU	13	F		
TUVU	60	M	▨	▨
TUVU	75	M	▨	▨
TUVU	90	M	▨	▨
TUVU	91	M	▨	▨
TUVU	123	M		▨
BLVU	08	M	▨	
BLVU	12	M	▨	▨
BLVU	22	F	▨	▨
BLVU	47	F	▨	▨
BLVU	48	M	▨	
BLVU	57	F		
BLVU	92	F	▨	▨
BLVU	108	M		▨
BLVU	126	M		▨

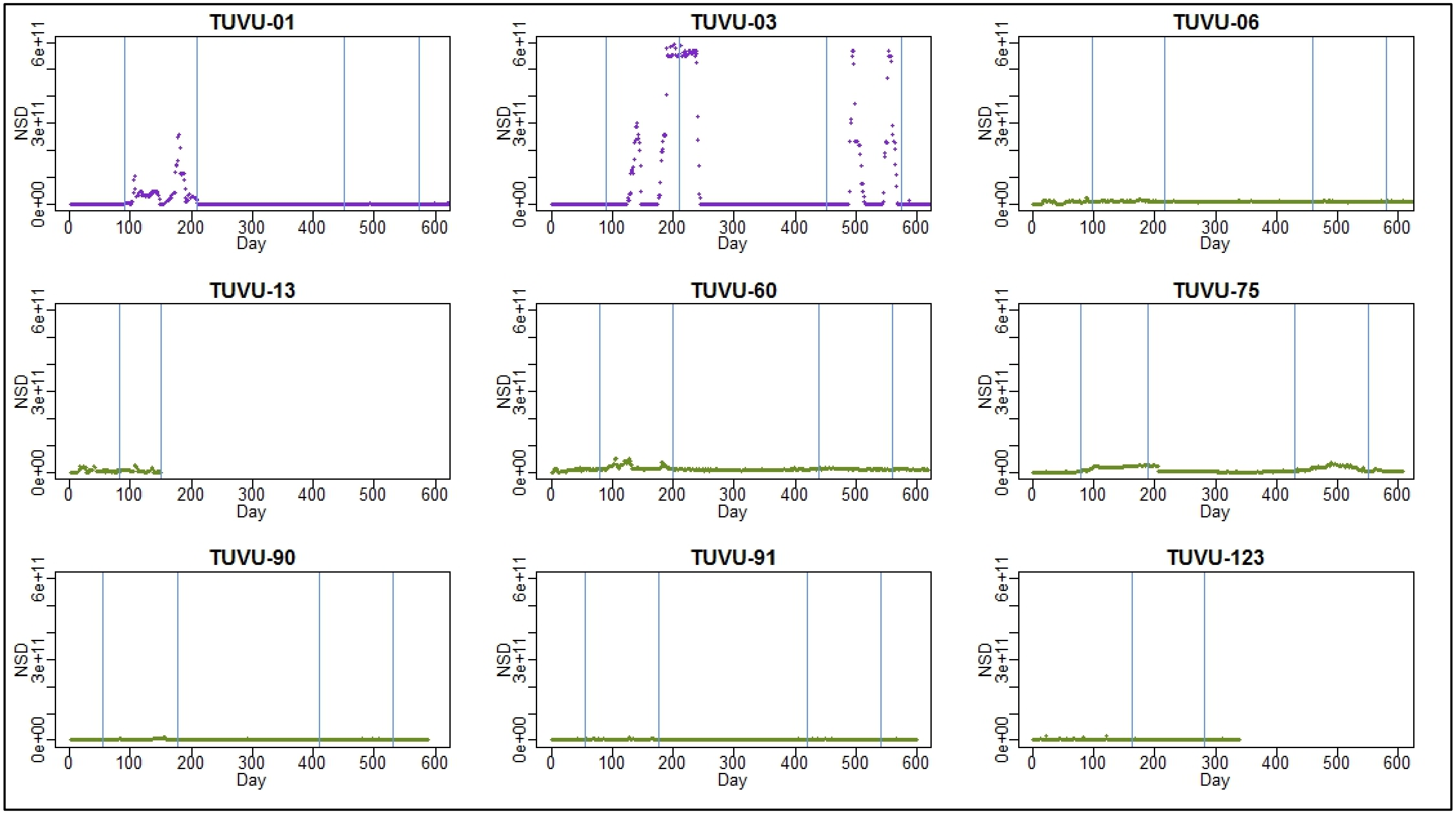

Figure 2-1. Net-squared displacement from evening roost locations for 2 female (purple) and 7 male (olive) turkey vultures (TUVU; *Cathartes aura*) derived from GPS location data from 16 August 2013 – 9 June 2015. TUVU-ID#=Patagial tag identification number. Migratory movements shown by elevated peaks within winter seasons (7 October – 8 February) bounded by blue-grey boxes. Migratory movements evident for 2 female turkey vultures: TUVU-01 and TUVU-03.

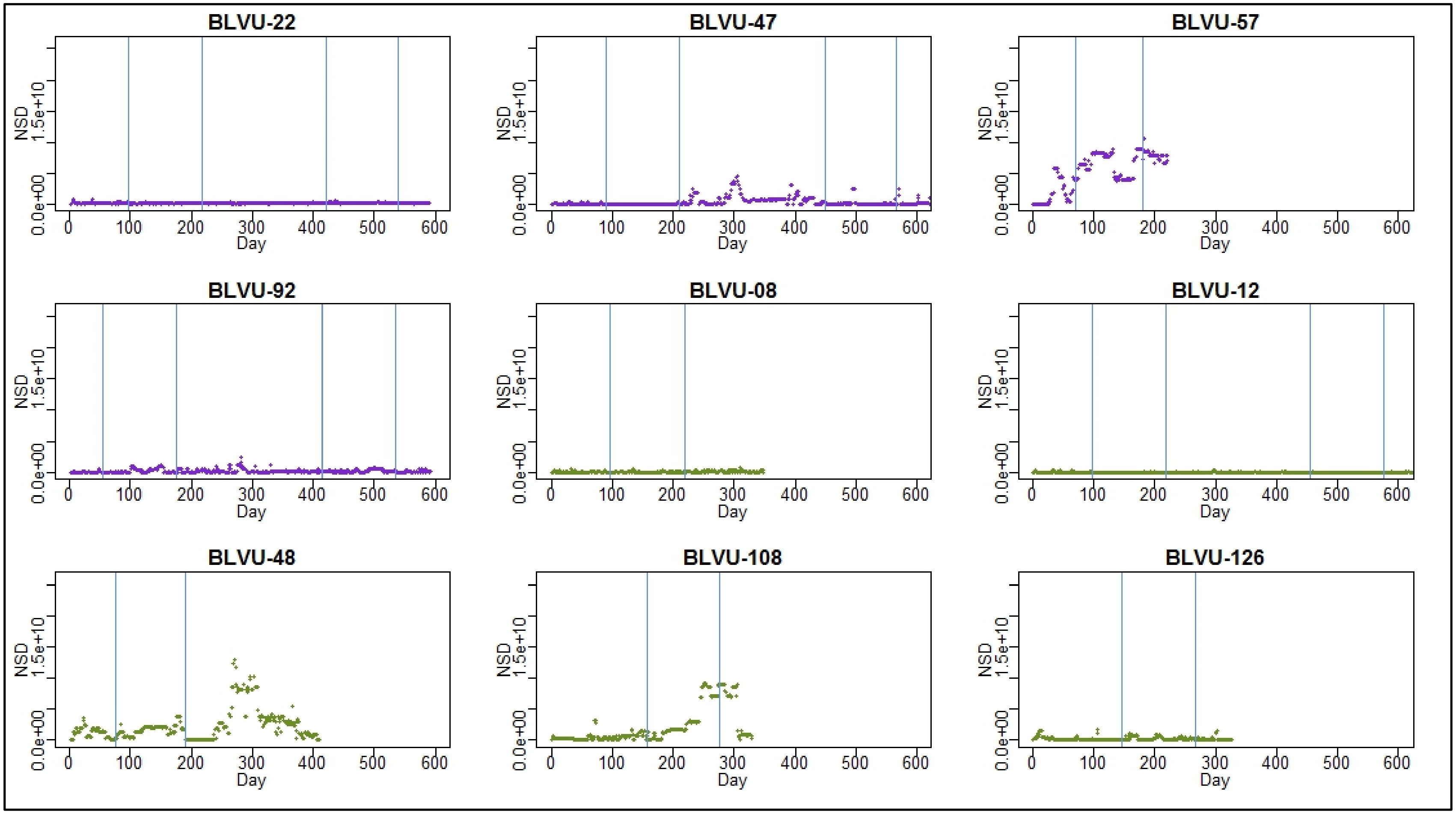

Figure 2-2. Net-squared displacement from evening roost locations for 4 female (purple) and 5 male (olive) black vultures (BLVU; *Coragyps atratus*) derived from GPS location data from 16 August 2013 – 9 June 2015. BLVU-ID#=Patagial tag identification number. Migratory movements would be shown by elevated peaks within winter seasons (7 October – 8 February) bounded by blue-gray boxes. No migratory movements evident for black vultures in this analysis.

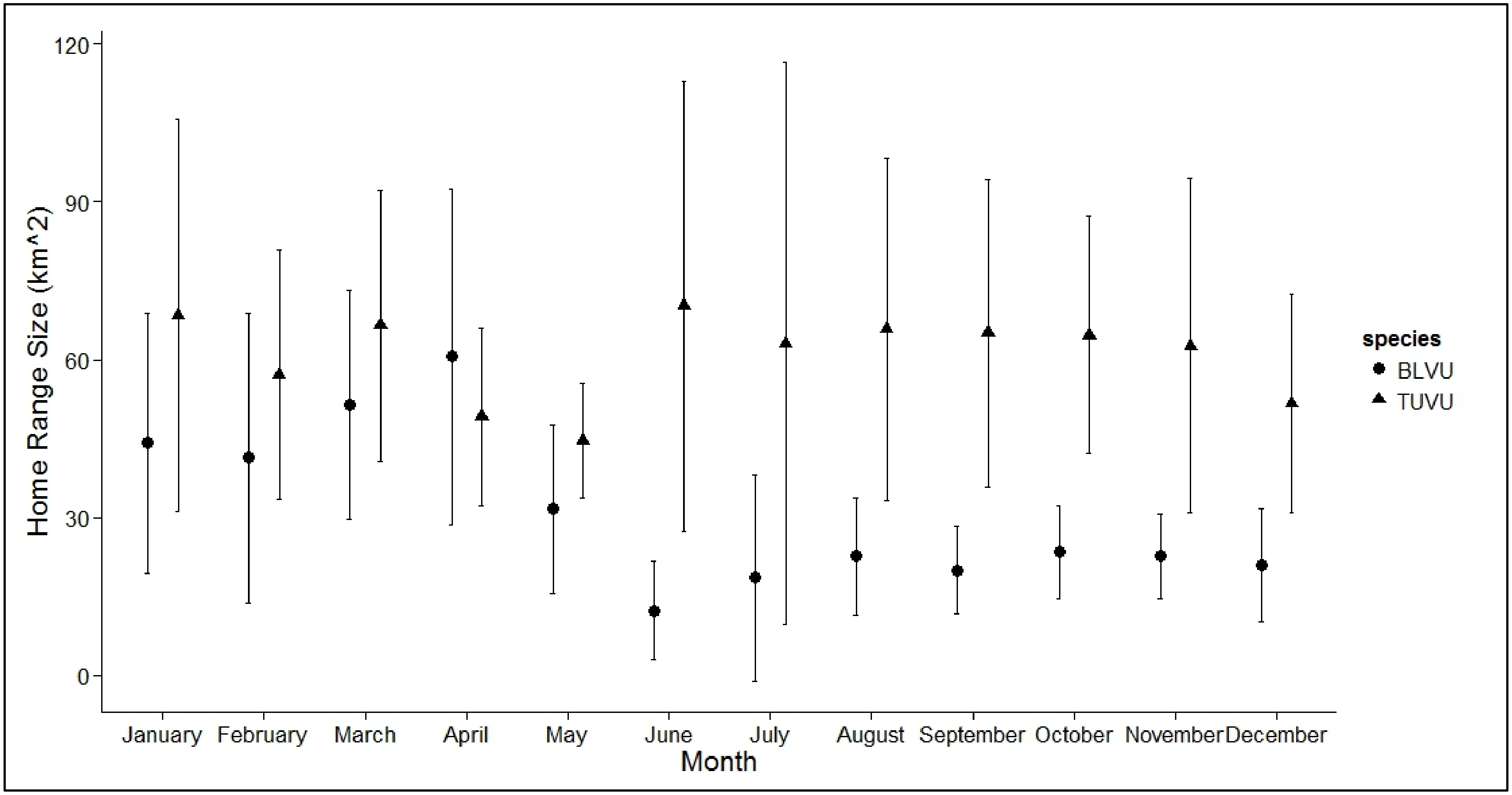

Figure 2-3. Median (±95% CIs) monthly 95% home range sizes (km^2) for 9 black (*Coragyps atratus*; total locations=804,470; mean locations/month=8,429, max=14,391, min=895) and 9 turkey (*Cathartes aura*; total locations=1,372,194; mean locations/month=9,026, max=16,566, min=531) vultures calculated from GPS locations collected 1 September 2013 - 31 August 2015. BLVU=black vulture; TUVU=turkey vulture. Home ranges developed using the dynamic Brownian Bridge Movement Model.

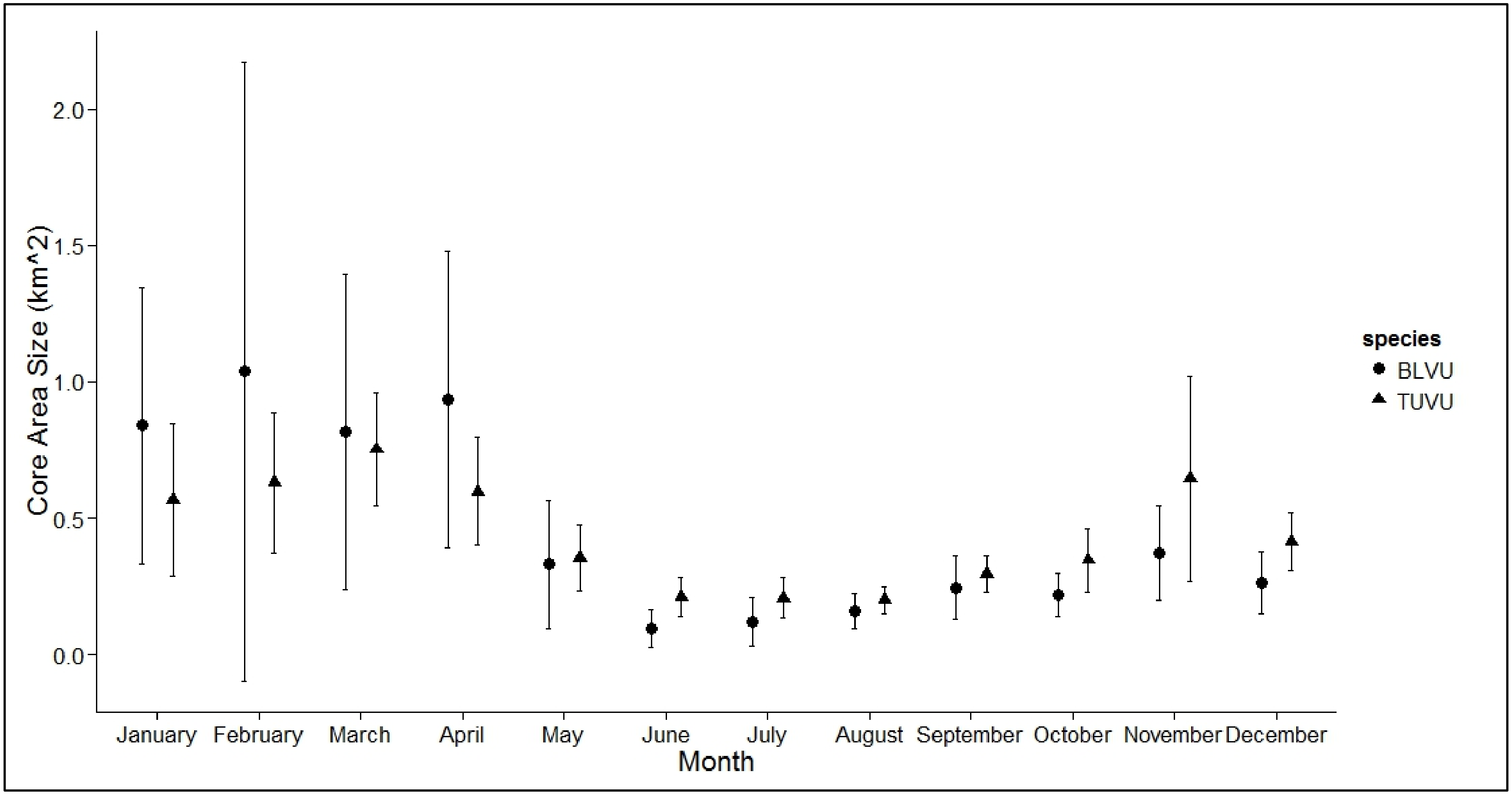

Figure 2-4. Mean (±95% CIs) monthly 50% core area sizes (km^2) for 9 black (*Coragyps atratus*; total locations=804,470; mean locations/month=8,429, max=14,391, min=895) and 9 turkey (*Cathartes aura*; total locations=1,372,194; mean locations/month=9,026, max=16,566, min=531) vultures calculated from GPS locations collected 1 September 2013 - 31 August 2015. BLVU=black vulture; TUVU=turkey vulture. Core areas developed using the dynamic Brownian Bridge Movement Model.

