Using multiple data sources to investigate foraging niche partitioning in sympatric obligate avian scavengers

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Abstract. As carrion feeders competing for a limited and ephemeral resource, avian scavengers are ideal model organisms to study mechanisms of niche partitioning. Previous work has focused on observations of species' interactions at carcasses, and although fruitful, the inclusion of behavior beyond that at carcasses, such as movement patterns, could yield a more comprehensive understanding of mechanisms of foraging niche partitioning. Our goal was to assess how differences in physiological, morphological, and social characteristics between sympatric black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*) manifest interspecific variation in movement patterns, foraging habitats, and carcass use to reduce direct competition. Both species are obligate scavengers that co-occur across much of the New World. Turkey vultures are solitary foragers with enhanced olfactory capabilities and wings optimized for energy-efficient low-altitude soaring. Black vultures are aggressive, heavier bodied, and forage socially. We assessed interspecific variation in carcass exploitation using experimental carcass trials encompassing a range of habitats, carcass sizes, and seasons, and used GPS telemetry to compare how soaring conditions influenced daily space use and diurnal patterns of movement activity for each species. Turkey vultures occurred more often at small (i.e., rabbit) carcasses, and those obscured by forest cover than black vultures, and were the first vultures recorded at 94% of carcasses visited by both species. Both species increased movement rates and daily ranges when soaring conditions were favorable; however, turkey vultures had higher travel rates regardless of soaring conditions. Our results suggest the olfactory sense of turkey vultures allows them to locate smaller and visually obscured carcasses more efficiently than black vultures, facilitated by wing morphology that allows them to forage over large areas efficiently. Socially foraging black vultures appear specialized at locating larger carcasses in open habitats, which does not require as much foraging flight as turkey vultures. Our study illustrates how inclusion of movement ecology into niche partitioning studies provides a more complete understanding of the mechanisms of coexistence in avian scavenger guilds. This approach may provide important information to guide conservation efforts, such as supplemental feeding, of imperiled vulture species.

Key words: black vulture; *Cathartes aura*; *Coragyps atratus*; movement ecology; niche differentiation; resource specialization; telemetry; turkey vulture.

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INTRODUCTION

To coexist, ecologically similar species must evolve mechanisms of niche differentiation to limit direct competition for resources (Schoener 1974, Brown 1989). Niche differentiation can occur through the development of divergent behavioral, physiological, or morphological traits, which result in specialized abilities of individual species to exploit resources. This variation in resource specialization reduces interspecific competition and facilitates coexistence (Tilman 1987). By studying how sympatric species occupying a similar trophic position exploit resources, insight can be gained into the processes that structure assemblages of ecologically similar species.

Avian scavenger guilds are diverse assemblages of obligate (e.g., vultures) and facultative (e.g., eagles, kites, and corvids) carrion feeders that compete for a limited food resource that, under natural conditions, is spatially and temporally unpredictable and ephemeral (DeVault et al. 2003, Beasley et al. 2015). Despite this, carrion offers considerable biomass for relatively little energetic investment compared to predation, and multi-species guilds of obligate avian scavengers have evolved independently in both the Old and New World (Hertel 1994). Avian scavengers are interesting species in which to investigate foraging niche partitioning given their specialization for, and reliance on, carrion as a food source. Much previous work in this field was based on observations at natural or experimentally located carcasses (Wallace and Temple 1987, Lemon 1991, Buckley 1996, Cortés-Avizanda et al. 2012, Kendall 2014). While informative, carcass observations can be limiting in that other potentially important behavioral mechanisms of niche partitioning are unobserved.

Comparatively, little work has examined the movement ecology of sympatric avian scavengers. Morphological characteristics, such as wing loading (ratio of body mass to wing area), have important implications for the energetic performance of soaring birds (Pennycuick 1983, Shepard and Lambertucci 2013) and variation in such characteristics should result in variation in soaring efficiency, creating a situation in which some species are able to travel and forage in an energetically efficient manner in conditions in which competitors are less able to do so. This in turn may lead to differentiation in activity budgets and daily foraging ranges (Shepard and Lambertucci 2013). Although a potentially important aspect of niche differentiation, the data needed to quantify fine-scale movements of such species have been traditionally difficult to obtain. However, recent advancements in solar-powered GPS tracking technology now allow researchers to track movements of vultures at high temporal resolutions for periods >1 yr (Byrne et al. 2017), making such studies feasible.

Black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*) are widely distributed New World vultures, with a high degree of range overlap in North and South America. Both species are obligate scavengers that are abundant year-round in the southeastern portion of North America, where they are the only vulture species present. Despite their similar trophic position, it is believed direct competition between species is reduced by the interaction of key differences in morphology, physiology, and social behavior that create differences in realized foraging niche. Morphologically, turkey vultures have lower body mass and lighter wing loading capacity than black vultures, which should create interspecies variation in soaring efficiency (Shepard and Lambertucci 2013). Physiologically, turkey vultures have a well-developed olfactory system (Bang and Cobb 1968, Wenzel and Sieck 1972), which is believed to help locate carcasses when foraging (Stager 1964, Houston 1986, Grigg et al. 2017). Conversely, there is no evidence to suggest black vultures rely on olfaction when foraging. Behaviorally, black vultures are socially gregarious, forming long-term coalitions of related adults (Parker et al. 1995) and using social cues to enhance foraging efficiency (Rabenold 1987, Buckley 1997), whereas there is little evidence to suggest social foraging in turkey vultures. Black vultures are aggressive and, when present in numbers, commonly usurp or severely limit feeding opportunities of other avian scavengers, including turkey vultures (Buckley 1996, Carrete et al. 2010).

We combined movement ecology and experimental carcass observations to test several hypotheses regarding variation in movement and carcass exploitation patterns expected to arise from morphological, physiological, and behavioral differences between species. We used

experimental carcass trials along a gradient of canopy cover to test the hypothesis that turkey vultures are more likely to locate small and visually obscured carcasses. We also hypothesized turkey vultures will arrive at carcasses prior to black vultures, especially carcasses under forest cover. We used GPS telemetry to test the hypothesis that turkey vultures are less reliant on strong thermal formation and that regardless of soaring condition, turkey vultures travel more than black vultures. We also hypothesized each species may exhibit different diurnal movement patterns, as turkey vultures may forage more than black vultures during hours characterized by poor soaring conditions, such as early morning and evening.

METHODS

Study site

All carcass trials and vulture capture occurred on the Savannah River Site (SRS), a 78,000-ha limited-access nuclear production and research facility owned by the U.S. Department of Energy located near Aiken, South Carolina, USA. Savannah River Site is located in the upper Atlantic Coastal Plain, and the topography is relatively flat with elevation ranging from 30 to 115 m above sea level (White and Gaines 2000). The landscape is primarily forested (~94%), with approximately 64% of the total area planted in loblolly pine (*Pinus taeda*), longleaf pine (*P. palustris*), and slash pine (*P. elliottii*) managed for timber production by the U.S. Forest Service (Workman and McLeod 1990). The remaining forest cover consists primarily of bottomland hardwood forests located along lower lying drainages and the Savannah River (Workman and McLeod 1990). Interspersed within the forest matrix are a number of nuclear industrial and research facilities.