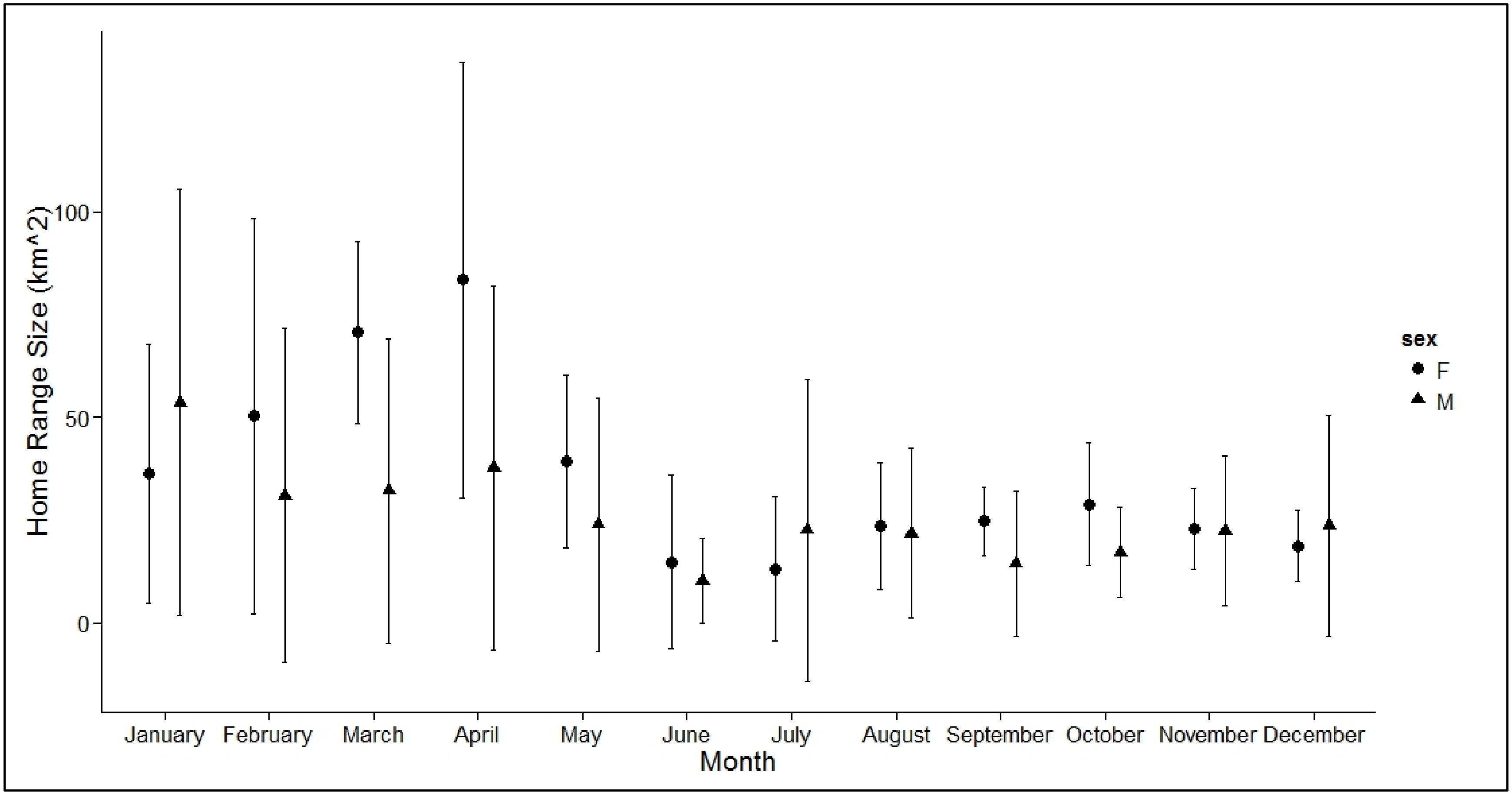

Figure 2-5. Mean (±95% CIs) monthly 95% home range sizes (km^2) for 5 male (total locations=437,629; mean locations/month=8,429, max=14,391, min=3,164) and 4 female (total locations=363,210; mean locations/month=7,753, max=13,340, min=895) resident black vultures (*Coragyps atratus*) calculated from GPS locations collected 1 September 2013 - 31 August 2015. Home ranges developed using the dynamic Brownian Bridge Movement Model.

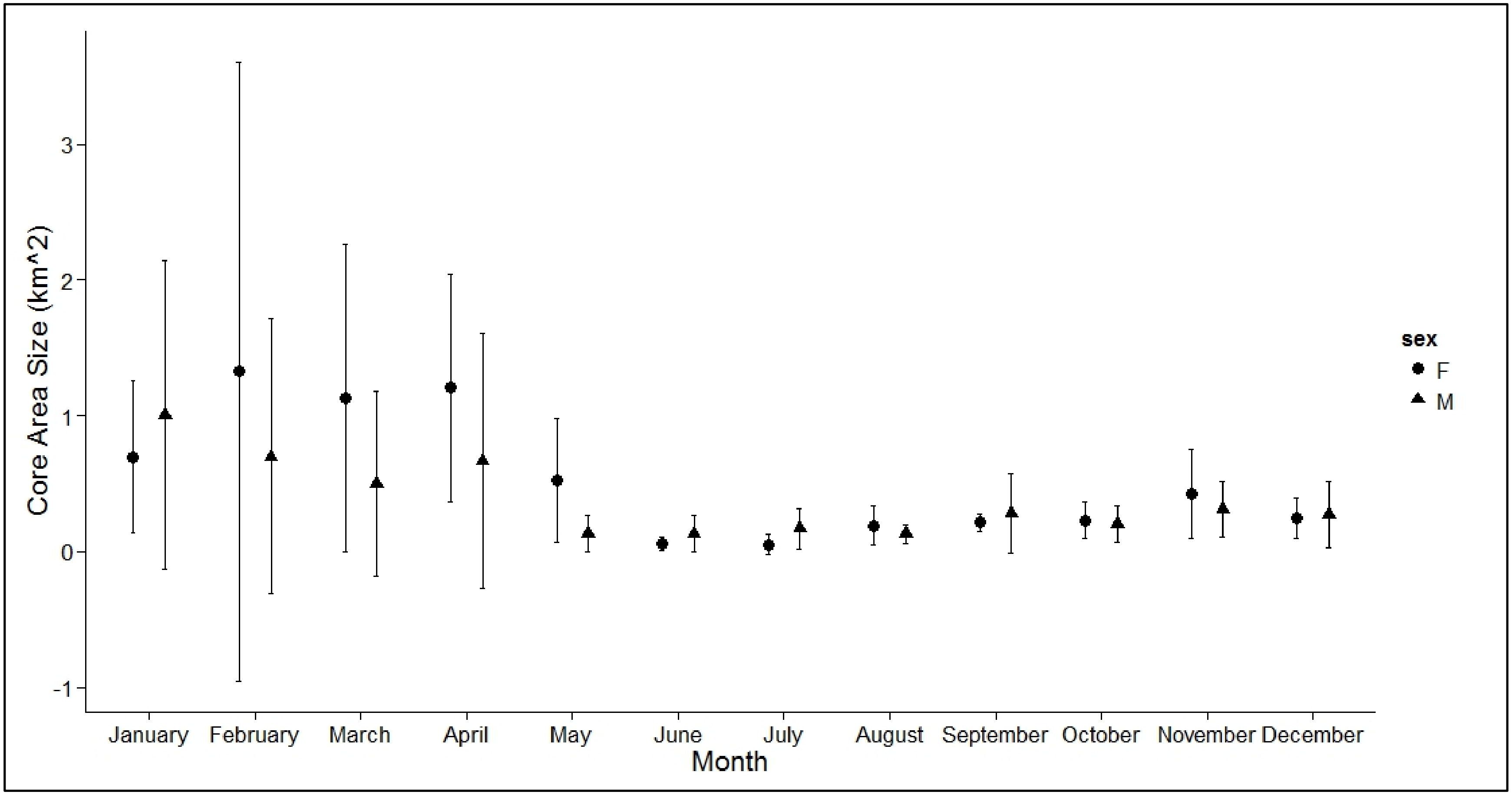

Figure 2-6. Mean (±95% CIs) monthly 50% core area sizes (km^2) for 5 male (total locations=437,629; mean locations/month=8,429, max=14,391, min=3,164) and 4 female (total locations=363,210; mean locations/month=7,753, max=13,340, min=895) resident black vultures (*Coragyps atratus*) calculated from GPS locations collected 1 September 2013 - 31 August 2015. Core areas developed using the dynamic Brownian Bridge Movement Model.

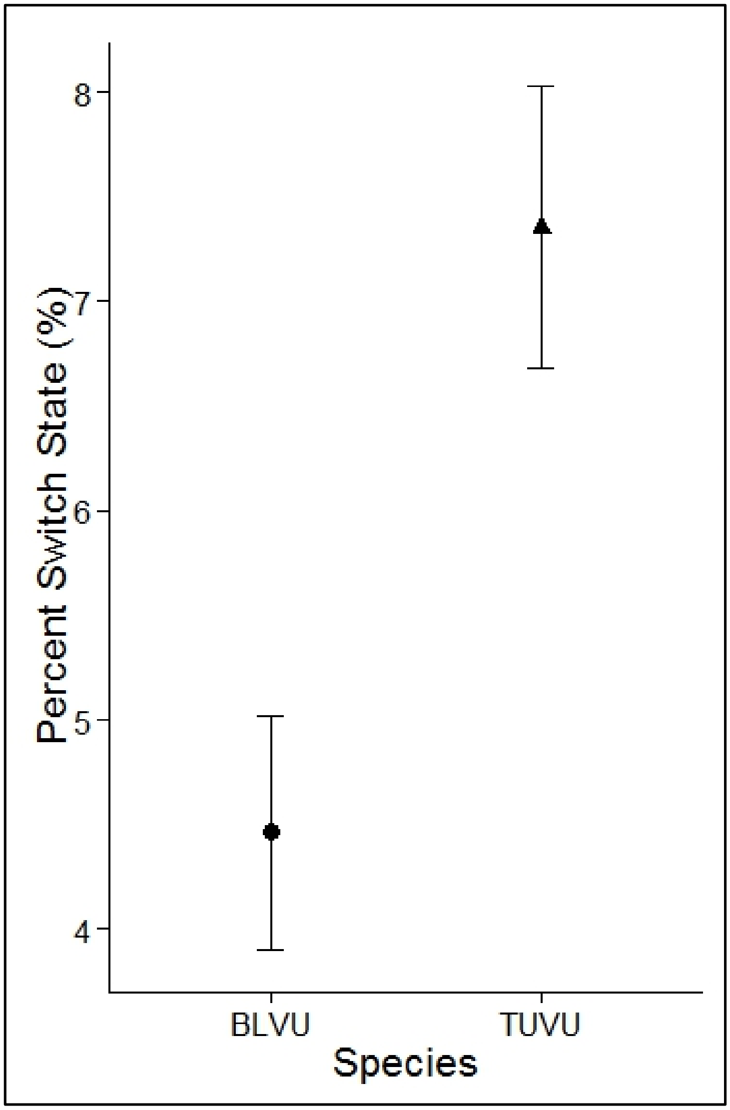

Figure 2-7. Mean (±95% CIs) proportion of switch (i.e., transitions between movement and stationary) state locations from among GPS locations collected for 9 black (*Coragyps atratus*; total locations=990,289; mean=110,032; max=171,932; min=29,808) and 9 turkey (*Cathartes aura*; total locations=1,595,225; mean=177,247; max=241,187; min=38,694) vultures from 1 September 2013 to 31 August 2015. BLVU=black vulture; TUVU=turkey vulture.

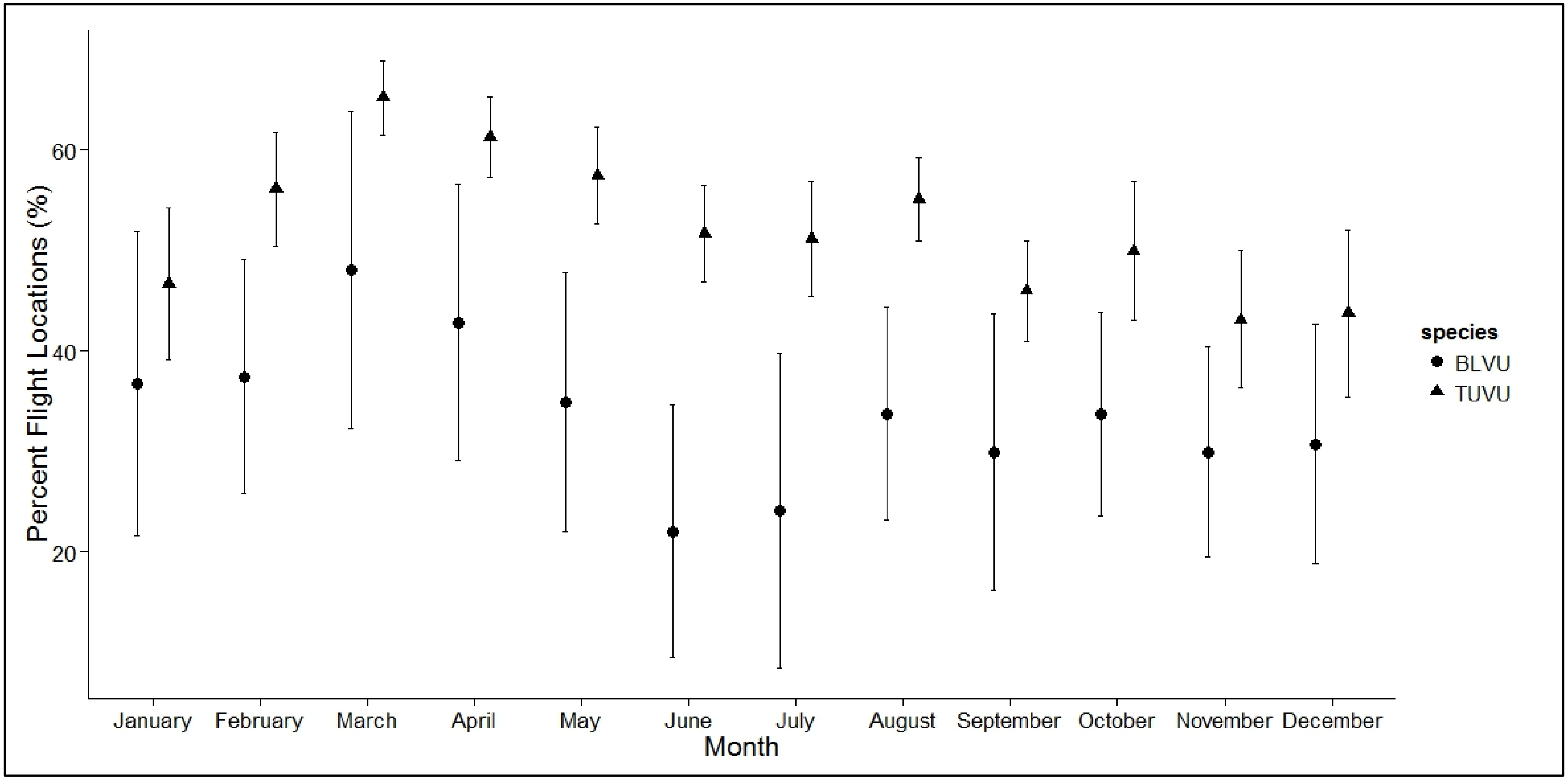

Figure 2-8. Mean (±95% CIs) proportion of locations characterized as transit (i.e., flight) state by month from among GPS locations collected for 9 black (*Coragyps atratus*; total locations=990,289; mean=110,032; max=171,932; min=29,808) and 9 turkey (*Cathartes aura*; total locations=1,595,225; mean=177,247; max=241,187; min=38,694) vultures from 1 September 2013 to 31 August 2015. BLVU=black vulture; TUVU=turkey vulture.