Carcass trials

Carcass trials were conducted as part of a larger study of scavenger community dynamics on the SRS during 2013–2014 (Turner et al. 2017). We used rabbit (*Sylvilagus* spp.) and wild pig (*Sus scrofa*) carcasses to represent small and large carrion items, respectively. Rabbit carcasses ranged from 0.79 to 1.53 kg, and wild pig (hereafter; pig) carcasses from 23 to 57 kg. Frozen rabbit

carcasses were purchased from a commercial provider (RodentPro.com, Inglefield, Indiana, USA). Pig carcasses consisted of euthanized animals acquired from ongoing pig management practices on SRS. Whenever possible, pigs were deployed immediately following euthanasia and otherwise were stored either by refrigeration (<72 h) or by freezing (>72 h). Frozen carcasses were thawed indoors before deployment. Trials occurred across four habitat types (clear cut, immature pine, mature pine, and hardwood forests) and two seasons (warm and cool). Clear cuts were created during forestry operations in 2011–2013 and had no canopy cover. Immature pine stands were dense, minimally thinned planted stands ~11–26 yr old characterized by dense canopy. Mature pine stands (>26 yr) included understory vegetation (e.g., hardwood saplings) and canopy cover that allowed some sunlight to reach the forest floor. Hardwood forests were non-planted, mixed-species patches with canopy cover that varied seasonally with leaf senescence. The warm season (May 2013–September 2013) was delineated based on months with average high temperatures >26.7°C, and the cool season (December 2013–March 2014) by months with average low temperatures <4.4°C.

Twelve sites ≥10 ha of each habitat type were selected, with a minimum distance of 1 km between sites. Sites were used in both seasons, and during each season, a single rabbit and pig carcass was placed at a randomly selected point within each site (96 total trials for each carcass type, 24 in each habitat across two seasons). Only one carcass was placed within a site at a time. Carcasses within a site were located ≥100 m from each other. An infrared remote sensing camera (Reconyx, Holmen, Wisconsin, USA) set ~2 m from each carcass was programmed to take a burst of three pictures followed by a 1-min rest period. Carcasses were staked to the ground to prevent scavengers from moving them out of camera view.

Trial length varied with carcass size and season, and represented the approximate amount of time expected for carcasses to be fully decomposed or scavenged based on pilot studies. During the warm season, pig carcasses were monitored for ≥2 weeks with a 2-week lag period before another carcass type was placed in that site. The lag period was assumed sufficient for scavengers to lose

interest and no longer periodically return. Rabbit carcasses were monitored for ≥1 week with a lag period of 1 week. During the cool season, trial lengths were extended to account for reduced invertebrate and microbial activity (Putnam 1978, DeVault et al. 2003) to 3 and 4 weeks for rabbit and pig carcasses, respectively.

Following each trial, camera images were viewed and the presence or absence of each vulture species was recorded, along with the time of the first record of each species. We used logistic regression to model the probability of each species occurring at a carcass as a function of carcass type, habitat type, and season. Occurrence was defined as whether a species was recorded at a carcass. All predictor variables (carcass, habitat, and season) were categorical with "pig," "clear cut," and "cool" representing the respective reference conditions.

As pig carcasses were visited extensively by both species in each season (see *Results*), we measured time-to-arrival of the first member of each species at pig carcasses to test the hypothesis that turkey vultures locate carcasses quicker than black vultures. Similar to Houston (1986), we measured time-to-arrival in hours of daylight elapsed since the carcass was placed in the environment because (1) carcasses were placed at different times of day, and (2) vultures did not forage nocturnally.

Carcass observations may be influenced by changes in relative abundance of either species on our study area. Although we were not able to quantify vulture population densities on SRS directly, several lines of evidence lead us to believe there were no significant changes. Both species are commonly observed on the SRS year-round, and previous tracking indicates many individuals of both species are resident to the immediate area (DeVault et al. 2004). Eleven years of monthly counts of vultures observed in flight at Augusta Regional Airport (<10 km from SRS) suggests seasonal changes in total abundance; however, relative abundance between species is consistent year-round (Appendix S1: Fig. S1).

Capture and tracking

We captured vultures using an air-propelled net launcher (Wildlife Control Supplies, East Granby, Connecticut, USA) at sites baited with

pig carcasses interspersed throughout the SRS during June–August 2013, and April 2014. We measured wing chord length (cm) and weight (kg) of each vulture and used the wing length-to-body mass ratio as a proxy for wing loading, where a larger ratio corresponds to lighter wing loading. We fit a subset of vultures with 70 g solar-powered GPS transmitters (Microwave Telemetry, Columbia, Maryland, USA) attached via Teflon ribbon backpack harness. Transmitters collected GPS locations on a dynamic schedule that varied from 1- to 120-min intervals during daylight hours contingent on battery charge. Transmitters were programmed to remotely transmit data daily via the Global System for Mobile Communication. We targeted non-migratory individuals by trapping outside the migration seasons (Kirk and Mossman 1998, Buckley 1999). All vultures were released at the capture site immediately after processing. Transmitter weights were <4% of vulture body weight, which was unlikely to cause significant negative impacts (Phillips et al. 2003, Sergio et al. 2015), and all capture and handling was in accordance with the University of Georgia Animal Care and Use Protocol No. A2013 02-004-Y2-A2.

We filtered outlying GPS locations by first removing all 2D fixes and then applying a speed filter to remove locations associated with estimated mean minimum horizontal flight speeds ≥90 km/h, a conservative cutoff speed based on top-speed observations of a migrating turkey vulture (68 km/h; Mandel et al. 2008). We limited our analysis to summer (June–August) and winter (December–February) seasons because these are (1) periods of relative weather stability, (2) outside of primary migration seasons, and (3) outside of primary nesting seasons for both species, limiting the potentially confounding influence of nesting-related behaviors. To ensure individuals were resident during study periods, we visually examined movement paths and removed any days that were indicative of migratory behavior.

The dynamic collection schedule of the GPS transmitters resulted in locations taken at variable time intervals. In order to standardize data and make meaningful behavioral comparisons, we fit a continuous-time correlated random walk model (CTCRW; Johnson et al. 2008) to each vulture's track using the package "crawl" (Johnson

2015) in R (R Core Team 2015). The CTCRW is a state-space model of animal movement that accounts for measurement error and temporally irregular data. We used a variation of the model that allows movement to halt when vultures were stationary by incorporating instantaneous speed reported with GPS fixes as a stopping covariate (Johnson et al. 2008). Previous testing indicated speed was a reliable index to whether a vulture was moving or stationary (e.g., roosting or resting; Byrne et al. 2017). Thus, we assumed when a GPS location reported a speed estimate of 0 km/h the vulture was not flying. We used fitted models to predict vulture locations at 10-min intervals, a compromise between high-resolution movement information and temporal variability in GPS location data.