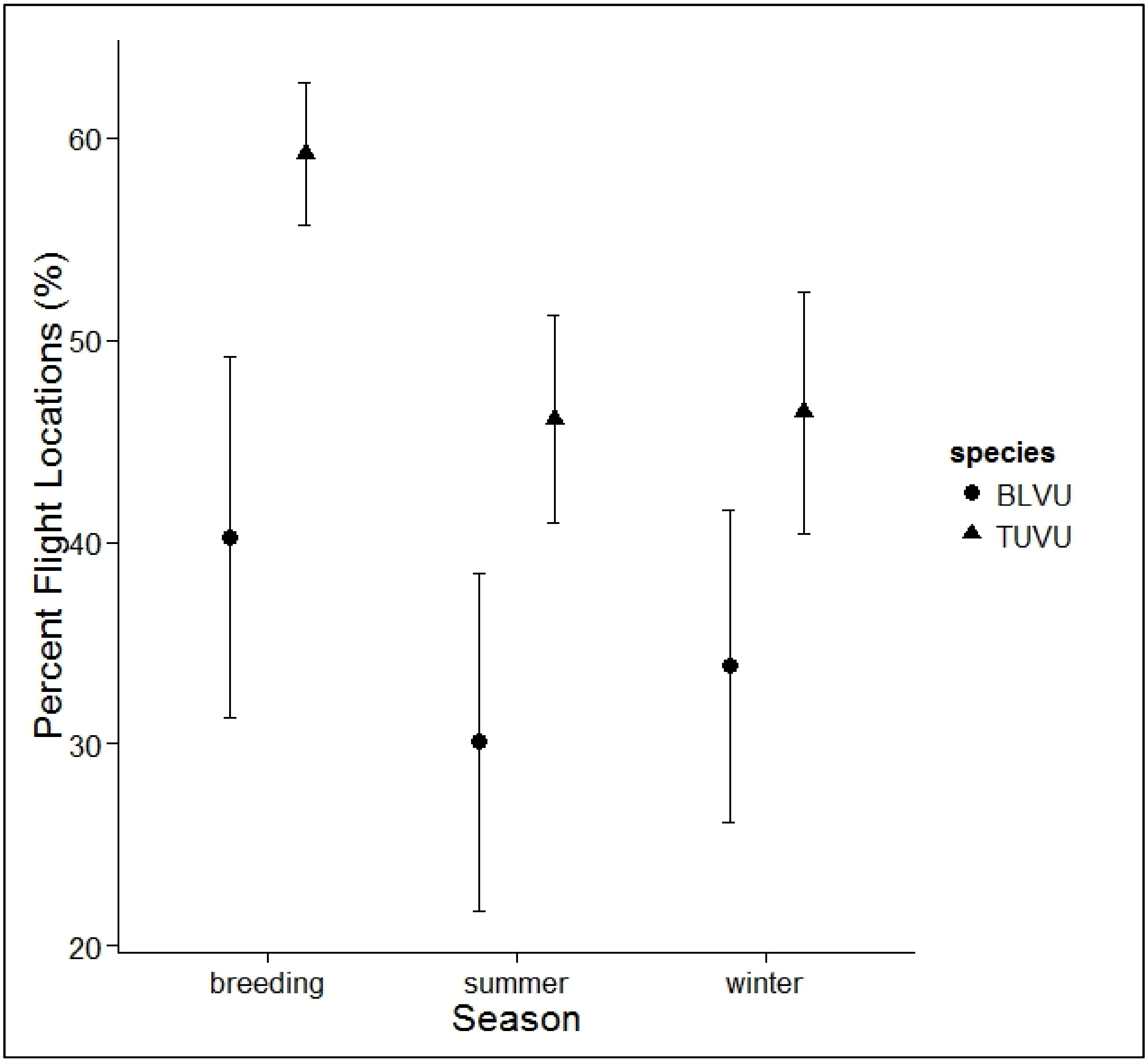

Figure 2-9. Mean (±95% CIs) proportion of locations characterized as transit (i.e., flight) state by season from among GPS locations collected for 9 black (*Coragyps atratus*; total locations=990,289; mean=110,032; max=171,932; min=29,808) and 9 turkey (*Cathartes aura*; total locations=1,595,225; mean=177,247; max=241,187; min=38,694) vultures from 1 September 2013 to 31 August 2015. BLVU=black vulture; TUVU=turkey vulture.

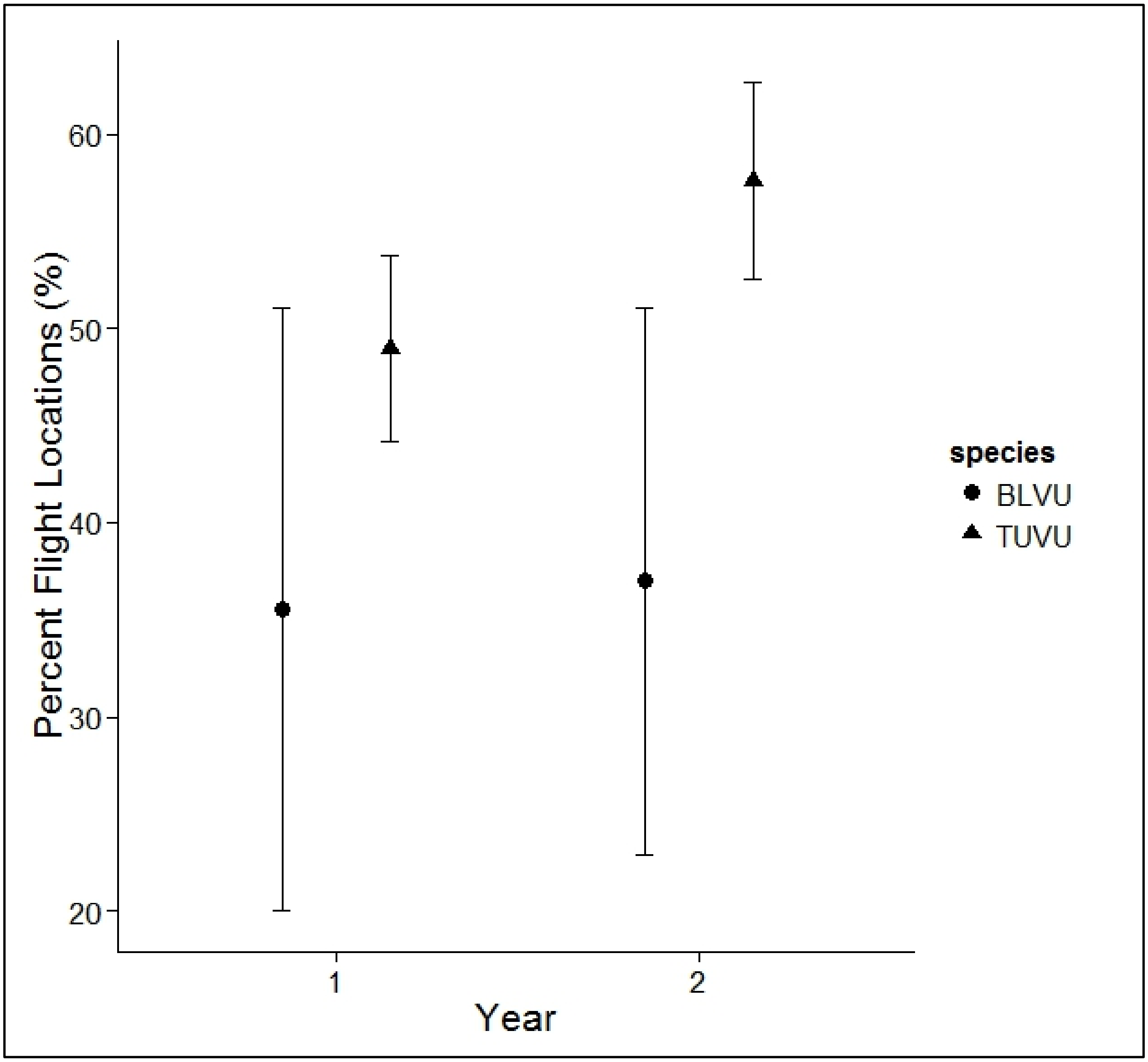

Figure 2-10. Mean (±95% CIs) proportion of locations characterized as transit (i.e., flight) state by year from among GPS locations collected for 9 black (*Coragyps atratus*; total locations=990,289; mean=110,032; max=171,932; min=29,808) and 9 turkey (*Cathartes aura*; total locations=1,595,225; mean=177,247; max=241,187; min=38,694) vultures from 1 September 2013 to 31 August 2015. BLVU=black vulture; TUVU=turkey vulture.

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CHAPTER 3

CHARACTERISTICS OF RESOURCE SELECTION FOR BLACK AND TURKEY VULTURES IN THE SOUTHEASTERN UNITED STATES[2]

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[2] Holland, A. E., M. E. Byrne, J. Hepinstall-Cymerman, A. L. Bryan, T. L. DeVault, O.E. Rhodes, and J. C. Beasley. To be submitted to *Landscape Ecology*.

ABSTRACT

As obligate scavengers utilizing similar habitats, interspecific competition undoubtedly occurs over the annual cycle between resident black (*Coragyps atratus*) and turkey (*Cathartes aura)* vultures. In the interest of exploring how sympatric species coexist through habitat segregation, I examined resource selection of resident vultures in the southeastern United States for evidence of niche differentiation. Using fine-scale movement data, I assessed characteristics of habitats associated with roost sites, roost reuse frequency and roost site fidelity, and aspects of resource selection based on utilization distributions of 9 black and 9 turkey vultures tracked from September 2013 to August 2015 using GSM/GPS transmitters. Specifically, using > 2.8 million GPS locations, I assessed seasonal selection of evening roost site habitat attributes, quantified monthly, seasonal, and annual differences in the roost reuse frequency and roost site fidelity of black and turkey vultures, and elucidated differences in monthly resource selection with consideration to species and sex at multiple temporal scales. Results of these analyses revealed interspecific differences in habitats associated with evening roost sites as turkey vulture roosts comprised a significantly greater proportion of forest habitat, and black vulture roosts were associated with areas with greater proportions of developed/urban habitat. Roost reuse frequency was significantly lower in turkey vultures than black vultures, although roost site fidelity did not differ by species. Comparisons of space use between male and female vultures were only possible for black vultures for which monthly selection did not differ. Patterns of habitat selection within the home range varied across the annual cycle with selection for wetland habitats strongest for both species. Results of this study demonstrate differences in resource selection and provide evidence for habitat segregation and niche differentiation by these vulture species, for which competition exists in areas of sympatry.

INTRODUCTION

In areas of sympatry, competition between resident, non-migratory species occurs throughout the annual cycle when resource requirements are similar; however, niche differentiation reduces competition and allows for resource partitioning and coexistence. Interspecific competition is a particular issue for vultures (i.e., obligate scavengers) as both Old and New World species are specifically adapted to relying on carrion as a primary food resource (Hertel 1994). Large bodies, broad wings for soaring, excellent vision, and highly acidic stomachs are just some of the various morphological and physiological adaptations vultures possess providing evolutionary advantages in carrion detection and consumption over other facultative scavenging species (DeVault et al., *in press*). In areas where multiple vulture species coexist, niche differentiation is demonstrated through variation in morphological characteristics relating to feeding strategies such as body size, skull, beak, and mandible metrics (Hertel 1994). However, when body sizes and feeding strategies are not notably distinct between coexisting vulture species, the need to avoid direct interspecific competition drives spatial and temporal niche separation and may be evidenced through habitat segregation.

In areas of sympatry, interspecific competition undoubtedly occurs between black and turkey vultures as both species are diurnal, obligate scavengers utilizing similar roosting (Buckley 1998, Avery et al. 2002, Evans and Sordahl 2009) and nesting habitats (Kirk and Mossman 1998, Buckley 1999). However, turkey vultures primarily forage solitarily or in pairs and have an enhanced sense of smell, allowing them to exploit carrion in areas where visual detection is limited (Kirk and Mossman 1998) such as in forested areas with dense canopy cover. Conversely, black vultures often forage with conspecifics (Buckley 1999), maintaining large social groups and responding to visual cues of other scavenging birds for improved carcass detection as they have a limited sense of smell (Buckley 1996, Buckley 1999). Furthermore, black vultures are generally more aggressive and dominant and thus able to displace turkey vultures at carcass sites (Buckley 1996, Buckley 1999). Resident vultures in the southeastern United States are an ideal population to examine in the interest of exploring how seemingly similar vulture species coexist through habitat segregation.

Although black and turkey vultures are relatively common and abundant throughout their ranges, there remains a scarcity of studies elucidating the ecology and resource selection for these species. Moreover, many prior assessments of home range and resource selection have been limited by the capabilities of tracking devices available at the time – i.e, physical observation (Novaes and Cintra 2013), VHF radio telemetry (Arrington 2003, Coleman and Fraser 1989), and fixed-wing aerial radio telemetry (DeVault et al. 2004). Recent advancements in GPS tracking technologies allow for intense sampling of vulture movements and, when coupled with high-resolution land cover data, detailed examination of resource selection and evidence for resource partitioning at finer temporal resolutions than previously possible (Fischer et al. 2013). Characteristics of roost selection and measures of roost reuse and roost site fidelity are additional aspects of vulture ecology where little is known. At increasingly finer spatial and temporal scales, differences in resource utilization between sympatric vulture species may be evident. To date, no prior studies have examined variation in black and turkey vulture resource selection across fine temporal scales (e.g., monthly) and with consideration to sex-specific differences.

Using fine-scale movement data from sympatric black and turkey vultures in the southeastern United States, the objective of this study is to elucidate spatial and temporal differences in resource selection throughout the annual cycle as a function of species and sex with finer resolution than any previous study of these species to date. These data will further develop our understanding of vulture ecology, allowing us to uncover distinctions in resource selection toward evidencing niche differentiation in sympatric vulture species at fine spatial and temporal resolutions. The specific goals of this study are to assess selection of habitat attributes associated with vulture evening roost sites seasonally, quantify seasonal differences in the reuse frequency and site fidelity of vultures to evening roost sites, and elucidate differences in monthly resource selection with consideration to species and sex. From this assessment, I hypothesize evening roost habitat selection, roost reuse frequency, and roost site fidelity will vary by season and species. Specifically, I expect roosts to be composed of greater proportions of forest habitat in winter months due to enhanced thermal cover. Considering that there are no perceptible differences between sexes in body size or parental roles for either species, I have little reason to expect differences in roost habitat selection, reuse frequency, or site fidelity between males and females of either species. Furthermore, I expect monthly resource selection will vary between species, and because nesting activities generally occur in areas of low-disturbance (Kirk and Mossman 1998, Buckley 1999), I expect both species will utilize undisturbed (low human-impact) areas during breeding season months more frequently than those of the non-breeding season. In terms of revealing evidence for niche differentiation through habitat segregation, and with consideration to these species' morphological and behavioral differences in carcass-detection and acquisition, I hypothesize turkey vultures will utilize greater proportions of forested habitats, and black vultures will utilize greater proportions of open areas, roads, agricultural areas, and other developed/human-disturbed areas (urban, landfills, etc.). I further expect temporal resource partitioning between sympatric black and turkey vultures will be apparent at these finer-scales as evidenced through variation in monthly habitat selection.

METHODS

Study Area

This research was conducted at the Savannah River Site (SRS), which is located along the border of Georgia and South Carolina in the southeastern United States. Populations of black and turkey vultures are abundant on the SRS as it provides important roosting, nesting, and foraging habitat for both species (DeVault et al. 2004, DeVault et al. 2005). The SRS is a 780-km^2, limited-access nuclear research facility owned and operated by the U.S. Department of Energy (DOE; White et al. 2000). Elevations range from <30 m to 115 m above sea level (White et al. 2000). Much of SRS is relatively undisturbed by DOE activities and is primarily forested (White et al. 2000). The SRS is composed of planted pine forests managed by the U.S. Forest Service, bottomland hardwood, wetland, and various industrial areas including five decommissioned nuclear reactors, radioactive materials processing plants, and landfills (White et al. 2000). The composition of largely undisturbed natural areas and pockets of human-use industrial areas at the SRS make this site an ideal location in which to study resident vulture resource selection.

Vulture Trapping & Handling

During summer 2013 and spring 2014, I captured 295 black and turkey vultures. Of these, 13 adult black and 14 adult turkey vultures were randomly selected and affixed with a solar-powered 70-g Groupe Spécial Mobile/Global Positioning System (GSM/GPS) transmitter (Microwave Telemetry, Inc. 2013). The transmitters reported locations (lat/long coordinates) at variable intervals, with 76% of all locations collected with durations of 3 minutes or less between fixes (see Chapter 2). Vultures were handled in accordance with the University of Georgia Animal Care and Use Protocol No. A2013 02-004-Y2-A2. All trapping was conducted during the non-migration season in an attempt to target only resident vultures. Non-migration/residency was verified by assessing each vulture’s net-squared displacement (NSD; see Chapter 2) from evening roost sites. All vultures were affixed with numbered patagial tags for individual identification, measured for standard morphological characteristic, and aged (adult or juvenile) based on coloration and wrinkling of the head (Kirk and Mossman 1998, Buckley 1999). Given that black and turkey vultures are sexually monomorphic (Kirk and Mossman 1998, Buckley 1999), it was not possible to control for balanced ratios of male and female black and turkey vultures from among those randomly selected to receive GPS tracking devices. I collected a feather and blood from a leg or brachial vein for use in sex determination via sex-specific DNA markers and polymerase chain reaction (PCR). All genetic analyses were conducted at the Savannah River Ecology Laboratory in Aiken, South Carolina (see Chapter 2 for details).

Roost Habitat Characteristics, Roost Reuse and Roost Site Fidelity

Habitat characteristics of evening roosts, seasonal roost reuse frequency and roost site fidelity were quantified using location data collected for 9 black and 9 turkey vultures from 16 August 2013 to 9 June 2015. Location data were subset into three seasons (breeding, summer and winter) and included all fixes received within equal durations of 121 days, with the exception of the first summer which only includes data from the final 52 nights of the season because the GPS transmitters were first deployed mid-summer 2013. Breeding season durations are similar for black and turkey vultures (Jackson 1983, Kirk and Mossman 1998, Buckley 1999), although in areas of sympatry, black vultures typically nest two weeks earlier than turkey vultures (1 February - 10 June for black vultures and 15 February - 24 June for turkey vultures; Jackson 1983, Kirk and Mossman 1998, Buckley 1999). Therefore, breeding seasons in this analysis included fixes from 8 February to 8 June, which represent the median dates of those described for vultures breeding at 32°-33° latitudes (Jackson 1983), and encompass the range of dates wherein adult black and turkey vultures are both influenced by breeding phenology, and standardized for ease of comparison. Fixes received within the tertiles preceding and following the breeding season were defined as winter (9 October - 7 February) and summer (9 June - 8 October), respectively.

Evening roosts were standardized such that only those nights in which all birds had a detectable roost location were included in this analysis, resulting in the exclusion of 3% (22 of 662) of all nights within the study period. To identify evening roosts, I extracted the average location from among fixes received between 20:00-00:00 hours for each vulture. For nights where no fixes were received between 20:00-00:00 hours, evening roosts were determined manually by examining location data for series of fixes within nighttime hours where the bird clearly did not move for several hours throughout the evening and into the following morning (00:00-04:00), reporting the evening roost as the average of those locations. Evening roost locations were buffered by 75 m and rounded to incorporate location error (±23 m, based on the manufacturer's estimate (Microwave Telemetry, Inc. 2013)). Neighboring roosts within 100 m of one another were merged together using ArcMap GIS software (Esri 2012), incorporating habitats between roosts to form a single roost in order to remove distinctions between locations that may be proximally considered the same roost by a vulture.

Within each buffered roost, I quantified the proportion of each habitat type: i.e. including proximity to roads, binned into two distance classes of 0-500m and 500-1,000m (based on Euclidian distance) and derived from USA Major Roads map layer (Esri 2014); proximity to landfills, binned into three distance classes of 0-500m, 500-1,000m, and >1,000m (based on Euclidian distance) and derived from active solid waste landfill locations for Georgia (GSB-

EPD-GADNR 2000), South Carolina (SCDHEC-BLWM 2006), Florida (FLDEP 2015), and North Carolina (NCDENR-DWM 2014); and five habitat types distinguished by ground-visibility and relative level of human-impact disturbance (see Table 3-1) including wetlands (emergent herbaceous and woody), forest (deciduous, evergreen and mixed), open developed, open undeveloped (rock/clay/sand, barren land), and developed (low, medium and high intensity) derived from 30m resolution land cover data from the National Land Cover Database (NLCD2011, Homer et al. 2015). Normality was tested using the Shapiro-Wilk test and data failing to meet the assumption of normality were square-root transformed. For normal and square-root transformed data, I used unbalanced repeated-measures linear mixed effects models with an unstructured covariance structure to assess differences in composition of habitat types by species, sex and season, as well as interactions using the ‘lme4’ package (Bates et al. 2015) in the R program (R Core Team 2014). I conducted a separate analysis for each habitat type and in all models, species, sex, and season were included as fixed effects and individual was incorporated as a random effect.

Roost site fidelity quantifies the percentage of evenings a vulture spends at its most frequently re-used roost site. In other words, it gives a relative amount of time spent at the one roost site that was most frequented by that bird. Roost site fidelity is thus calculated by dividing the maximum number of nights at a single roost by the total number of nights sampled. Frequency of roost reuse quantifies the percentage of evenings a vulture spends at any roost site used once before. In other words, it reveals the frequency at which a bird reverts to any previously used roost site as well as the inverse of utilization of new roosts. Roost reuse is thus calculated by dividing the number of nights spent at any roost that was used more than once by the total number of nights tracked. Normality was tested using the Shapiro-Wilk test and roost site fidelity data were log-transformed to meet assumptions of normality. I used unbalanced repeated-measures linear mixed effects models with unstructured covariance structure to assess differences in roost reuse and log(site fidelity) by species, sex and season, as well as interactions using the ‘lme4’ package (Bates et al. 2015) in the R program (R Core Team 2014). Analysis between sexes was not possible for turkey vultures due to low numbers of monitored female turkey vultures. In both models, species, sex, and season were included as fixed effects and individual was incorporated as a random effect.

Utilization Distributions

Filtered locational data were used to develop monthly utilization distributions (UDs) for individual vultures using the dynamic Brownian Bridge Movement Model (dBBMM; Kranstauber et al. 2012) with the ‘move’ package (Kranstauber and Smolla 2014) in the R program (R Core Team 2014). An advantage of the dBBMM method is that it accounts for both temporal autocorrelation and variation in trajectories between points (Kranstauber et al. 2012). Location data were filtered to remove erroneous data as well as any outliers according to the root mean square (rms) algorithm of McConnell et al. (1992; see Chapter 2). To fit the dBBMM to vulture movement paths and allow for comparisons across each model, parameters were standardized (window=47, margin=11, raster=30) with a location error of ±23 m based on the manufacturer’s estimate (Microwave Telemetry, Inc. 2013). To increase the certainty that UDs developed through the dBBMMs produced reliable estimates of actual space use, vertical and horizontal accuracy of the GSM/GPS transmitters were validated through with a series of static tests (see Chapter 2).

Monthly Resource Selection

I assessed variation in vulture resource selection by delineating monthly UDs and relating probabilities of black and turkey vulture use of specific habitat types within UDs relative to their availability within the home range. Data for all vultures were subset and standardized to include only fixes received within equal timeframes (i.e., monthly). Specifically, for monthly utilization, data from September 2013 to August 2015 were sorted by month based on calendar definitions (e.g., June contained fixes from 1 June 2015 00:00:00 EST to 30 June 2015 23:59:59 EST). Monthly UDs were developed using the dBBMM (Kranstauber et al. 2012) in the ‘move’ package (Kranstauber and Smolla 2014) in R (R Core Team 2014; see Chapter 2) for 9 black (4 female, 5 male) and 9 turkey (3 female, 6 male) vultures monitored from 1 September 2013 to 31 August 2015. UDs provide an array of cell values based on probability of use throughout a home range (Van Winkle 1975, Millspaugh et al. 2010). Areas receiving more use are represented by cells of the UD with higher probability values, and substantial use of an area may suggest importance in terms of quality or quantity of a resource therein. Contours defining 100% home ranges were delineated from UDs and proportions of habitat types therein were used as an estimate of available habitat.

Only habitat attributes expected to be important in providing vulture roosting, nesting, and foraging resources were included in analyses of resource selection. Carrion is typically ephemeral and difficult to predict spatially and temporally except along roads due to roadkill. Landfills also are commonly used by vultures as they provide consistent and relatively reliable foraging opportunities year-round. Roost selection by these species is influenced by level of human disturbance (Coleman and Frasier 1989, Thompson et al. 1990), and can also be influenced by proximity to food (Novaes and Cintra 2013), nests (Davis 1983), conditions facilitating flight (Thompson et al. 1990), and social interactions (Rabenold 1986, 1987, Buckley 1996, 1997). Therefore, habitat variables in my analyses included distances to roads and landfills, as well as land cover characteristics distinguished by both ground-visibility (i.e., open areas vs. forests with canopy cover) and relative level of human-impact disturbance (developed vs. undeveloped; Table 3-1; see section: *Roost Habitat Characteristics, Roost Reuse and Roost Site Fidelity*). ArcMap GIS software (Esri 2012) was used to develop raster layers at 30 m resolution of all input data for habitat types encompassing the spatial extent of the study area. Study area was determined by buffering the outer edge of the 100% minimum convex polygon (MCP) of all pooled vulture locations by 1000 km, which resulted in a study area roughly four-times larger than the size of all combined vulture MCP 100% home range areas (Figure 3-1).

Resource selection was determined by ratios of proportional use to availability of each habitat type within the home range. Use of each habitat type was determined with the expected probabilities of occurrence derived from monthly UDs using the “Zonal Statistics” tool in ArcMap GIS software (Esri 2012). Resource selection ratios (*ln*(rf)) were calculated for each bird/year/month/habitat following the method of Rivers et al. (2013) where:

$$Y_{bird,year,month,habitat} =$$

$$ln\left(rf_{bird,year,month,habitat}\right) =$$

$$ln\left(\frac{\text{Proportion Use}_{bird,year,month,habitat}}{\text{Proportion Available}_{bird,year,month,habitat}}\right)$$

I removed months where available habitat was zero, resulting in the exclusion of ~5% (124/2496) of total possible selection ratios. For retained months where a habitat was available but not used, I replaced zero values of use with $1e^{-100}$ to constrain the output of the equation to real numbers. Resource selection ratios were *ln*-transformed such that “a selection ratio of ½ is the same distance away from 1 as a selection ratio of 2” (Rivers et al. 2013). Selection ratios

(ln(rf)) for each habitat type were assessed for normality using the Shapiro-Wilk test and subsequently square-root transformed based on skew of the distribution (e.g., $\sqrt{(ln(\mathrm{rf}) + |\min(ln(\mathrm{rf}))|)}$). For each habitat type, I developed 10 resource selection models *a-priori* using linear mixed-effects models with unstructured covariance structure with the 'lme4' package (Bates et al. 2015) in R (R Core Team 2014). Fixed effects for each model included species, month, and sex, combinations thereof, and species*sex and species*month interactions. Individual was included as a random effect in the models. Models were ranked using Akaike's Information Criterion (AIC) and model weights and all models within 2 ΔAIC were considered supported.

RESULTS

Seasonal Roost Characteristics

Habitat characteristics for seasonal (breeding, summer and winter) roosts were quantified from 662 nights for 9 black vultures (4 female, 5 male) and 9 turkey vultures (3 female, 6 male) from 16 August 2013 to 8 June 2015. Proportions of habitat types were calculated for an average of 106 (min=50, max=123) nights across all seasons (Table 3-2). I observed a significant difference in the proportion of forested habitat within evening roosts between black and turkey vultures ($F_{1,80}=21.97$, $P<0.001$) across all seasons ($F_{3,79}=10.536$, $P<0.001$), with turkey vulture roosts comprising significantly greater proportions of forest than those of black vultures (28.37 ± 1.6%, 14.62 ± 1%; Figure 3-2c). Mean proportions of developed/urban habitat types comprising black vulture evening roosts (3.24 ± 0.96%) were greater than those of turkey vultures (0.79 ± 0.16%) amongst all seasons, although differences by species were not significant ($F_{1,80}=2.408$, $P=0.32$; Figure 3-2b). Mean proportions of developed/urban habitat in evening roosts was substantially greater in female black vultures (5.21 ± 1.7%) than male black vultures (1.06 ±

0.3%) roosts, although differences were not significant ($F_{1,7}$=1.63, *P*=0.24; Figure 3-5a). Mean proportions of road distances 0-500m comprising turkey vulture evening roosts (19.4 ± 1.4%) were greater than those of black vultures (13.6 ± 2.1%) across all seasons, although differences were not significant ($F_{1,80}$=16.17, *P*=0.32; Figure 3-3b). Proportions of evening roost developed/open habitat did not differ between black and turkey vultures (10.9 ± 1.3%, 7.6 ± 0.8%; $F_{1,80}$=1.682, *P*=0.213; Figure 3-2d). Although proportions of wetland habitat utilized at evening roosts by black and turkey vultures did not differ between species (55.7 ± 2.7%, 47.2 ± 2.2%; $F_{1,80}$=2.861, *P*=0.109), use differed significantly by season for both black ($F_{2,79}$=3.541, *P*=0.043) and turkey ($F_{2,79}$=4.493, *P*=0.018) vultures, with use of wetland habitats highest in winter (Figure 3-2a). Similarly, proportions of undeveloped/open habitat at evening roosts of black and turkey vultures did not differ by species (13.6 ± 0.7%, 15.3 ± 1.1%; $F_{1,80}$=0.540, *P*=0.47), however use differed significantly by season ($F_{2,79}$=5.633, *P*<0.001; Figure 3-3a) with use highest in the breeding season. Finally, I found no differences in evening roost use of landfill distances 0-500m ($F_{1,80}$=0.724, *P*=0.407) and 500-1000m ($F_{1,80}$=1.846, *P*=0.19) by black and turkey vulture roosts, although use did vary by season ($F_{1,80}$=4.68, *P*=0.019; and $F_{1,80}$=14.17, *P*<0.001), and was highest in the summer (Figure 3-3c,d).

Roost Reuse Frequency and Site Fidelity

Roost site fidelity did not differ between black (30.71 ± 4.23%) and turkey vultures (19.91 ± 1.51%; $F_{1,82}$=1.03, *P*=0.325; Figure 3-6b). The frequency of roost reuse was significantly higher in black vultures (74.29 ± 2.11%) than turkey vultures (57.50 ± 2.41%; $F_{1,82}$=15.805, *P*=0.002; Figure 3-6a). Roost reuse also varied significantly among seasons for both black ($F_{2,36}$=4.54, *P*=0.02) and turkey vultures ($F_{2,36}$=4.23, *P*=0.02; Figure 3-6a). Specifically, roost reuse was highest in winter (79.5 ± 2.1%) over breeding (74 ± 4.3%) and summer (69.4 ± 4%) seasons for black vultures, and highest in breeding (65.8 ± 2.7%) over winter (57.3 ± 5%) and summer (50 ± 3.7%) seasons for turkey vultures. Roost reuse did not vary between male and female black vultures ($F_{1,36}$=0.248, *P*=0.633; Figure 3-7a) and there was no evidence for a sex by season interaction ($F_{2,36}$=1.24, *P*=0.306).

Monthly Resource Selection

Monthly resource selection within the home range was calculated for 9 black vultures (4 female, 5 male) and 9 turkey vultures (3 female, 6 male) from September 2013 to August 2015. I assessed resource selection for an average of 16 (min=6, max=24) months for individual black vultures and 18 (min=3, max=24) months for turkey vultures. Results of my mixed model analyses for resource selection within the home range showed strongest support for monthly effects on selection for most habitat types (Table 3-3). There was little evidence that selection differed by species for developed/urban, developed/open, habitats with distances of 0-500m from roads, and habitats with distances of 500-1,000m from landfills. For selection of wetland habitats, there was evidence for an effect of species and sex interactions. For selection of habitats within distance of 0-500m of landfills, I found strong support for a species and month interaction effect. I found consistent evidence for selection of wetlands (Figure 3-8) whereas nearly all other habitat types were used somewhat less than their availability (Figures 3-9 – 3-15). Month was the strongest factor influencing selection for developed/urban habitats.

DISCUSSION

This study provides evidence for niche differentiation in sympatric black and turkey vultures by demonstrating habitat segregation at a finer temporal resolution than previous studies. Using over 2.8 million locations collected from GPS-tracked vultures, my results demonstrate differences in roost site characteristics, roost reuse frequency, and resource selection between these species at multiple spatial and temporal scales. These data undoubtedly reflect differences in physiology, behavior, and social structure and thus represent underlying mechanisms of niche differentiation between species.

Although black and turkey vultures are observed concurrently at roost sites (Thompson et al. 1990), my data provide strong evidence for niche differentiation in evening roost site characteristics as both species differed in the proximity of evening roosts to forest and developed/urban habitats. Specifically, turkey vulture evening roosts comprised a significantly greater proportion of forest habitat, whereas black vulture evening roosts comprised a greater proportion of developed/urban habitat. Distinctions in the level of disturbance associated with these habitats are substantial and suggest black and turkey vultures may differ in their sensitivity to human disturbance at roost sites. Black vultures are generally described as bold compared to turkey vultures (Buckley 1996, Buckley 1999) and their tolerance to roosting in developed areas near human activity may be higher due to their inherent boldness as well as propensity to roost in large groups of conspecifics, reducing predation risk (Buckley 1999). Turkey vultures likely roost in forest habitats significantly more than black vultures because of their ability to exploit carrion resources in forested areas through enhanced olfaction, while black vultures must rely more so upon visual detection, which is limited in forested habitats (Kirk and Mossman 1998, Buckley 1999). Furthermore, although I did not examine specific finer-scale roost characteristics within the generalized habitats (i.e., tree type within forest or building/structure within developed/urban habitat), black vultures may be utilizing communication towers and other tall human structures within developed/urban habitats in order to gain in visual perspective. The composition of other measured habitats at roost sites did not differ between species, although use of wetlands varied by season. Specifically, use of wetlands was highest in winter and lowest in breeding season for both species. In winter, wooded wetlands are likely used for thermal properties as protection from adverse weather conditions (Thompson et al. 1990), and equally may provide desirable cooling conditions with shade, water, and abundant perch structures for resting in warm summer conditions.

Roost reuse and roost site fidelity also can be informative parameters differentiating behaviors of sympatric black and turkey vultures. I used roost reuse frequency to elucidate a measure of a vulture’s exploratory behavior and general success in finding new foraging opportunities. When a vulture spends an evening in a new location, it is likely that it chose that site after some searching and in response to having found something of value; most probably a carcass. Roost reuse frequency measures the amount of time a vulture returns to any previously used roost site, and thus the inverse of roost reuse may be a useful measure of successful explorations for novel carrion sources. Roost reuse frequency was significantly lower in turkey vultures than black vultures, and turkey vultures thus spent more nights in novel roosts than did black vultures. This finding likely reflects the fact that turkey vultures have enhanced olfaction and are typically the first to arrive at a carcass (Kirk and Mossman 1998, Roen and Yahner 2005). Moreover, the higher roost reuse frequency observed by black vultures may be indicative that individuals return to familiar roosts more often in order to maintain social connections and continue to benefit from responding to cues of other vultures for carrion resources (Buckley 1999). I found no significant evidence for differences in seasonal roost site fidelity by species or sex, suggesting that all vultures return to dominant evening roost sites at relatively similar rates; however, mean roost site fidelity was higher in black vultures than turkey vultures, which supports my original hypothesis. These results can have important implications for vulture management and conservation as roost habitat characteristics can be further examined to understand aspects driving selection for and differences between these primary, reused and novel roosts.

Analyses of monthly resource selection revealed significant selection for wetland habitats by both species, while all other habitat types were selected to substantially lesser degrees. It is important to note that proportions of habitat availability were not relative to other habitats in this analysis, but rather relative to actual availability within the home ranges. For example, habitats within distances of 0-500m from roads could also be composed of various proportions of forest, developed/open, wetland, or any other habitat combinations included in this analysis. Therefore, selection and use of one habitat did not necessarily suggest non-use or avoidance of others. Wetland habitats included both emergent and wooded wetlands. This analysis did not distinguish between wetland types; however, strong selection for wetlands was evident by both species and is likely due to the substantial composition of wooded wetlands within the study area which provides a variety of desirable conditions for a vulture including suitable flight conditions, roosting and nesting structures, and reliable and consistent foraging opportunities due to high biodiversity typical of wetlands (Dudgeon et al. 2006).

Vulture habitat selection varied by month for nearly all habitat types. Selection for habitats within distances of 0-500m from roads, and within 0-1,000m of landfills did not differ significantly by species, and varied similarly across months with lowest selection occurring during winter and breeding months, especially for black vultures. Decreased selection for roads and landfills during the winter months, however nominal, may suggest that more desirable scavenging opportunities were available in less-disturbed habitats during winter months. Although landfills and roads provide a relatively reliable source of scavenging opportunities throughout the annual cycle, risks are associated with selection for carrion at these sites. Vultures foraging on carcasses along roads risk colliding with passing vehicles, and trash at landfills is constantly churned and plowed over by maintenance vehicles creating a relatively disruptive environment for foraging vultures. Therefore, nominal selection for these habitat types may suggest that roads and landfills are not preferentially selected, but rather may only be used in times of desperation, when safer alternatives are not available or abundant.