We extracted all location estimates from 30 min before sunrise to 30 min after sunset daily and used the Env-DATA tool in Movebank (www.movebank.org) to obtain an estimate of thermal uplift (TU) specific to each location (Dodge et al. 2013). Thermal uplift is a measure of the upward velocity (m/s) of airflow caused by heating of the land by solar radiation. These updrafts (i.e., thermals) are commonly exploited by soaring birds to facilitate energy-efficient travel (Bohrer et al. 2012). Thus, stronger TU should correlate with increased thermal formation and serve as a measure of favorable flight conditions. Thermal uplift was calculated using equations detailed in Bohrer et al. (2012) based on data from the European Center for Medium-Range Weather Forecasts ERA-Interim global atmospheric reanalysis, which archives climatic data at a spatial resolution of 0.7° and a temporal resolution of 6 h. Location-specific estimates of thermal uplift were obtained by bilinear interpolation from the four nearest grid-cell centers.

Daily space use

We used dynamic Brownian bridge movement models (dBBMM) to estimate space use daily for each vulture (Kranstauber et al. 2012). A dBBMM allows estimation of the utilization distribution (UD) for a given time period conditioned on an animal's movement path while accounting for heterogeneity in behavior (Kranstauber et al. 2012). We fit a dBBMM to the full movement path of each vulture seasonally using the package "move" in R (Kranstauber and Smolla 2016), then estimated UDs daily on a 20-m^2 spatial grid based on movements between sunrise and sunset (Byrne et al. 2014). We quantified ranges as the area within the 99% isopleth of each daily UD, providing a measure of the area traversed by a vulture each day. We used the maximum TU value associated with diurnal locations each day as a measure of soaring conditions and modeled daily ranges of each species seasonally as a function of maximum TU using generalized linear mixed-effects models (GLMM; gamma distribution) with vulture ID included as a random effect. To account for temporal autocorrelation, we included ranges of preceding days directly as independent covariates (Hamel et al. 2012). We sequentially added covariates corresponding to lagged daily ranges (1 d prior, 2 d prior, etc.) until autocorrelation function plots (ACF) indicated no residual correlation. We used the fixed-effects estimates of GLMM models to predict and compare daily ranges of each species as a function of TU for each season.

Diurnal movement patterns

To quantify diurnal patterns of movement, we calculated the minimum distance traveled hourly from 05:00 to 20:00 hours daily for each vulture by summing the step length distances between each pair of locations. We modeled hourly movement using GLMMs (gamma distribution) with hour as a categorical fixed-effect independent variable, and vulture ID as a random effect. We modeled each species and season separately. We used the fixed-effects estimates from each model to predict expected hourly travel distances for each species/season combination.

RESULTS

Carcass trials

After censoring sites with malfunctioning cameras, we successfully recorded activity at 92 rabbit and 85 pig carcasses, with black and turkey vultures recorded at 63 and 106 carcasses, respectively (Table 1). Black vultures were never recorded at a carcass that was not also visited by turkey vultures. Turkey vultures were the first vulture species recorded at 94% of carcasses. Black vultures were recorded first at only four carcasses (exclusively pig carcasses during the warm season), and at three of those carcasses,

Table 1. Number of wild pig and rabbit carcasses visited by black and turkey vultures in four habitat types during warm (May–September) and cool (December–March) seasons on the Savannah River Site, South Carolina, USA, 2013–2014.

Carcass	Season	Habitat	N	Black Vulture	Turkey vulture
Rabbit	Warm	Clear cut	11	4	11
		Hardwood	12	0	1
		Immature pine	12	0	4
		Mature pine	11	0	2
	Cool	Clear cut	12	1	5
		Hardwood	11	0	1
		Immature pine	11	0	0
		Mature pine	12	0	1
Pig	Warm	Clear cut	12	12	12
		Hardwood	10	9	10
		Immature pine	9	8	9
		Mature pine	9	9	9
	Cool	Clear cut	12	8	12
		Hardwood	9	3	8
		Immature pine	12	4	12
		Mature pine	12	5	10

Note: N, number of carcasses with camera data.

the timestamps between pictures of the first black and turkey vulture differed by <3 min.

Season, habitat, and carcass type influenced probability of occurrence for both species (Appendix S1: Table S1). For both species, probability of occurrence was greater during the warm season, in clear cuts relative to forested habitats, and at pig carcasses relative to rabbit carcasses (Fig. 1). Probability of occurrence was high at pig carcasses in all habitats during the warm season (Fig. 1), with turkey vultures recorded at all pig carcasses during the warm season (Table 1). During the cool season, turkey vultures were recorded less frequently at pig carcasses in forested habitats compared to the warm season; however, they were still recorded at all carcasses in clear cuts. Probability of black vulture occurrence at pig carcasses during the cool season was lower than during the warm season in all habitats, particularly forested habitats (Fig. 1).

Turkey vultures were recorded at rabbit carcasses with much greater frequency than black vultures (Table 1). Turkey vultures were recorded at all rabbit carcasses in clear cuts during the warm season, and 33.3%, 18.2%, and 8.3% of rabbit carcasses in immature pine, mature pine, and hardwood plots, respectively.

Cool season occurrence of turkey vultures at rabbit carcasses was primarily limited to clear cuts (71.4%), with no records in immature pine plots. Black vultures were rarely recorded at rabbit carcasses, with only a single record during the cool season. Black vulture occurrence at rabbit carcasses was exclusive to clear cuts in both seasons.

During the warm season, mean time-to-arrival of the first member of either species at pig carcasses was nearly identical; black vulture = 28.5 h, turkey vulture = 28.6 h. Both species arrived at pig carcasses in clear cuts faster (mean = 16.7 h) than in forested habitats (mean = 33.9 h; Fig. 2). At 47% of pig carcasses visited by both species during the warm season, the first individuals of each species were recorded on the same day.

Time-to-arrival at pig carcasses was considerably longer in the cool season, with mean time-to-arrival = 111.2 and 97.2 h for black and turkey vultures, respectively. Although time-to-arrival for both species was similar in clear cuts during the cool season, black vultures lagged well behind turkey vultures in forested habitats (Fig. 2). Only once during the cool season were the first members of each species recorded on the same day.