Certain distinctions in habitat selection were evident by species. Fluctuations in monthly selection for undeveloped/open habitats was relatively similar by species, although selection for undeveloped/open habitats by turkey vultures was substantially higher across all months, especially in the breeding season. Additionally, selection for forest habitats was greater in turkey vultures throughout nearly all months except the end of summer. Black vulture selection for habitats within distance of landfills at 0-1,000m dropped significantly while selection for developed/open habitats increased substantially in the months of June and July, which coincide with the range of dates over which chicks hatch. Black vultures tasked with chick-rearing in the early stages may take greater precautions during foraging events and thus preferentially selected less-disturbed habitats than landfills.

Resource selection by black and turkey vultures varies over the course of an annual cycle, and differences previously undetected emerge at finer scales. Results of this study demonstrate differences in resource selection and provide evidence for habitat segregation and niche differentiation by these vulture species for which competition exists in areas of sympatry. These data build upon our understanding of vulture spatial ecology, providing insights into underlying behavioral mechanisms facilitating niche differentiation between species and ultimately should provide critical insights into the conservation and management of this important group of birds.

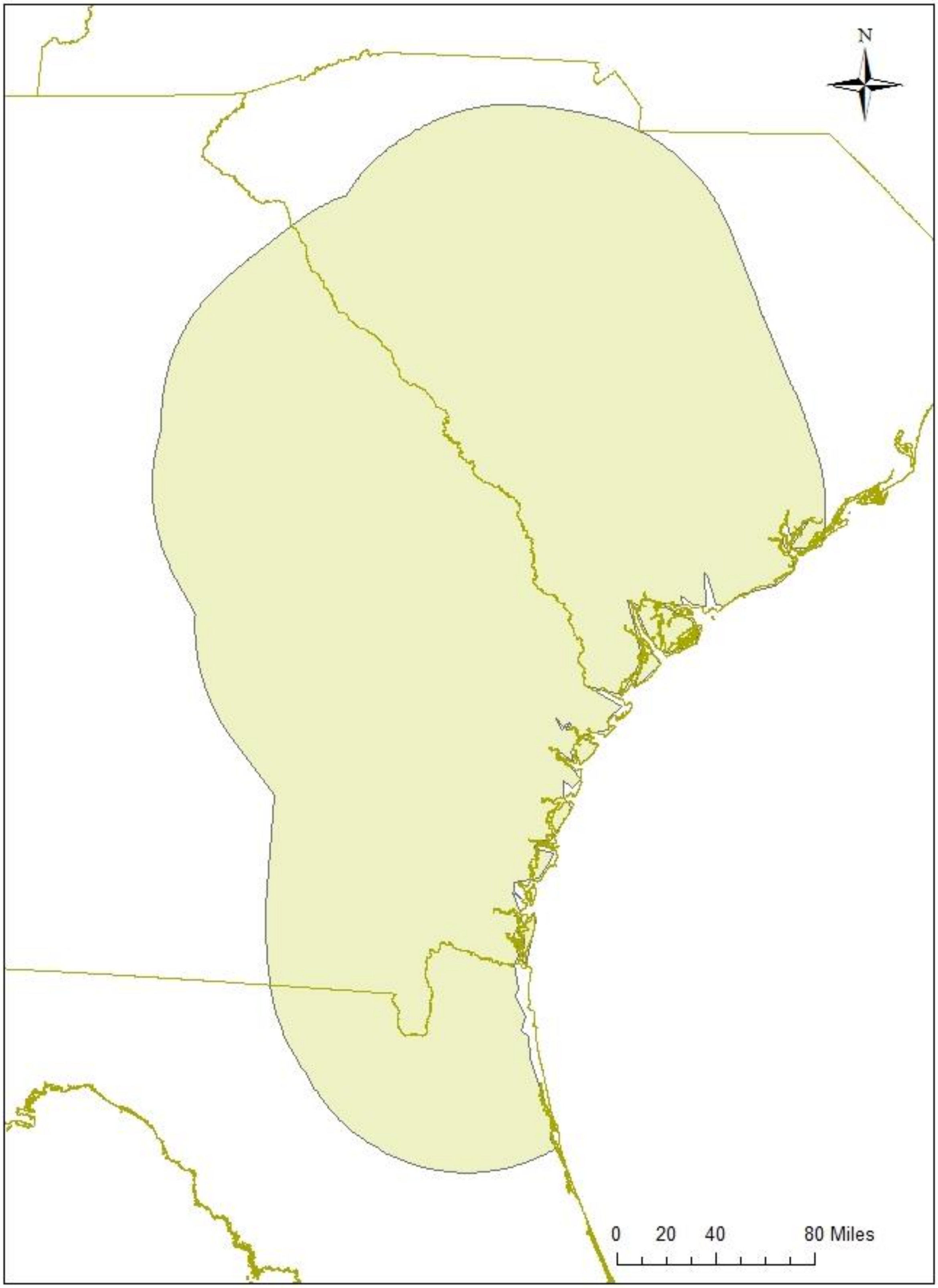

Figure 3-1. Extent of study area for resource selection analysis including major portions of South Carolina, Georgia and Florida in the southeastern United States.

Table 3-1. Habitat variables and associated descriptions for resource selection analyses conducted for black and turkey vultures monitored with GPS transmitters in the southeastern U.S.

Habitat Variable		**Class Descriptions**
Wetland	90*	Woody Wetland
	95*	Emergent Herbaceous Wetland
Forest	41*	Deciduous Forest
	42*	Evergreen Forest
	43*	Mixed Forest
Developed	22*	Developed, Low Intensity
	23*	Developed, Medium Intensity
	24	Developed, High Intensity
Developed, Open	21*	Developed, Open Space
	31*	Barren Land (Rock/Sand/Clay)
	81*	Pasture/Hay
	82*	Cultivated Crops
Undeveloped, Open	52*	Shrub/Scrub
	71*	Grassland/Herbaceous
Landfill #1	--	Distance: 0-500 m
Landfill #2	--	Distance: 500-1,000 m
Road #1	--	Distance: 0-500 m

*Class\Value from National Land Cover Database 2011 (NLCD 2011)

Table 3-2. Table of individual vultures (ID) included in seasonal roost habitat analyses and number of nights (n) included per season. Species: BLVU=black vulture (*Coragyps atratus*), TUVU=turkey vulture (*Cathartes aura*); ID#: Patagial Tag Identification Number; Sex: F=female, M=male. ✓: included; -: not included in analyses.

Species	**ID**	**Sex**	**Summer 2013**	**Winter 2014**	**Breeding 2014**	**Summer 2014**	**Winter 2014**	**Breeding 2015**
			n=50	**n=119**	**n=117**	**n=110**	**n=123**	**n=121**
TUVU	01	F	✓	✓	✓	✓	✓	✓
TUVU	03	F	✓	✓	✓	✓	✓	✓
TUVU	06	M	✓	✓	✓	✓	✓	✓
BLVU	08	M	✓	✓	✓	-	-	-
BLVU	12	M	✓	✓	✓	✓	✓	✓
TUVU	13	F	✓	-	-	-	-	-
BLVU	22	F	✓	✓	✓	✓	✓	✓
BLVU	47	F	✓	✓	✓	✓	✓	✓
BLVU	48	M	✓	✓	✓	-	-	-
BLVU	57	F	✓	✓	-	-	-	-
TUVU	60	M	✓	✓	✓	✓	✓	✓
TUVU	75	M	✓	✓	✓	✓	✓	✓
TUVU	90	M	✓	✓	✓	✓	✓	✓
TUVU	91	M	✓	✓	✓	✓	✓	✓
BLVU	92	F	✓	✓	✓	✓	✓	✓
BLVU	108	M	-	-	-	✓	✓	✓
TUVU	123	M	-	-	-	✓	✓	✓
BLVU	126	M	-	-	-	✓	✓	✓

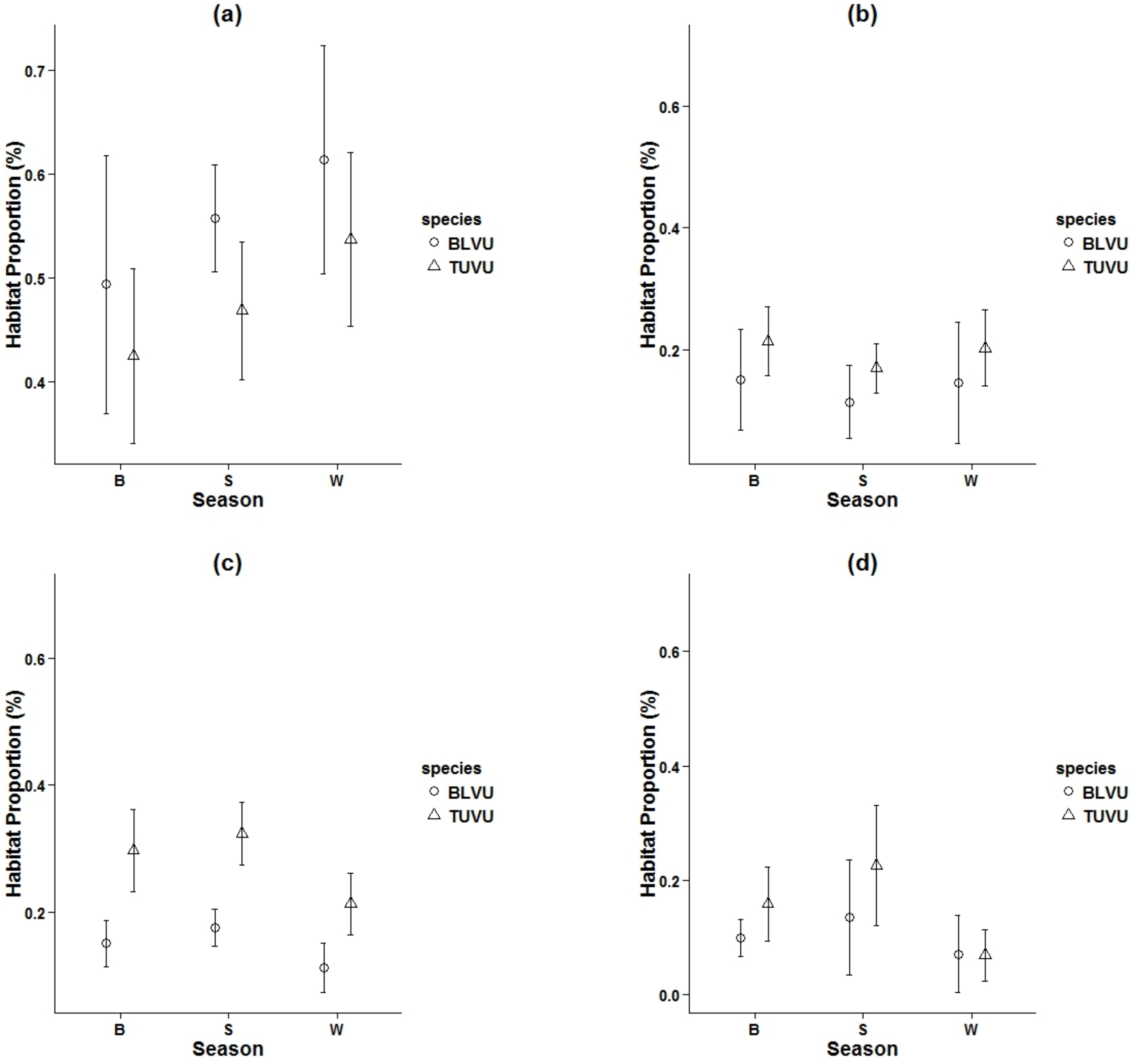

Figure 3-2. Mean (±95% CI) proportions of (a) wetland, (b) developed/urban, (c) forest, and (d) developed/open habitat types comprising evening roosts across breeding (B), summer (S), and winter (W) seasons for 9 black (BLVU; *Coragyps atratus*), and 9 turkey (TUVU; *Cathartes aura*) vultures monitored with GPS transmitters in the southeastern U.S.

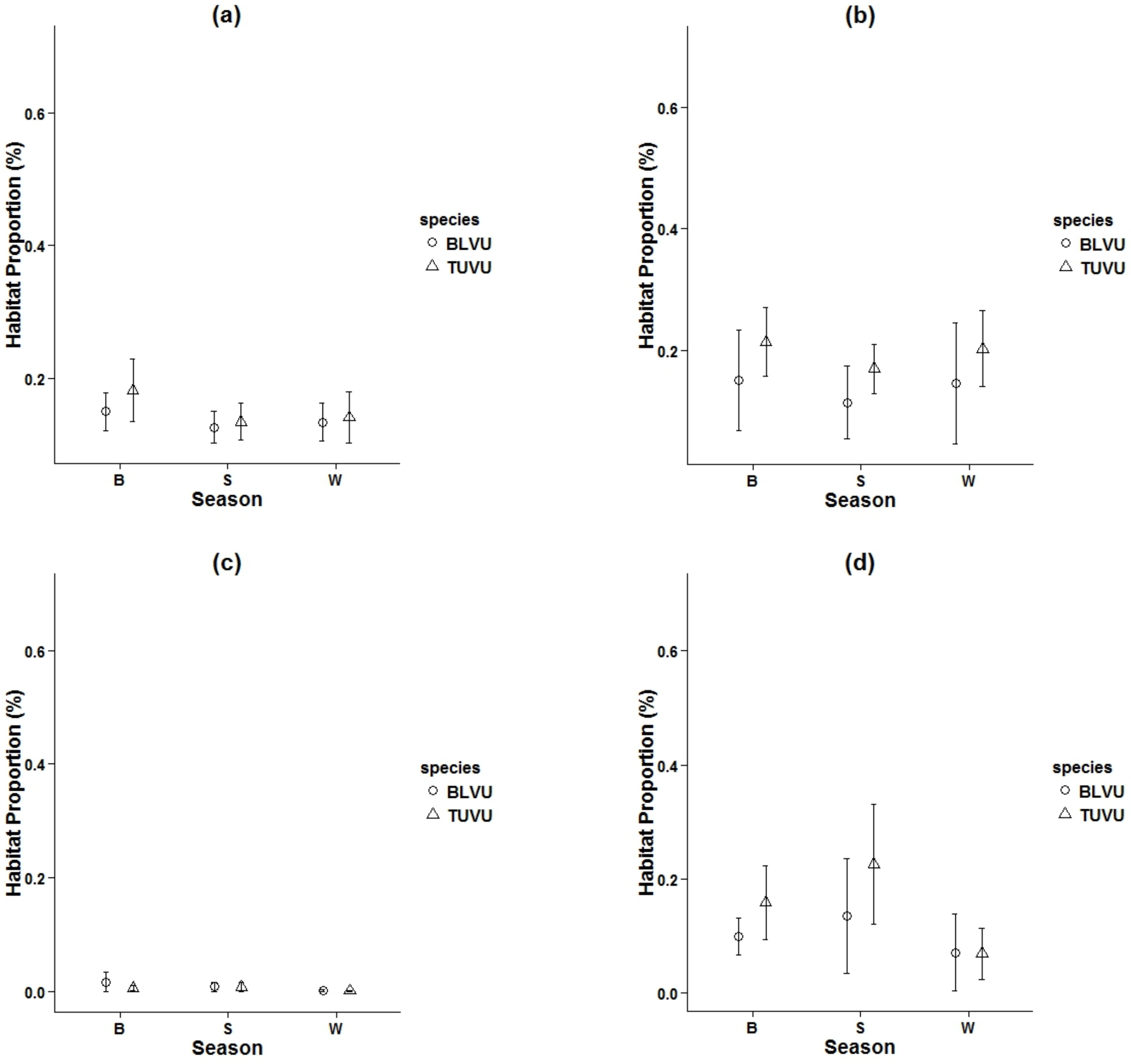

Figure 3-3. Mean (±95% CI) proportions of (a) undeveloped/open, (b) distances of 0-500m from road (c) distances of 0-500m from landfill, and (d) distances of 500-1,000m from landfill habitat types comprising evening roosts across breeding (B), summer (S), and winter (W) seasons for 9 black (BLVU; *Coragyps atratus*), and 9 turkey (TUVU; *Cathartes aura*) vultures monitored with GPS transmitters in the southeastern U.S.

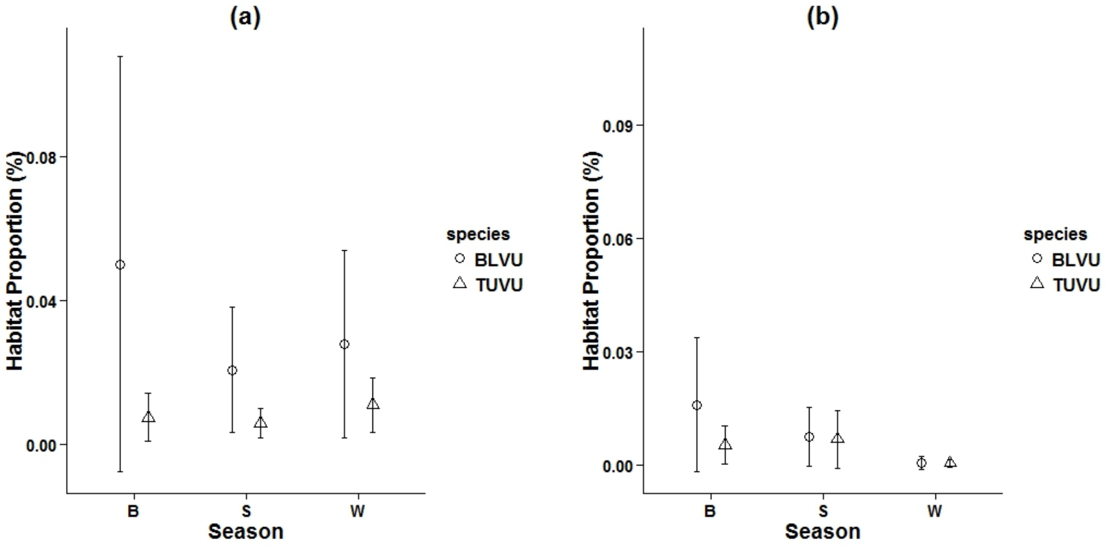

Figure 3-4. Mean (±95% CI) proportions of (a) developed/urban, and (b) distances of 0-500m from landfill habitat types comprising evening roosts across breeding (B), summer (S), and winter (W) seasons for 9 black (BLVU; *Coragyps atratus*), and 9 turkey (TUVU; *Cathartes aura*) vultures monitored with GPS transmitters in the southeastern U.S.

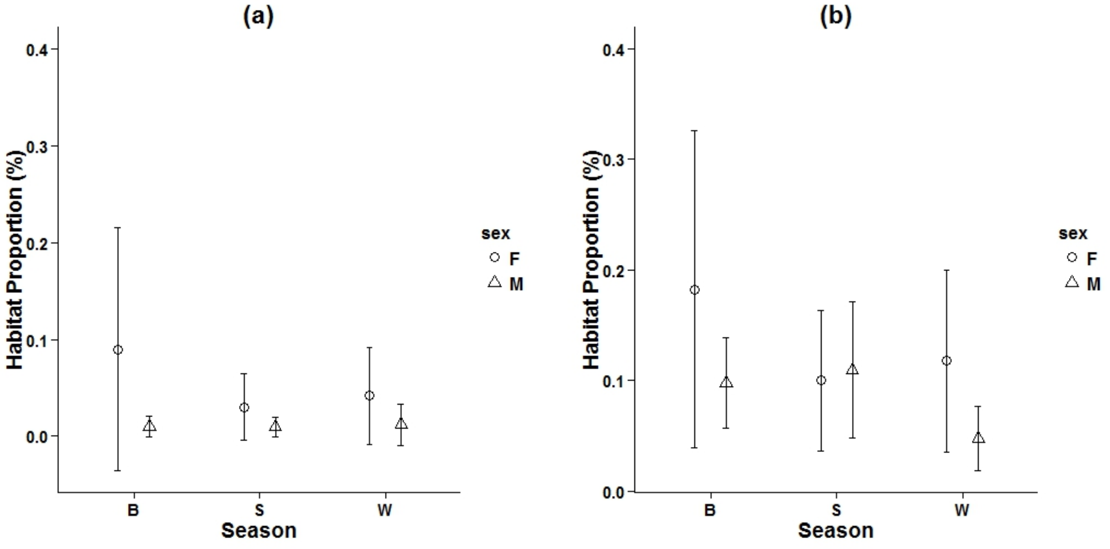

Figure 3-5. Mean (±95% CI) proportions of (a) developed/urban and (b) developed/open habitat types comprising evening roosts across breeding (B), summer (S), and winter (W) seasons of 5 male and 4 female black vultures (*Coragyps atratus*) monitored with GPS transmitters in the southeastern U.S.

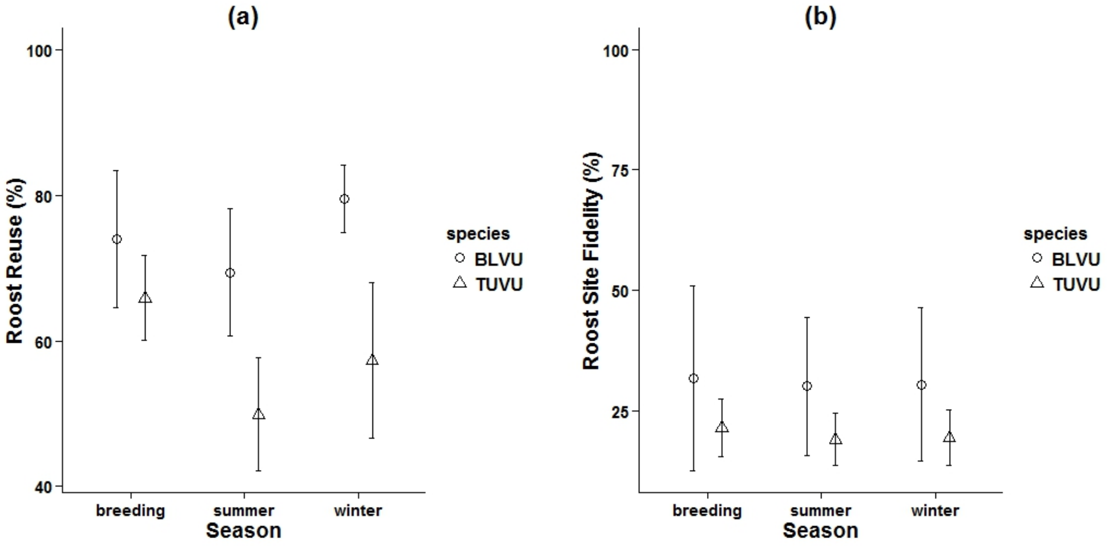

Figure 3-6. (a) Roost reuse (±95% CI) and (b) site fidelity (±95% CI) across breeding, summer, and winter seasons for 9 black (BLVU; *Coragyps atratus*), and 9 turkey (TUVU; *Cathartes aura*) vultures monitored with GPS transmitters in the southeastern U.S.

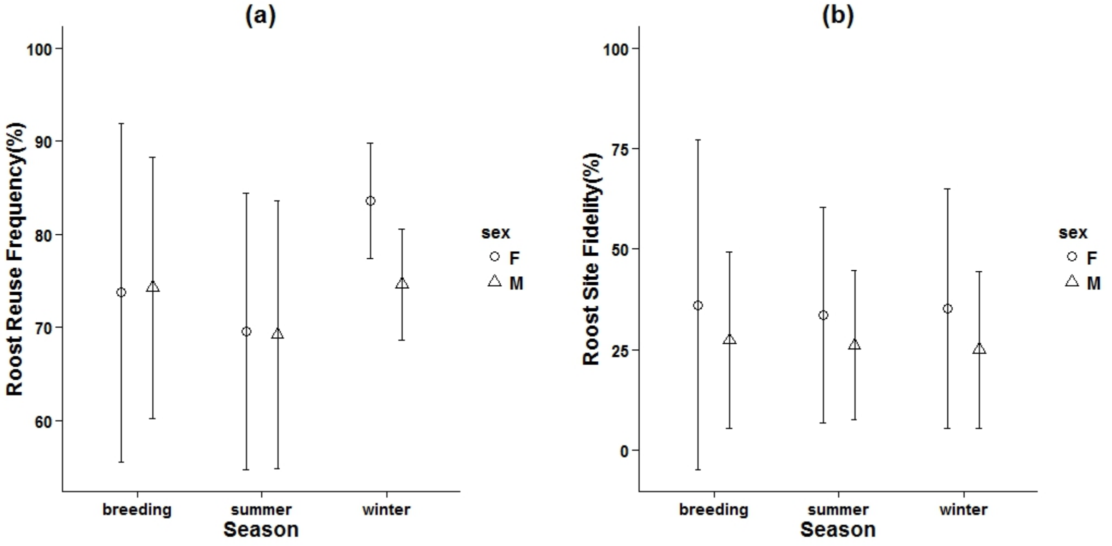

Figure 3-7. (a) Roost reuse (±95% CI) and (b) site fidelity (±95% CI) across breeding, summer, and winter seasons for 5 male and 4 female black vultures (*Coragyps atratus*) monitored with GPS transmitters in the southeastern U.S.

Table 3-3. Model selection results for repeated measures mixed model analyses based on selection ratios (sr) for individual habitat types by species (spp), month (mo) and sex (sex) within 100% home ranges with individual animal (id) as random effect.

Habitat Type	**Model**	**AIC wt**	**ΔAIC**	**AIC**	**Dev**
Wetland	sr~spp*sex+mo+(1|id)	0.85	0.00	335.60	321.6
	sr~spp+sex*mo+(1|id)	0.14	3.60	339.20	285.2
	sr~spp*sex*mo+(1|id)	0.00	10.80	346.40	246.4
	sr~spp+sex+mo+(1|id)	0.00	18.50	354.10	322.1
	sr~mo+(1|id)	0.00	19.30	354.90	326.9
	sr~spp+mo+(1|id)	0.00	20.80	356.40	326.4
	sr~spp*mo+(1|id)	0.00	30.30	365.90	313.9
	sr~1+(1|id)	0.00	33.70	369.30	363.3
	sr~spp+sex+(1|id)	0.00	33.70	369.30	359.3
	sr~spp*sex+(1|id)	0.00	35.00	370.60	358.6
	sr~spp+(1|id)	0.00	35.30	370.90	362.9
Forest	sr~spp+mo+(1|id)	0.33	0.00	358.30	328.3
	sr~spp+sex+mo+(1|id)	0.27	0.40	358.74	326.7
	sr~spp*sex*mo+(1|id)	0.19	1.10	359.40	259.4
	sr~spp*sex+mo+(1|id)	0.10	2.40	360.70	326.7
	sr~spp+sex*mo+(1|id)	0.05	3.70	362.00	308.0
	sr~mo+(1|id)	0.04	4.30	362.60	334.6
	sr~spp*mo+(1|id)	0.03	5.10	363.40	311.4
	sr~spp+(1|id)	0.00	8.90	367.20	359.2
	sr~spp+sex+(1|id)	0.00	9.40	367.70	357.7
	sr~spp*sex+(1|id)	0.00	11.40	369.70	357.7
	sr~1+(1|id)	0.00	13.40	371.70	365.7
Developed	sr~mo+(1|id)	0.40	0.00	1005.50	977.5
	sr~spp*mo+(1|id)	0.27	0.80	1006.30	954.3
	sr~spp+mo+(1|id)	0.17	1.70	1007.20	977.2
	sr~spp+sex+mo+(1|id)	0.09	3.10	1008.60	976.6
	sr~spp*sex+mo+(1|id)	0.07	3.60	1009.10	975.1
	sr~1+(1|id)	0.00	10.70	1016.20	1010.2
	sr~spp+(1|id)	0.00	12.50	1018.00	1010.0
	sr~spp+sex+(1|id)	0.00	13.90	1019.40	1009.4
	sr~spp*sex+(1|id)	0.00	14.10	1019.60	1007.6
	sr~spp+sex*mo+(1|id)	0.00	15.80	1021.30	967.3
	sr~spp*sex*mo+(1|id)	0.00	22.20	1027.70	927.7

Table 3-3. Model selection results for repeated measures mixed model analyses based on selection ratios (sr) for individual habitat types by species (spp), month (mo) and sex (sex) within 100% home ranges with individual animal (id) as random effect.

Habitat Type	Model	AIC wt	ΔAIC	AIC	Dev
Developed, Open	sqrt(sr+|min(sr)|)~mo+(1|id)	0.46	0.00	41.50	13.5
	sqrt(sr+|min(sr)|)~spp*sex+mo+(1|id)	0.27	1.10	42.60	8.6
	sqrt(sr+|min(sr)|)~spp+mo+(1|id)	0.18	1.90	43.40	13.4
	sqrt(sr+|min(sr)|)~spp+sex+mo+(1|id)	0.07	3.90	45.40	13.4
	sqrt(sr+|min(sr)|)~spp*mo+(1|id)	0.03	5.50	47.00	-5.0
	sqrt(sr+|min(sr)|)~spp+sex*mo+(1|id)	0.00	14.80	56.30	2.3
	sqrt(sr+|min(sr)|)~1+(1|id)	0.00	18.90	60.40	54.4
	sqrt(sr+|min(sr)|)~spp*sex+(1|id)	0.00	19.80	61.30	49.3
	sqrt(sr+|min(sr)|)~spp+(1|id)	0.00	20.90	62.40	54.4
	sqrt(sr+|min(sr)|)~spp+sex+(1|id)	0.00	22.90	64.40	54.4
	sqrt(sr+|min(sr)|)~spp*sex*mo+(1|id)	0.00	25.50	67.00	-33.0
Undeveloped, Open	sr~spp*sex+mo+(1|id)	0.23	0.00	381.10	347.1
	sr~spp*sex+(1|id)	0.21	0.20	381.30	369.3
	sr~spp+mo+(1|id)	0.14	1.00	382.10	352.1
	sr~spp+(1|id)	0.11	1.50	382.60	374.6
	sr~mo+(1|id)	0.09	1.80	382.90	354.9
	sr~1+(1|id)	0.07	2.30	383.40	377.4
	sr~spp+sex+mo+(1|id)	0.07	2.30	383.40	351.4
	sr~spp+sex+(1|id)	0.06	2.70	383.80	373.8
	sr~spp*mo+(1|id)	0.00	9.20	390.30	338.3
	sr~spp+sex*mo+(1|id)	0.00	10.30	391.40	337.4
	sr~spp*sex*mo+(1|id)	0.00	24.30	405.40	305.4
Landfill Distance (0-500m)	sqrt(sr+|min(sr)|)~spp*mo+(1|id)	0.57	0.00	525.40	473.4
	sqrt(sr+|min(sr)|)~spp+mo+(1|id)	0.16	2.50	527.90	497.9
	sqrt(sr+|min(sr)|)~spp+sex+mo+(1|id)	0.12	3.20	528.60	496.6
	sqrt(sr+|min(sr)|)~mo+(1|id)	0.09	3.70	529.10	501.1
	sqrt(sr+|min(sr)|)~spp*sex+mo+(1|id)	0.05	4.80	530.20	496.2
	sqrt(sr+|min(sr)|)~spp+sex*mo+(1|id)	0.01	9.10	534.50	480.5
	sqrt(sr+|min(sr)|)~spp+(1|id)	0.00	16.60	542.00	534.0
	sqrt(sr+|min(sr)|)~spp+sex+(1|id)	0.00	17.30	542.70	532.7
	sqrt(sr+|min(sr)|)~1+(1|id)	0.00	17.60	543.00	537.0
	sqrt(sr+|min(sr)|)~spp*sex+(1|id)	0.00	18.00	543.40	531.4
	sqrt(sr+|min(sr)|)~spp*sex*mo+(1|id)	0.00	26.00	551.40	451.4

Table 3-3. Model selection results for repeated measures mixed model analyses based on selection ratios (sr) for individual habitat types by species (spp), month (mo) and sex (sex) within 100% home ranges with individual animal (id) as random effect.

Habitat Type	**Model**	**AIC wt**	**ΔAIC**	**AIC**	**Dev**
Landfill Distance (500-1000m)	sqrt(sr+|min(sr)|)~mo+(1|id)	0.40	0.00	539.50	511.5
	sqrt(sr+|min(sr)|)~spp+mo+(1|id)	0.28	0.70	540.20	510.2
	sqrt(sr+|min(sr)|)~spp*mo+(1|id)	0.15	2.00	541.50	489.5
	sqrt(sr+|min(sr)|)~spp+sex+mo+(1|id)	0.12	2.40	541.90	509.9
	sqrt(sr+|min(sr)|)~spp*sex+mo+(1|id)	0.05	4.10	543.60	509.6
	sqrt(sr+|min(sr)|)~1+(1|id)	0.00	19.80	559.30	553.3
	sqrt(sr+|min(sr)|)~spp+(1|id)	0.00	19.90	559.40	551.4
	sqrt(sr+|min(sr)|)~spp+sex*mo+(1|id)	0.00	21.10	560.60	506.6
	sqrt(sr+|min(sr)|)~spp+sex+(1|id)	0.00	21.70	561.20	551.2
	sqrt(sr+|min(sr)|)~spp*sex+(1|id)	0.00	23.10	562.60	550.6
	sqrt(sr+|min(sr)|)~spp*sex*mo+(1|id)	0.00	33.90	573.40	473.4
Road Distance (0-500m)	sqrt(sr+|min(sr)|)~mo+(1|id)	0.51	0.00	452.60	424.6
	sqrt(sr+|min(sr)|)~spp+mo+(1|id)	0.27	1.30	453.90	423.9
	sqrt(sr+|min(sr)|)~spp+sex+mo+(1|id)	0.14	2.60	455.20	423.2
	sqrt(sr+|min(sr)|)~spp*sex+mo+(1|id)	0.06	4.30	456.90	422.9
	sqrt(sr+|min(sr)|)~1+(1|id)	0.01	8.00	460.60	454.6
	sqrt(sr+|min(sr)|)~spp+(1|id)	0.01	9.20	461.80	453.8
	sqrt(sr+|min(sr)|)~spp+sex+(1|id)	0.00	10.60	463.20	453.2
	sqrt(sr+|min(sr)|)~spp*sex+(1|id)	0.00	12.40	465.00	453.0
	sqrt(sr+|min(sr)|)~spp*mo+(1|id)	0.00	14.30	466.90	414.9
	sqrt(sr+|min(sr)|)~spp+sex*mo+(1|id)	0.00	19.40	472.00	418.0
	sqrt(sr+|min(sr)|)~spp*sex*mo+(1|id)	0.00	54.30	506.90	406.9