GPS tracking and movement

We captured 147 black vultures and 137 turkey vultures. Wing:body mass ratio of turkey vultures (mean = 28) was significantly higher than black vultures (mean = 19; $t = -31.2$, df = 195, $P < 0.001$). We tracked 12 black vultures and nine turkey vultures with GPS between 18 June 2013 and 31 March 2015, and all but one black vulture was tracked continuously over multiple seasons (Appendix S1: Table S2). Data filtering resulted in <1% of GPS locations being removed. Mean number of GPS locations reported during daylight hours was 222 (standard deviation [SD] = 123) and 133 (SD = 114) in summer and winter, respectively. GPS-tracked turkey vultures ranged over a larger geographical area than black vultures; however, there was considerable overlap in species distributions in both seasons (Fig. 3). Median daily ranges of black vultures were 13 km^2 (range: 0.9–460 km^2) during summer and 14 km^2 (range: 1–250 km) during winter. Median daily ranges of turkey vultures were 39 km^2 (range: 2–973 km^2) in summer and 24 km^2 (range: 2–585 km^2) in winter.
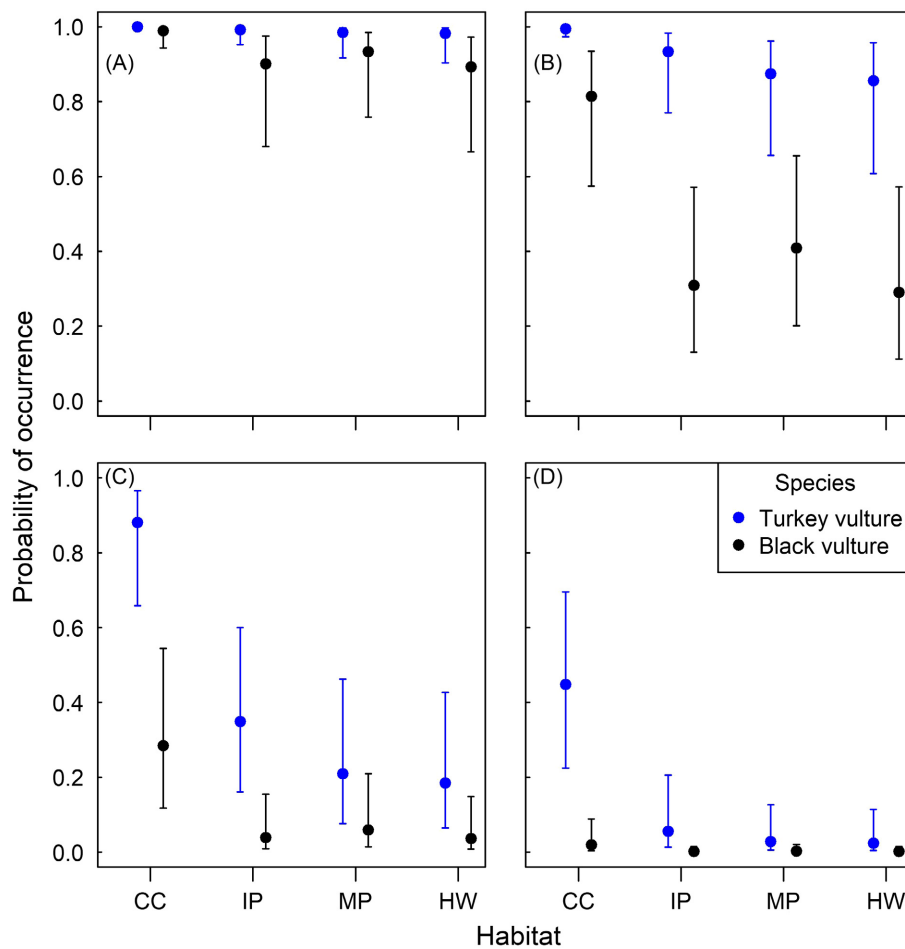
Fig. 1. Probability of occurrence of black and turkey vultures at wild pig carcasses during the warm (A) and cool (B) seasons, and at rabbit carcasses during the warm (C) and cool (D) seasons in four habitat types (CC, clear cut; IP, immature pine; MP, mature pine; and HW, hardwood) at the Savannah River Site, South Carolina, 2013–2014, based on logistic regression models. Bars = 95% confidence intervals.

Autocorrelation function plots indicated inclusion of a 1-d lag was sufficient to account for temporal autocorrelation in daily ranges for both species during summer, while a 2- and 1-d lag was sufficient for black and turkey vultures, respectively, in winter. There was a positive correlation between daily range size and maximum daily TU in all seasons for both species (coefficient values available in Appendix S1: Tables S3 and Table S4). Predicted daily ranges of turkey vultures were greater than black vultures in all seasons and conditions (Fig. 4). Predicted response of turkey vultures to TU was similar between seasons, whereas black vultures exhibited a more pronounced response during winter,

resulting in a large seasonal discrepancy between species in summer. When holding previous day's range sizes constant at species/season-specific median values, the predicted daily ranges of turkey vultures ranged from 7.3–27 km^2 larger than black vultures in winter, and 11–55 km^2 larger in summer (Fig. 4).

Diurnal activity patterns were similar for both species, with hourly travel rates peaking during mid-day (Fig 5). Hourly movement patterns generally corresponded to diurnal patterns of TU (Fig. 5), which also peaked mid-day indicating both species traveled more when soaring conditions were most favorable. Although diurnal activity patterns were similar between species, turkey
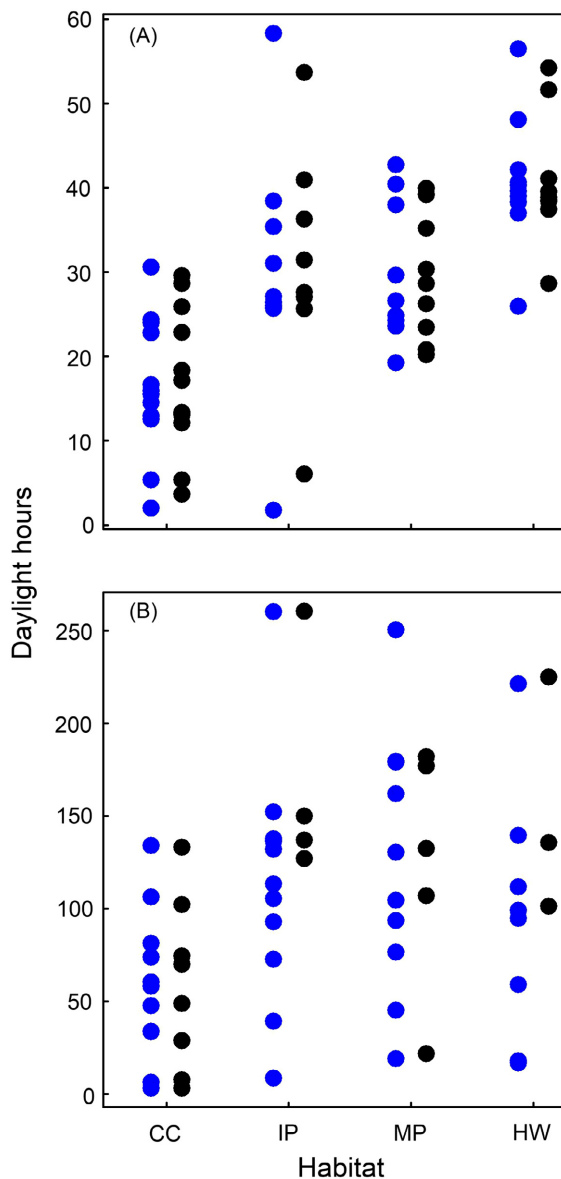
Fig. 2. Time of arrival of the first black vulture (black dots) and turkey vulture (blue dots) recorded at pig carcasses during the warm (A) and cool (B) seasons in four habitat types (CC, clear cut; IP, immature pine; MP, mature pine; and HW, hardwood) at the Savannah River Site, SC, 2013–2014. Each dot represents an individual observation. Note the different *y*-axis scales.

Discussion

Our study illustrates how hypothesized relationships between different physiological (e.g., olfactory sensitivity), morphological (e.g., wing loading), and behavioral (e.g., solitary vs. social foraging) characteristics of each species translate into different patterns of movement, foraging habitat, and carcass use that reduce direct foraging competition, despite both species occupying a similar trophic position. Specifically, turkey vultures appear to use their olfactory sense to locate smaller and obscured carcasses. This method of foraging likely requires turkey vultures to sample large portions of the landscape and thus spend more time in daily foraging flight, which is reflected in observed movement patterns and facilitated by wing morphology that allows efficient low-altitude soaring in a wide range of conditions. Black vultures, by way of social foraging and the ability to locate food by observing and following other avian scavengers such as turkey vultures (Rabenold 1987, Buckley 1999), likely do not need to spend as much time in foraging flight, and their morphology and observed flight behavior reflect this. The adaptations of turkey vultures expand their foraging niche breadth and allow them to become more generalist scavengers (Coleman and Fraser 1987, Hiraldo et al. 1991, Ballejo et al. 2017), supporting the hypothesis that turkey vultures are able to exploit carcasses not easily located by black vultures to reduce direct competition.

Carcass observations supported our hypotheses, based on olfaction capabilities, that turkey vultures were more likely to exploit small carcasses and carcasses in forested habitats than black vultures, as well as the hypothesis that turkey vultures are likely to locate carcasses before black vultures. Our results closely match those of similar studies conducted in other ecosystems where these species co-occur (Coleman and Fraser 1987, Wallace and Temple 1987, Lemon 1991, Buckley 1996), suggesting a well-established mechanism of resource specialization resulting from a long evolutionary history of co-occurrence. Additionally, we observed seasonal variation in patterns of carcass exploitation. Notably, turkey vulture use of small carcasses decreased in the cool season, particularly in forested habitats, and time-to-arrival of turkey
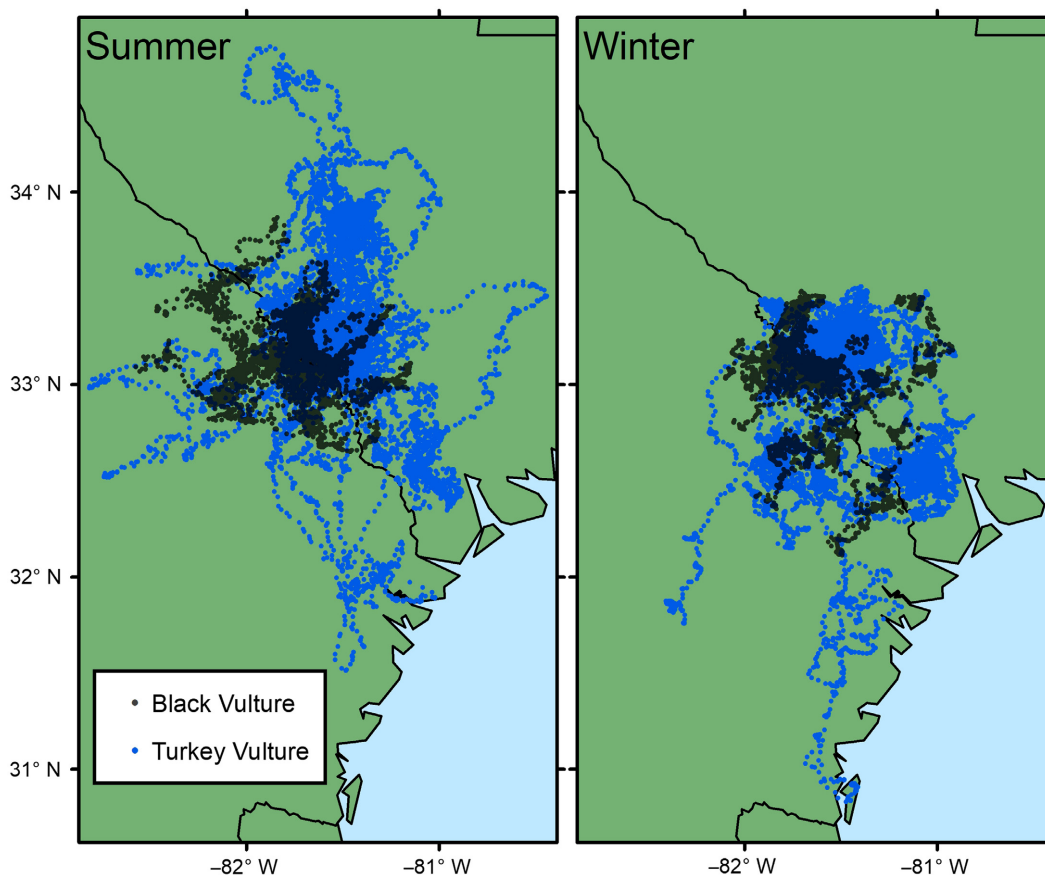
vultures traveled more than black vultures at all diurnal hours (Fig 5). For example, during the 12:00 hour, turkey vultures were predicted to travel on average ~3.1 and ~2.1 km further than black vultures in summer and winter, respectively.

Fig. 3. Distribution of movements of black (n = 12) and turkey vultures (n = 9) tracked with GPS telemetry during summer (June–August) and winter (December–February), 2013–2014.

vultures at carcasses was later in the cool season. Colonization of carrion by microbes and arthropods is slow in cold temperatures (Putnam 1978, DeVault et al. 2003, Beasley et al. 2015), and the patterns we observed are likely the result of slower decomposition rates during the cool season delaying the release of scent cues. This may also explain why seasonal discrepancies were most apparent in forested habitats where visual obstruction would require a heavier reliance on olfactory signals.

GPS telemetry revealed turkey vultures were more mobile than black vultures, flying on average greater distances and traversing larger daily ranges. Our results confirm previous studies that suggested turkey vultures spend more time in flight than black vultures (Coleman and Fraser 1989, DeVault et al. 2005, Avery et al. 2011, Holland et al. 2017), and are consistent with

expectations that soaring advantages conferred by lighter wing loading allows turkey vultures to travel more efficiently. Use of olfaction likely requires turkey vultures to search the landscape extensively when foraging and spend more time in flight, which would be facilitated by morphological adaptations that enhance soaring efficiency, similar to many pelagic seabirds (Nevitt et al. 2008). This may be especially important in locating smaller food items quickly before they are consumed by mammalian scavengers or decompose completely, or in finding larger items and feeding before being usurped by black vultures. Conversely, black vultures, which rely on vision, social cues, and the behavior of other scavengers to locate food, may not need to travel as extensively when foraging.