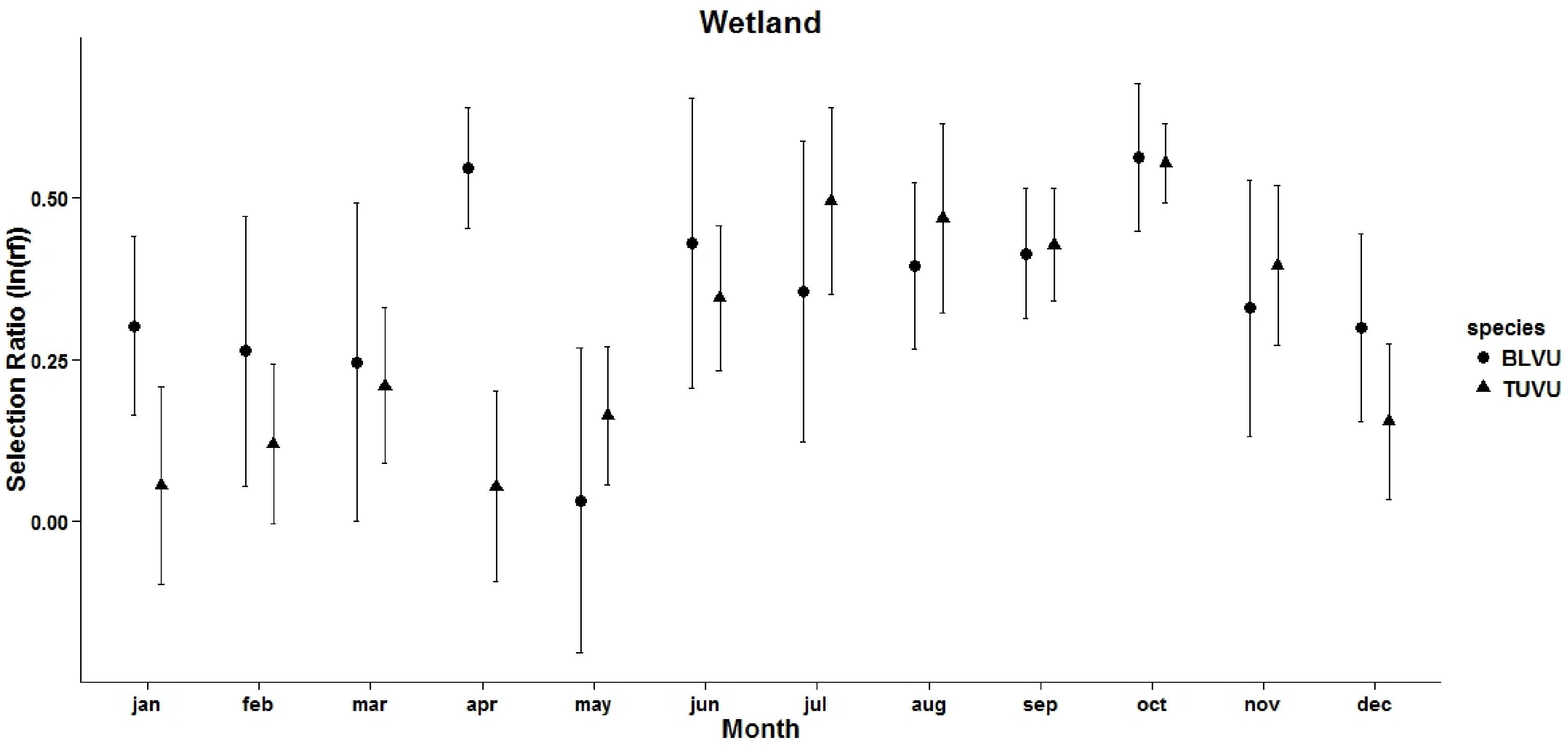

Figure 3-8. Mean (±SE) selection ratios (*ln*(rf)) for wetland habitat within 100% home ranges calculated from utilization distributions of 9 black (*Coragyps atratus*; BLVU;) and 9 turkey (*Cathartes aura*; TUVU) vultures tracked via GPS transmitters from September 2013 to August 2015.

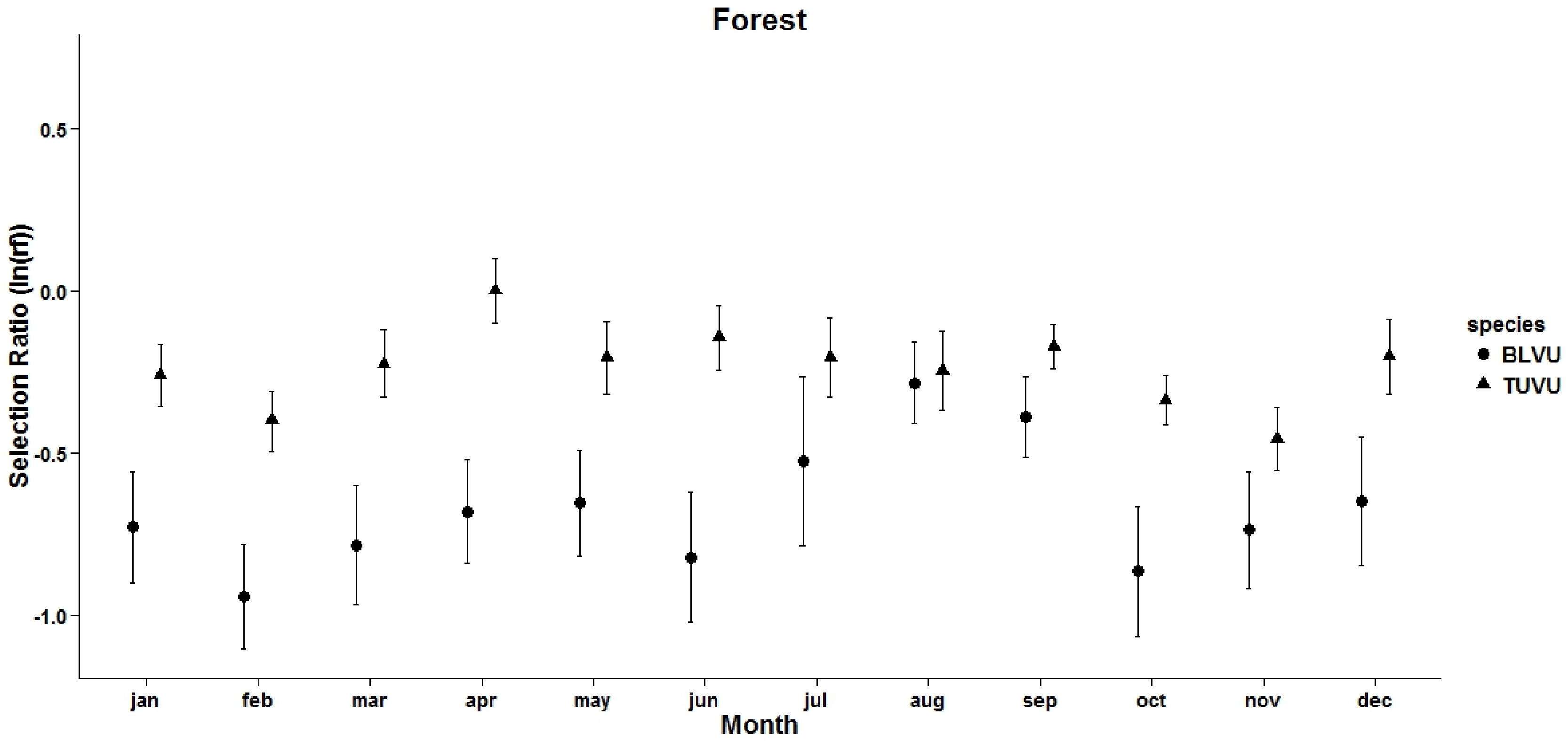

Figure 3-9. Mean (±SE) selection ratios (*ln*(rf)) for forest habitat within 100% home ranges calculated from utilization distributions of 9 black (*Coragyps atratus*; BLVU) and 9 turkey (*Cathartes aura*; TUVU) vultures tracked via GPS transmitters from September 2013 to August 2015.

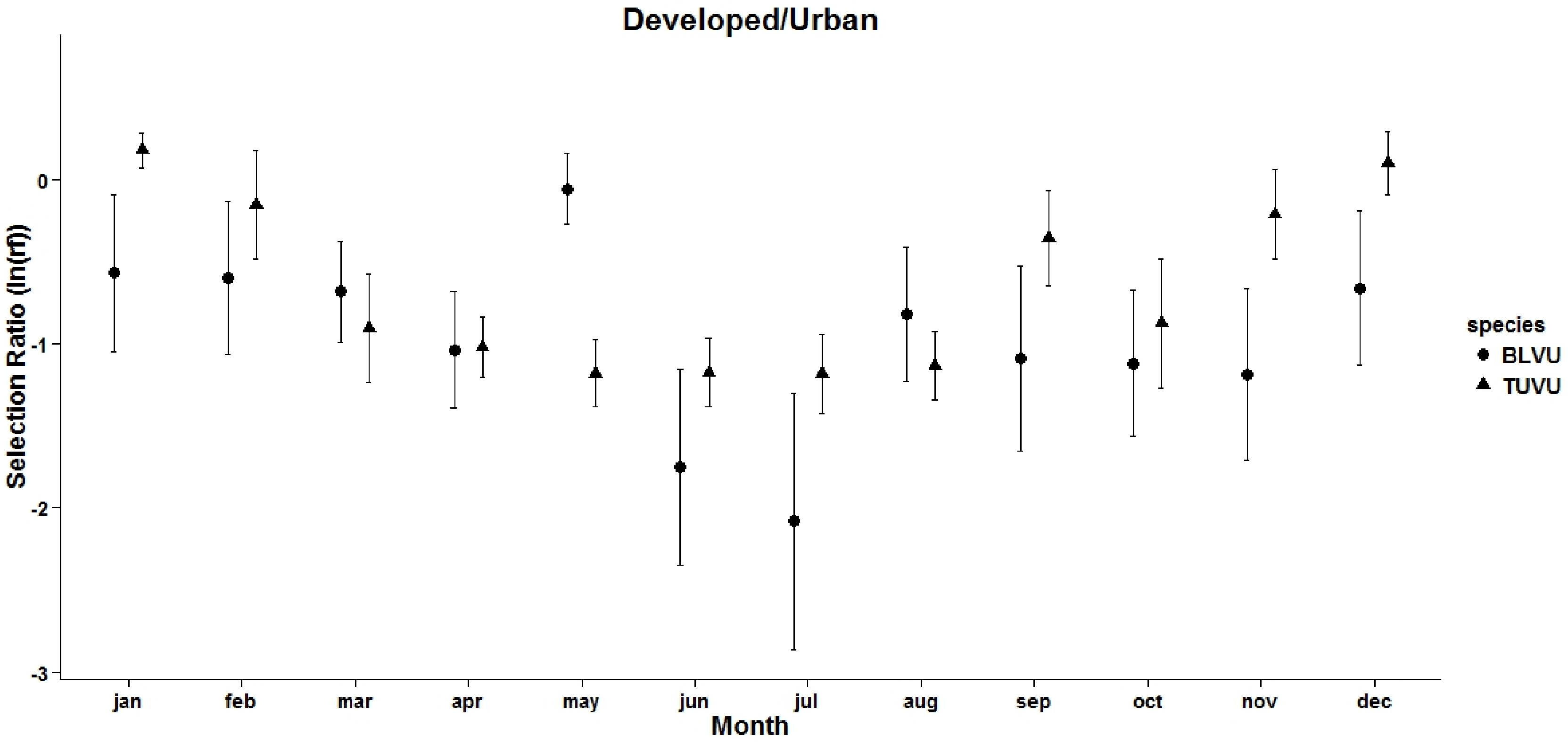

Figure 3-10. Mean (±SE) selection ratios (*ln*(rf)) for developed habitat within 100% home ranges calculated from utilization distributions of 9 black (*Coragyps atratus*; BLVU) and 9 turkey (*Cathartes aura*; TUVU) vultures tracked via GPS transmitters from September 2013 to August 2015.

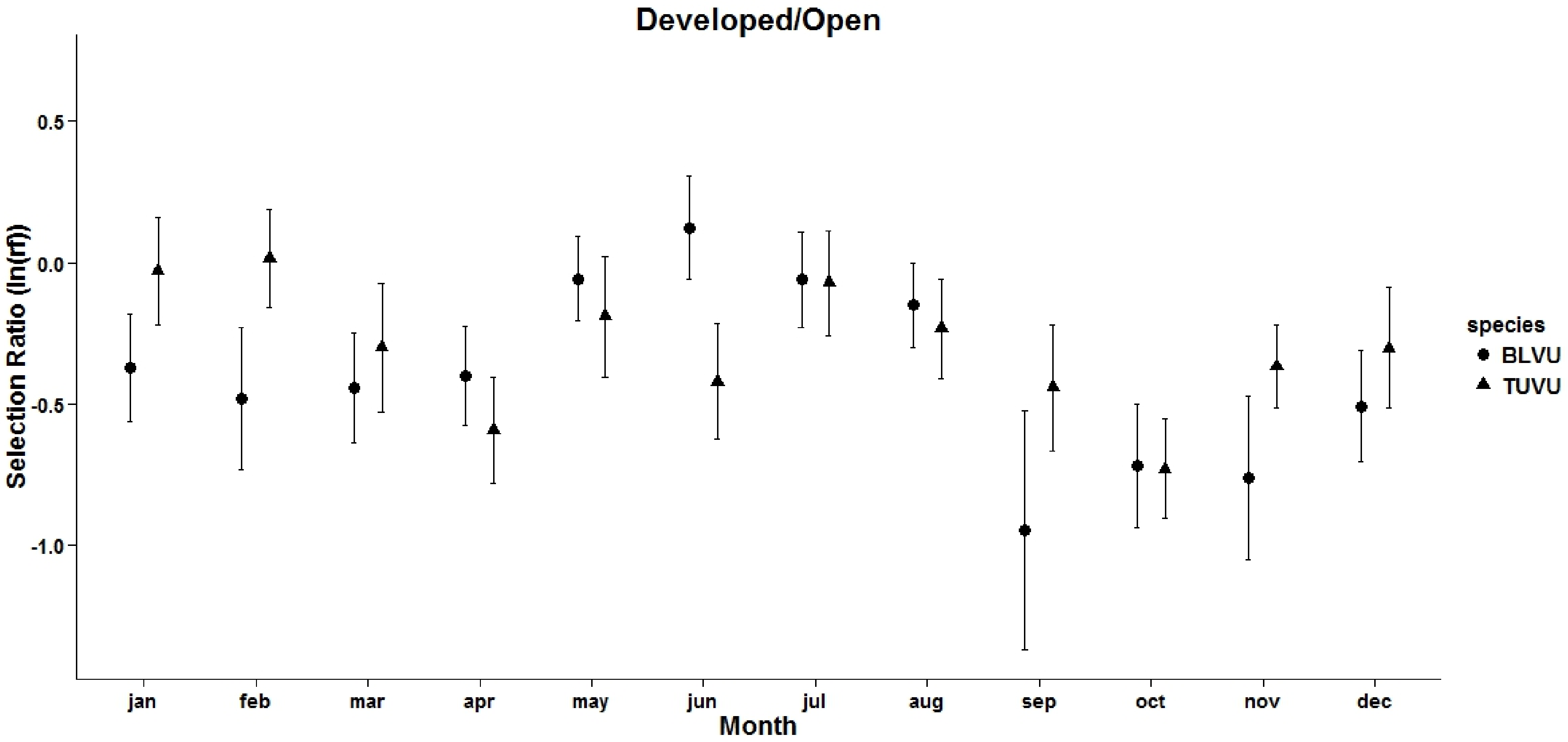

Figure 3-11. Mean (±SE) selection ratios (*ln*(rf)) for developed/open habitat within 100% home ranges calculated from utilization distributions of 9 black (*Coragyps atratus*; BLVU) and 9 turkey (*Cathartes aura*; TUVU) vultures tracked via GPS transmitters from September 2013 to August 2015.

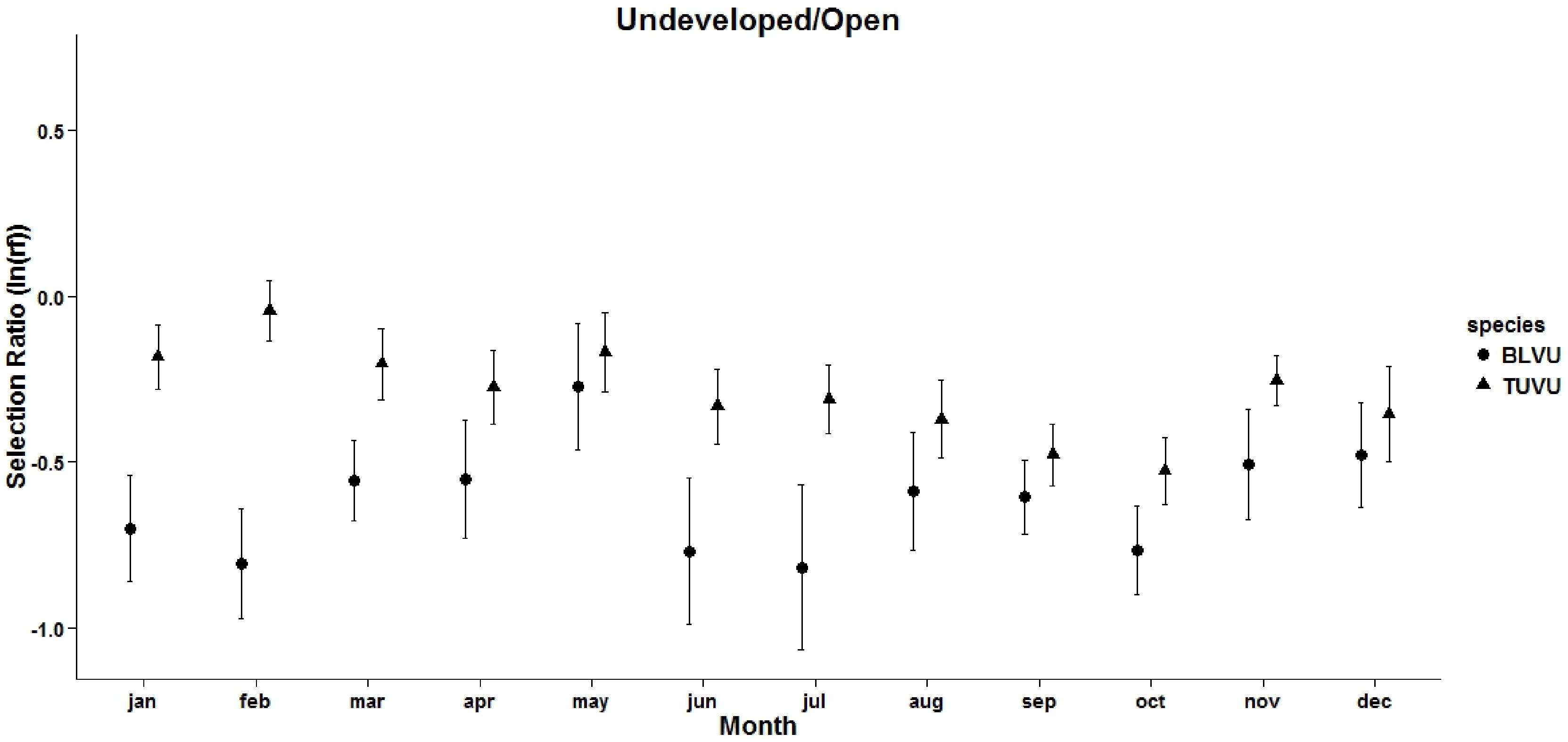

Figure 3-12. Mean (±SE) selection ratios (*ln*(rf)) for undeveloped/open habitat within 100% home ranges calculated from utilization distributions of 9 black (*Coragyps atratus*; BLVU) and 9 turkey (*Cathartes aura*; TUVU) vultures tracked via GPS transmitters from September 2013 to August 2015.