While previous studies have used VHF or GPS telemetry to quantify general patterns of space
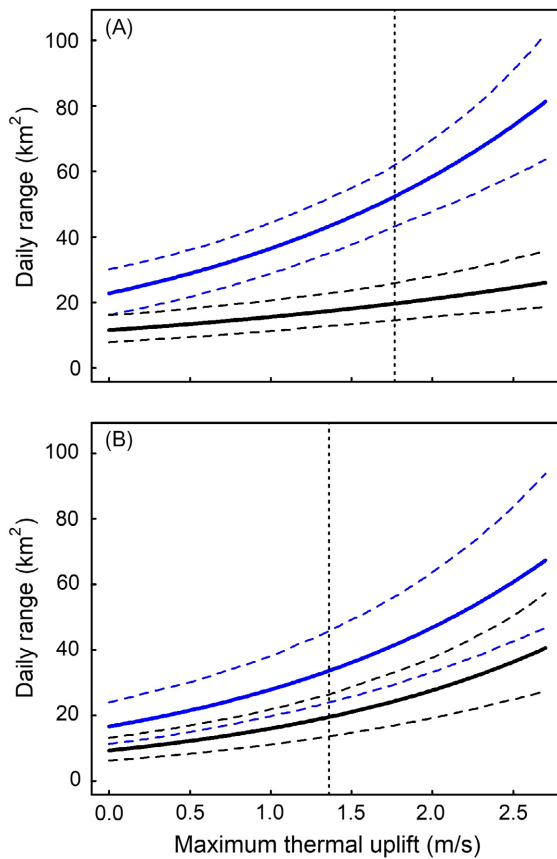
Fig. 4. Model-predicted daily ranges (solid lines) and 95% confidence intervals (dashed lines) for black vultures (black lines) and turkey vultures (blue lines) as a function of maximum daily thermal uplift during (A) summer (June–August) and (B) winter (December–February). For predictions, previous day's range held constant at species- and season-specific median values. Dotted vertical lines represent mean seasonal maximum daily thermal uplift.
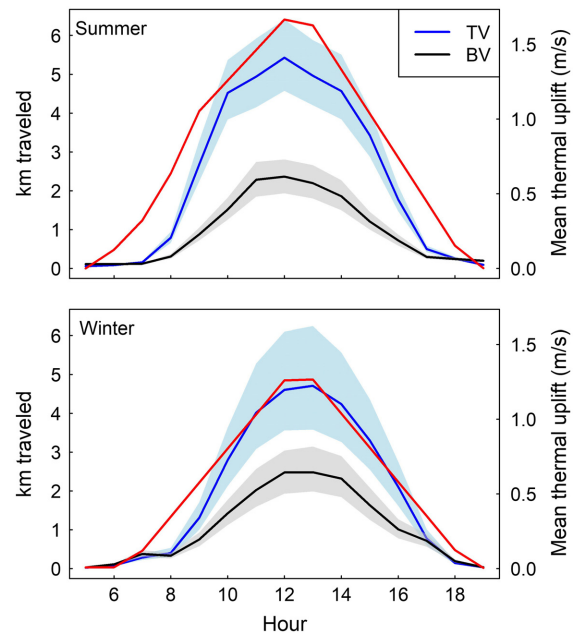

Fig. 5. Model-predicted estimates of hourly travel distances (solid lines) and 95% confidence intervals (shaded regions) of black and turkey vultures during summer (June–August) and winter (December–February). Red line indicates mean thermal uplift.

use and flight behavior of sympatric populations of these species (Coleman and Fraser 1989, DeVault et al. 2004, 2005, Avery et al. 2011, Fischer et al. 2013, Holland et al. 2017), a novel aspect of our work was the ability to use high-resolution GPS data to quantify movement patterns in relation to an environmental factor known to influence soaring efficiency. Both species increased travel rates as soaring conditions improved, with greater daily ranges associated with days characterized by high TU, and greatest movement during mid-day when TU reached its daily peak. Turkey vultures, however, showed a stronger response in terms of distance traveled to relative increases in TU than black vultures. This was consistent when looking at both daily ranges and diurnal patterns of travel and was especially apparent during summer. Although it has been shown that environmental conditions influence turkey vulture movement (Mandel et al. 2008, Bohrer et al. 2012, Dodge et al. 2014), this result is somewhat surprising as we expected black vultures to be more reliant on thermal formation given their higher wing loadings, and thus show a stronger response to changes in soaring conditions. Instead, it appears that while black vultures do take advantage of favorable soaring conditions, soaring adaptations of turkey vultures allows them to better exploit any increases in TU and consequently increase their travel ability more than black vultures for any given improvement in soaring conditions. Thus, while we observed no evidence of diurnal segregation of movement activity between species (travel of both species peaked mid-day), turkey vultures were consistently expected to forage over larger areas than black vultures. Beyond allowing

turkey vultures to sample more of the landscape, this may also provide a form of spatial segregation where turkey vultures are able to forage in areas of the landscape with reduced black vulture densities, and future studies may wish to explore this hypothesis.

While median daily ranges of turkey vultures differed by ~15 km^2 between seasons, black vultures maintained very similar daily range sizes. Larger summer ranges of turkey vultures appear to result from a combination of greater summer day length (mean = 3.4 h longer) providing more time to forage than winter, and capitalization of summer thermal formation to increase mid-day travel rates. However, maintenance of similar daily ranges in both seasons despite shorter day length indicates black vultures spent a greater proportion of the day traveling during winter. Additionally, the response to soaring conditions was much greater for black vultures during winter compared to summer, in that expected daily range size increased at a faster rate during winter as maximum daily TU increased. Avery et al. (2011) suggested the proportional increase in flight time during winter was a result of black vultures needing to spend more time foraging relative to the reduced hours of available daylight. In temperate regions, cold winter temperatures may physiologically stress black vultures, which historically had a more tropical and subtropical distribution (Buckley 1999), requiring increased energy consumption and thus foraging effort to meet increased metabolic requirements in cold weather (Swanson 2010). An additional consideration that may explain increased flight time in winter is a potential increase in intraspecific competition, as evidence suggests the density of black vultures in the area is greatest during winter (Appendix S1: Fig. S1), perhaps due to an influx of overwintering migratory individuals that nested further north. If black vultures must spend more effort foraging during winter, then the stronger response to uplift observed in winter may be representative of black vultures more fully exploiting any potential increase in favorable soaring conditions in order to maximize searching within a shorter daylight period.

Strength of interspecific competition is mediated by resource availability (Holbrook and Schmitt 1989). Populations of both species have increased in tandem over several decades in our study region based on North American Breeding Bird Survey data (https://www.pwrc.usgs.gov/bbs/), suggesting sufficient resources to allow foraging niche separation to limit direct competition. It is not practical to limit carrion resources experimentally over large spatial scales, which would be ideal to understand how patterns of movement and carrion use change under different levels of resource availability. However, a similar study conducted in portions of the turkey vulture's North American range where black vultures are absent may provide comparative insight into how foraging differs in the absence of a competing avian scavenger. For example, Hiraldo et al. (1991) found evidence of competitive release where turkey vultures in regions of Mexico where black vultures were absent consumed larger carcasses compared to regions where black vultures were abundant.

Although obligate avian scavengers are functionally unique in terrestrial systems, they share broad ecological similarities to guilds of pelagic seabirds (such as albatross) which also forage on patchily distributed and ephemeral food resources, are morphologically specialized for long-term foraging flight, include species that rely on olfaction to locate food (Verheyden and Jouventin 1994, Nevitt et al. 2008), and often share overlapping distributions (Phillips et al. 2008). Thus, we may expect similar mechanisms of foraging niche differentiation to manifest in seabirds and vultures. Evidence exists to support spatial segregation of foraging areas in both groups. Sympatric seabirds often segregate foraging areas characterized by different oceanographic habitat features (Hyrenbach et al. 2002, Wood et al. 2000, Navarro et al. 2009) and further partition foraging space based on variation in diving capability (Phillips et al. 2008), while our study and Lemon (1991) suggest sympatric New World vultures spatially segregate foraging along a canopy cover gradient. We observed differential exploitation patterns of large and small carcasses by black and turkey vultures suggesting specialization for different food items, analogous to trophic segregation often documented in sympatric seabirds (Navarro et al. 2009, 2013). Despite operating in very different ecosystems, these distinct yet functionally similar taxa appear to reduce direct foraging competition through

broadly similar mechanisms. One key difference is that unlike vultures in our study, many seabirds exhibit some degree of temporal segregation in foraging activity (Navarro et al. 2013, Conners et al. 2015). This difference is likely due to the primarily diurnal activity of vultures, whereas many seabirds are active during nocturnal and diurnal periods.

Given the conservation concerns of many vultures (Buechley and Şekercioğlu 2016), understanding drivers of specialization to carrion exploitation within scavenger guilds may have practical application to conservation efforts. Examples include guiding supplemental feeding efforts in Europe (Cortés-Avizanda et al. 2012) or mitigating negative competitive interactions of black vultures and Andean condors (*Vultur gryphus*) resulting from human-facilitated range expansions of black vultures in Patagonia (Carrete et al. 2010, Ballejo et al. 2017). Given recent advances in tracking technology, the inclusion of movement ecology will open up new avenues of research regarding how avian scavengers partition space and time when foraging, as well as the influence of environmental conditions, ultimately providing a more refined understanding of how these species evolved to coexist.

Acknowledgments

Literature Cited

Avery, M. L., J. S. Humphrey, T. S. Daughtery, J. W. Fischer, M. P. Milleson, E. A. Tillman, W. E. Bruce, and W. D. Walter. 2011. Vulture flight behavior and implications for aircraft safety. Journal of Wildlife Management 75:1571–1587.

Ballejo, F., S. A. Lambertucci, A. Trejo, and L. J. M. De Santis. 2017. Trophic niche overlap among scavengers in Patagonia supports the condor-vulture competition hypothesis. Bird Conservation International. https://doi.org/10.1017/S0959270917000211

Bang, B. G., and S. Cobb. 1968. The size of the olfactory bulb in 108 species of birds. Auk 85:55–61.

Beasley, J. C., Z. H. Olson, and T. L. DeVault. 2015. Ecological role of vertebrate scavengers. Pages 107–127 in E. M. Benbow, J. Tomberlin, and A. Tarone, editors. Carrion Ecology, Evolution and Their Applications. CRC Press, Boca Raton, Florida, USA.

Bohrer, G., D. Brandes, J. T. Mandel, K. L. Bildstein, T. A. Miller, M. Lanzone, T. Katzner, C. Maisonneuve, and J. A. Tremblay. 2012. Estimating updraft velocity components over large spatial scales: contrasting migration strategies of golden eagles and turkey vultures. Ecology Letters 15:96–103.

Brown, J. S. 1989. Desert rodent community structure: a test of four mechanisms of coexistence. Ecological Monographs 59:1–20.

Buckley, N. J. 1996. Food finding and the influence of information, local enhancement, and communal roosting on foraging success of North American vultures. Auk 113:473–488.

Buckley, N. J. 1997. Experimental tests of the information-center hypothesis with black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*). Behavioral Ecology and Sociobiology 41:267–279.

Buckley, N. J. 1999. Black vulture (*Coragyps atratus*). Pages 1–24 in A. Poole and F. Gill, editors. The Birds of North America, Number 411. Cornell Lab of Ornithology, New York, New York, USA.

Buechley, E. R., and C. H. Şekercioğlu. 2016. The avian scavenger crisis: looming extinctions, trophic cascades, and loss of critical ecosystem functions. Biological Conservation 198:220–228.

Byrne, M. E., A. E. Holland, A. L. Bryan, and J. C. Beasley. 2017. Environmental conditions and animal behavior influence performance of solar-powered GPS-GSM transmitters. Condor: Ornithological Applications 119:389–404.

Byrne, M. E., J. C. McCoy, J. W. Hinton, M. J. Chamberlain, and B. A. Collier. 2014. Using dynamic Brownian bridge movement modelling to measure temporal patterns of habitat selection. Journal of Animal Ecology 83:1234–1243.

Carrete, M., S. A. Lambertucci, K. Speziale, O. Ceballos, A. Travaini, M. Delibes, F. Hiraldo, and J. A. Donázar. 2010. Winners and losers in human-made habitats: interspecific competition outcomes in two Neotropical vultures. Animal Conservation 13:390–398.

Coleman, J. S., and J. D. Fraser. 1987. Food habits of black and turkey vultures in Pennsylvania and Maryland. Journal of Wildlife Management 51:733–739.

Coleman, J. S., and J. D. Fraser. 1989. Habitat use and home ranges of black and turkey vultures. Journal of Wildlife Management 53:782–792.

Conners, M. G., E. L. Hazen, D. P. Costa, and S. A. Shaffer. 2015. Shadowed by scale: subtle behavioral niche partitioning in two sympatric, tropical breeding albatross species. Movement Ecology 3:28.

Cortés-Avizanda, A., R. Jovani, M. Carrete, and J. A. Donázar. 2012. Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. Ecology 93:2570–2579.

DeVault, T. L., B. D. Reinhart, I. L. Brisbin Jr., and O.E. Rhodes Jr. 2004. Home ranges of sympatric black and turkey vultures in South Carolina. Condor 106:706–711.

DeVault, T. L., B. D. Reinhart, I. L. Brisbin Jr., and O.E. Rhodes Jr. 2005. Flight behavior of black and turkey vultures: implications for reducing bird-aircraft collisions. Journal of Wildlife Management 69:601–608.

DeVault, T. L., O. E. Rhodes Jr., and J. A. Shivik. 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102:225–234.

Dodge, S., et al. 2014. Environmental drivers of variability in the movement ecology of turkey vultures (*Cathartes aura*) in North and South America. Philosophical Transactions of the Royal Society B 369:20130195.

Dodge, S., G. Bohrer, R. Weinzierl, S. C. Davidson, R. Kays, D. Douglas, S. Cruz, J. Han, D. Brandes, and M. Wikelski. 2013. The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data. Movement Ecology 1:3.

Fischer, J. W., W. D. Walter, and M. L. Avery. 2013. Brownian bridge movement models to characterize birds' home ranges. Condor 115:298–305.

Grigg, N. P., J. M. Krilow, C. Gutierres-Ibanez, D. R. Wylie, G. R. Graves, and A. N. Iwaniuk. 2017. Anatomical evidence for scent guided foraging in the turkey vulture. Scientific Reports 7:17408.