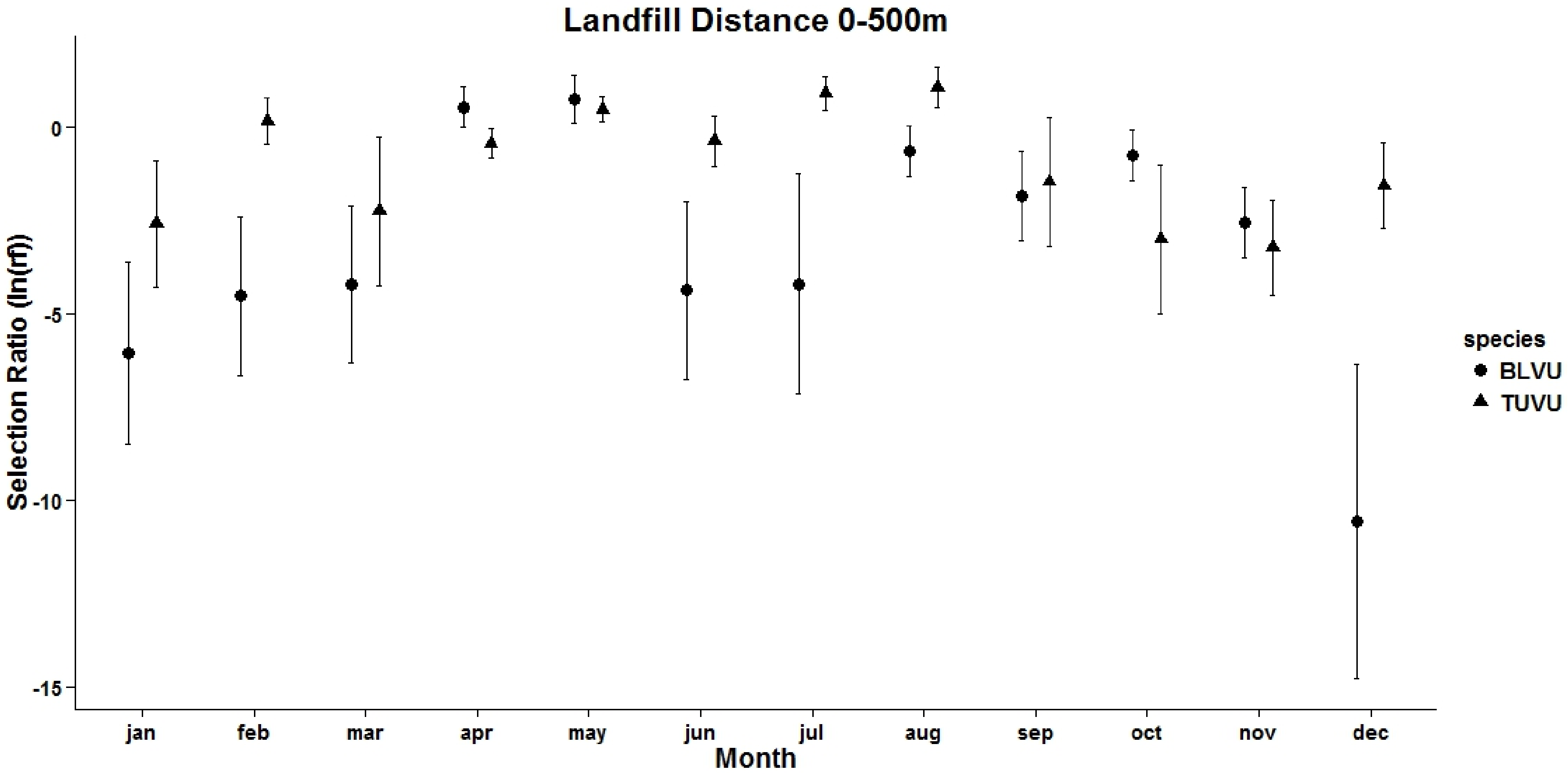

Figure 3-13. Mean (±SE) selection ratios (*ln*(rf)) for habitat within distances of 0-500m from landfill within 100% home ranges calculated from utilization distributions of 9 black (*Coragyps atratus*; BLVU) and 9 turkey (*Cathartes aura*; TUVU) vultures tracked via GPS transmitters from September 2013 to August 2015.

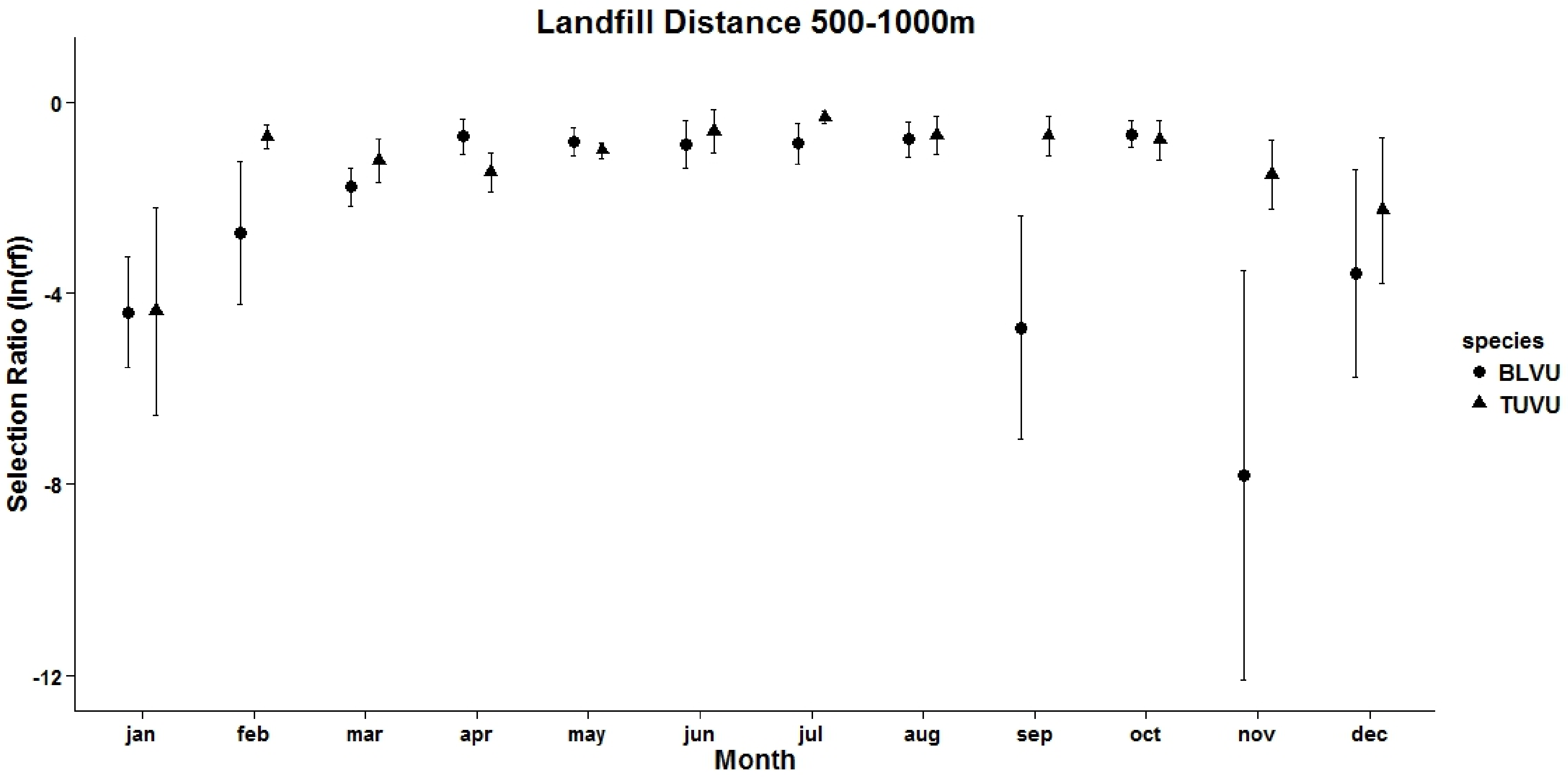

Figure 3-14. Mean (±SE) selection ratios (*ln*(rf)) for habitat within distances of 500-1,000m from landfill within 100% home ranges calculated from utilization distributions of 9 black (*Coragyps atratus*; BLVU) and 9 turkey (*Cathartes aura*; TUVU) vultures tracked via GPS transmitters from September 2013 to August 2015.

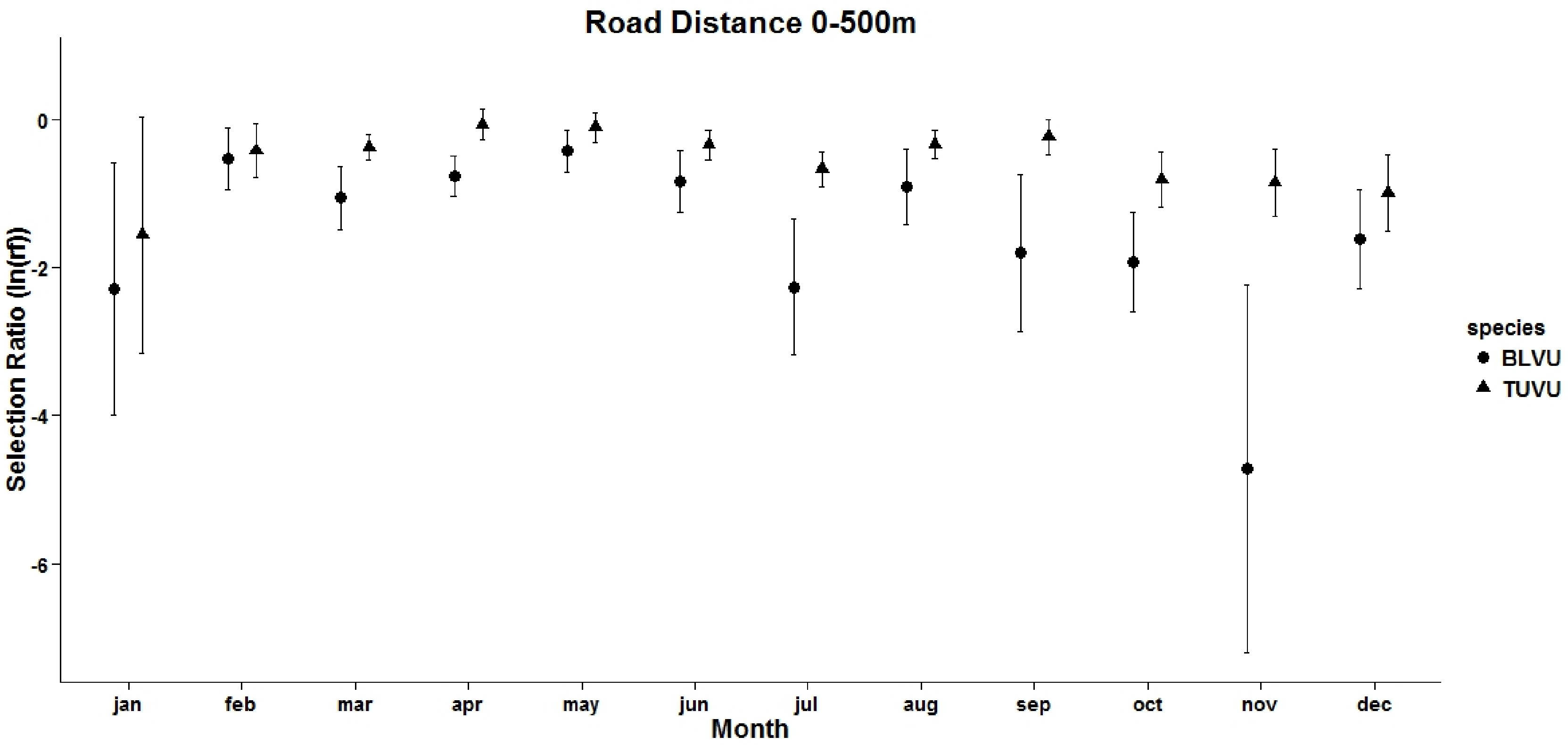

Figure 3-15. Mean (±SE) selection ratios (*ln*(rf)) for habitat within distances of 0-500m from road within 100% home ranges calculated from utilization distributions of 9 black (*Coragyps atratus*; BLVU) and 9 turkey (*Cathartes aura*; TUVU) vultures tracked via GPS transmitters from September 2013 to August 2015.

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CHAPTER 4. CONCLUSION

In the interest of filling important gaps in our understandings of vulture ecology, the objective of my master's research was to quantify space use, activity patterns, and resource selection of sympatric black (*Coragyps atratus*) and turkey (*Cathartes aura*) vultures with greater resolution than previous studies conducted on these species. Recent advancements in tracking device technologies allow the collection of fine-scale spatial data, which provide information that has been unattainable in many previous studies of vulture spatial ecology. In my research, I utilized GPS data collected using solar-powered GSM/GPS transmitters affixed to black and turkey vultures to monitor fine-scale vulture movements and to assess potential differences in resource utilization among individuals, species, sexes, and seasons.

In Chapter 2, I conducted the first assessment of monthly home range and core area sizes with consideration to sex for black and turkey vultures. I elucidated differences in monthly, seasonal, and annual activity patterns based on analyses of fine-scale movement data. I conducted these assessments based on 321 monthly 95% home ranges and 50% core areas derived from >2.8 million fixes collected from 9 black and 8 turkey vultures using the dynamic Brownian Bridge Movement Model (dBBMM). Using these data, I compared monthly home range and core area sizes by species and sex and found turkey vulture home ranges to be about two times larger than those of black vultures but only over a portion of the year. I also did not find any differences in core area sizes throughout the year, and home range sizes were comparable over months in the breeding season. I found no difference between home range and core area sizes of male and female black vultures; however, core areas of females were notably larger than those of males during March to May within the breeding season. I also compared monthly, seasonal, and annual proportions of flight, stationary, and switch states (transitions between flight and stationary) by species and found turkey vultures to have significantly higher activity rates than black vultures across all temporal scales, demonstrated by greater proportions of time spent in flight as well as higher switch states.

In Chapter 3, I assessed habitat characteristics of evening roosts, roost reuse and site fidelity, as well as aspects of monthly resource selection within home ranges based on utilization distributions (UDs) developed using the dBBMM. Evening roost locations were extracted from GPS location data from transmittered birds and I quantified proportions of habitats associated with roost sites and compared proportional use of roost habitats among species, sexes and seasons (breeding, summer and winter). Habitat variables included proximity to roads (distances of 0-500m), proximity to landfills (distance classes of 0-500m, and 500-1,000m), wetland, forest, developed, developed/open, undeveloped/open habitats types. I found turkey vulture evening roosts comprised a significantly greater proportion of forest habitat, whereas black vulture evening roosts comprised a greater proportion of developed/urban habitat. For both species, use of roost sites near wetlands was highest in winter and lowest in breeding seasons. I compared seasonal roost reuse frequency and site fidelity between species and found turkey vultures to have lower roost reuse frequencies than black vultures. Roost site fidelity was substantially higher in black vultures, although not significantly.

I also measured resource selection by black and turkey vultures by calculating ratios of use derived from UDs relative to the portion of available habitat within 100% home ranges. I developed a suite of *a-priori* resource selection models for each habitat type using linear mixed-effects models and ranked models using Akaike's Information Criterion. From these analyses I found month and species to be strong factors influencing selection for most habitats within the home range. I also found selection for wetland habitats to be strongest across all months for both species. Selection for habitat types within distances of 0-500m from roads and distances of 0-500m and 500-1,000m from landfills was limited and lowest during the winter months for both species. Selection of most habitats also fluctuated by month for both species. Selection for forest habitat was greatest in turkey vultures throughout all months except the end of summer. Similarly, I found black vulture selection of developed/open habitats to be significantly higher in the summer months.

The array of conclusions drawn from my master's research contributes new information to our understandings of the patterns and mechanisms underlying differences in space use, movement patterns and resource selection by sympatric black and turkey vultures. Specifically, spatio-temporal variations in the spatial ecology of black and turkey vultures are apparent when examining the movement behavior of these species at fine spatial and temporal scales. My data also revealed that space use by black and turkey vultures varies over the course of an annual cycle, which is a pattern previously undetected at coarser temporal scales. Differences in resource selection also emerged at finer spatial and temporal scales and provide evidence for habitat segregation and niche differentiation by these species, for which competition exists in areas of sympatry. These data build upon our understanding of vulture spatial ecology and provide insights into underlying behavioral mechanisms facilitating niche differentiation between species, which ultimately should provide critical insights into the conservation and management of this important group of birds.