Hamel, S., N. G. Yoccoz, and J. Gaillard. 2012. Statistical evaluation of parameters estimating autocorrelation and individual heterogeneity in longitudinal studies. Methods in Ecology and Evolution 3:731–742.

Hertel, F. 1994. Diversity in body size and feeding morphology within past and present vulture assemblages. Ecology 75:1074–1084.

Hiraldo, F., M. Delibes, and J. A. Donazar. 1991. Comparison of diets of turkey vultures in three regions of northern Mexico. Journal of Field Ornithology 62:319–324.

Holbrook, S. J., and R. J. Schmitt. 1989. Resource overlap, prey dynamics, and the strength of competition. Ecology 70:1943–1953.

Holland, A. E., M. E. Byrne, A. L. Bryan, T. L. DeVault, O. E. Rhodes, and J. C. Beasley. 2017. Fine-scale assessment of home ranges and activity patterns for resident black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*). PLoS ONE 12: e0179819.

Houston, D. C. 1986. Scavenging efficiency of turkey vultures in tropical forest. Condor 88:318–323.

Houston, D. C. 1988. Competition for food between Neotropical vultures in forest. Ibis 130:402–417.

Hyrenbach, K. D., P. Fernández, and D. J. Anderson. 2002. Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. Marine Ecology Progress Series 233:283–301.

Johnson, D.S. 2015. Crawl: fit continuous-time correlated random walk models to animal movement data. R package version 1.5. http://CRAN.R-project.org/package=crawl

Johnson, D. S., J. M. London, M. Lea, and J. W. Durban. 2008. Continuous-time correlated random walk model for animal telemetry data. Ecology 89:1208–1215.

Kendall, C. J. 2014. The early bird gets the carcass: temporal segregation and its effects on foraging success in avian scavengers. Auk 131:12–19.

Kirk, D. A., and M. J. Mossman. 1998. Turkey vulture (*Cathartes aura*). Pages 1–32 *in* A. Poole and F. Gill, editors. The Birds of North America, Number 339. Cornell Lab of Ornithology, Ithaca, New York, USA.

Kranstauber, B., R. Kays, S. D. LaPoint, M. Wikelski, and K. Safi. 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. Journal of Animal Ecology 81:738–746.

Kranstauber, B. and M. Smolla. 2016. Move: visualizing and analyzing animal track data. R package v 2.1.0 https://CRAN.R-project.org/package=move

Lemon, W. C. 1991. Foraging behavior of a guild of Neotropical vultures. Wilson Bulletin 103:698–702.

Mandel, J. T., K. L. Bildstein, G. Bohrer, and D. W. Winkler. 2008. Movement ecology of migration in turkey vultures. Proceedings of the National Academy of Sciences 105:19102–19107.

Navarro, J., M. G. Forero, J. González-Solís, J. M. Igual, J. Bécares, and K. A. Hobson. 2009. Foraging segregation between two closely related shearwaters breeding in sympatry. Biology Letters 5:545–548.

Navarro, J., S. C. Votier, J. Aguzzi, J. J. Chiesa, M. G. Forero, and R. A. Phillips. 2013. Ecological segregation in space, time, and trophic niche of sympatric planktivorous petrels. PLoS ONE 8:e62897.

Nevitt, G. A., M. Losekoot, and H. Weimerskirch. 2008. Evidence for olfactory search in wandering albatross, *Dimedea eulans*. Proceedings of the National Academy of Sciences 105:4576–4581.

Olson, Z. H., J. C. Beasley, and O. E. Rhodes Jr. 2016. Carcass type affects local scavenger guilds more than habitat connectivity. PLoS ONE 11:e0147798.

Parker, P. G., T. A. Waite, and M. D. Decker. 1995. Kinship and association in communally roosting black vultures. Animal Behaviour 49:395–401.

Pennycuick, C. J. 1983. Thermal soaring compared in three dissimilar tropical bird species, *Fregata magnificiens*, *Pelecanus occidentalis*, and *Coragyps atratus*. Journal of Experimental Biology 102:307–325.

Phillips, R. A., J. P. Croxall, J. R. D. Silk, and D. R. Briggs. 2008. Foraging ecology of albatrosses and petrels from South Georgia: two decades of insights from tracking technologies. Aquatic Conservation: Marine and Freshwater Ecosystems 17:S1–S21.

Phillips, R. A., J. C. Xavier, and J. P. Croxall. 2003. Effects of satellite transmitters on albatrosses and petrels. Auk 120:1082–1090.

Putnam, R. J. 1978. Patterns of carbon dioxide evolution from decaying carrion: decomposition of small mammal carrion in temperate systems, part 1. Oikos 31:47–57.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rabenold, P. P. 1987. Recruitment to food in black vultures: evidence for following from communal roosts. Animal Behaviour 35:1775–1785.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27–39.

Sergio, F., G. Tavecchia, A. Tanferna, L. L. Jiménez, J. Blas, R. D. Stephanis, T. A. Marchant, N. Kumar, and F. Hiraldo. 2015. No effect of satellite tagging on survival, recruitment, longevity, productivity and social dominance of a raptor, and the provisioning condition of its offspring. Journal of Applied Ecology 52:1665–1675.

Shepard, E. L. C., and S. A. Lambertucci. 2013. From daily movements to population distributions: Weather affects competitive ability in a guild of soaring birds. Journal of the Royal Society Interface 10:20130612.

Stager, K. E. 1964. The role of olfaction in food location by the Turkey Vulture (*Cathartes aura*). Los Angeles County Museum Contributions in Science 81:3–63.

Swanson, D. L. 2010. Seasonal metabolic variation in birds: functional and mechanistic correlates. Pages 75–129 *in* C. F. Thompson, editor. Current ornithology. Volume 17., Springer New York, New York, USA.

Tilman, D. 1987. The importance of the mechanisms of interspecific competition. American Naturalist 129: 769–774.

Turner, K. L., E. F. Abernethy, L. M. Conner, O. E. Rhodes Jr., and J. C. Beasley. 2017. Abiotic and biotic factors modulate carrion fate and vertebrate scavenging communities. Ecology 98:2413–2424.

Verheyden, C., and P. Jouventin. 1994. Olfactory behavior of foraging procellariiforms. Auk 111: 285–291.

Wallace, M. P., and S. A. Temple. 1987. Competitive interactions within and between species in a guild of avian scavengers. Auk 104:290–295.

Wenzel, B. M., and M. H. Sieck. 1972. Olfactory perception and bulbar electrical activity in several avian species. Physiology and Behavior 9:287–293.

White, D. L., and K. F. Gaines. 2000. The Savannah River Site: site description, land use and management history. Studies in Avian Biology 21:8–17.

Wood, A. G., B. Naef-Daenzer, P. A. Prince, and J. P. Croxall. 2000. Quantifying habitat use in satellite-tracked pelagic seabirds: application of kernel estimation albatross locations. Journal of Avian Biology 31:278–286.

Workman, S. W., and K. W. McLeod. 1990. Vegetation of the Savannah River Site: major community types. SRO-NERP-19. Savannah River Ecology Laboratory, Aiken, South Carolina, USA.

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