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Foraging shifts in a Neotropical Turkey Vulture (*Cathartes aura ruficollis*) in the presence and absence of a northern migrant (*C. a. meridionalis*)

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ABSTRACT—Intraspecific competition is believed to play a pivotal role in shaping the structure and resource use of migrant and resident bird communities. We compared seasonal movements and apparent survival of patagially-marked and radio-tagged individuals of a Neotropical subspecies of Turkey Vulture (*Cathartes aura ruficollis*) in central Venezuela in relation to the presence and absence of a larger, dominant, northern subspecies, *C. a. meridionalis*. We found that the *ruficollis* population was partially migratory during the periods when migrants arrived and departed. Tagged individuals used areas with higher and lower proportional forest and semi-open vegetation types, respectively, during the dry season than wet season months to avoid competition with migrants. Moreover, apparent survival of *ruficollis* was lower during sympatry than allopatry. Our study provided evidence that *C. a. meridionalis* competed with *C. a. ruficollis* during their tropical residence period, supporting the hypothesis that intraspecific competition contributes to niche separation between these subspecies.
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Key words: competition, land cover, Neotropics, resource partitioning, Venezuela.

Cambios de alimentación en una cataneja cabeza roja neotropical (*Cathartes aura ruficollis*) en presencia y ausencia de un migrante boreal (*C. a. meridionalis*)

RESUMEN (Spanish)—La competencia intraespecífica juega un papel fundamental en la estructura y uso de recursos de las comunidades de aves migratorias y residentes. Comparamos los movimientos estacionales y la sobrevivencia aparente de la cataneja cabeza roja neotropical (*Cathartes aura ruficollis*) marcada patagialmente y con radiotransmisores en el centro de Venezuela con relación a la presencia y ausencia de una subespecie boreal más grande y dominante, *C. a. meridionalis*. Encontramos que algunos individuos de *ruficollis* eran migrantes parciales durante la estación seca, utilizaban áreas con mayor y menor proporción de vegetación boscosa y ambientes semiabiertos, respectivamente, durante la estación seca en comparación con los meses de la estación húmeda para evitar la competencia con los migratorios boreales, y que la sobrevivencia aparente de *ruficollis* fue más baja durante simpatría que en alopatría. Nuestro estudio proporcionó evidencia de que *C. a. meridionalis* podría competir con *C. a. ruficollis* durante su período de residencia tropical, lo que respalda la hipótesis de que la competencia intraespecífica podría contribuir a la separación de nichos entre estas subespecies.

Palabras clave: cobertura del suelo, competencia, Neotrópico, reparto de recursos, Venezuela.

Migrant congeners coexist with more sedentary and resident individuals in many species of birds, including scavengers and raptors, during winter in the northern hemisphere (Bohall-Wood and Collopy 1986, Heredia et al. 1991). Theoretically, this should increase intraspecific or interspecific competition for food, as the wintering area is already occupied by resident birds (Greenberg 1986). Resident birds should be at an advantage to migrants because of their year-round knowledge of food sources and shelter from predators (Pérez-Tris and Tellería 2002, Morganti et al. 2017).

One way in which such food competition might be manifested is in differential habitat use or range/territorial shifts of resident birds in response to the presence and absence of migrants (Jedlicka et al. 2006). Alternatively, migrant birds have been presumed to occur in a wider range of land cover types than residents and they are more eurytopic (Leisler 1990). Some migrant species were believed to occupy more open or disturbed vegetation, exploit seasonally abundant food (Leck 1972, Karr 1976, Hutto 1988, Jones et al. 2010) or food of lower nutritional value than residents (Poulin and Lefebvre 1996), or be more flexible in their foraging behavior (Salewski et al. 2003). Among raptors, a resident American Kestrel subspecies (*Falco sparverius paulus*) and migrant subspecies (*F. s. sparverius*)

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showed preferences for different vegetation types during the period of sympatry and there was some evidence for a habitat shift in residents during the summer (Bohall-Wood and Collopy 1986). In southern Spain, resident Red Kites (*Milvus milvus*) used forest vegetation, while wintering migrants mostly used marshland for foraging. Migrant Red Kites displaced the Black Kites (*Milvus migrans*) that used marsh vegetation during the breeding season (Heredia et al. 1991).

Here we study 2 subspecies of Turkey Vulture (*Cathartes aura*) in the Llanos (heterogeneous savannas) of central Venezuela. Individuals of the subspecies *C. a. ruficollis* occur in the central lowlands of Central America and northern South America, where they coexist with the more numerous, larger, North American subspecies, *C. a. meridionalis* (Koester 1982, Kirk and Currall 1994, Kirk and Gosler 1994). *C. a meridionalis* migrate at the end of boreal summer in western and central North America (Hedlin et al. 2013) and arrive in the Llanos in late October or early November, returning to North America in March or April (Kirk 1988, Kirk and Currall 1994).

In this paper, we examine the effects of putative competition on the movements and land cover use of patagially-marked and radio-tagged *C. a. ruficollis* (hereinafter *ruficollis*). The immigration and emigration of *C. a. meridionalis* (hereinafter *meridionalis*) provided unique conditions for a natural experiment in which to investigate the behavior and land cover use of *ruficollis* in the presence and absence of North American migrants. Migrant *meridionalis* are larger in body size than *ruficollis* Turkey Vultures and dominate them in agonistic encounters at carcasses (Kirk and Houston 1995). Seasonal counts in different vegetation types also revealed that densities of migrant Turkey Vultures were much higher in open and semi-open cover types and much lower in forest; *ruficollis* demonstrated the reverse pattern (Kirk and Currall 1994). However, little is known about dietary differences between the 2 subspecies or seasonal changes in the availability of carrion; in the study area both subspecies tended to mostly forage on small carcasses of native mammal species, in contrast to Black Vultures (*Coragyps atratus*), which preferred carcasses of domestic livestock. Here, we predicted that if *meridionalis* competed for carrion resources with *ruficollis*, then individual *ruficollis* should alter their foraging behavior or movements accordingly and should exhibit differentiated habitat selection and lower survival, as a measure of residence time, during the period of sympatry versus allopatry. Specifically, we expected that *ruficollis* individuals should avoid open land cover types where they were more visible to other vultures and forage mostly in closed-canopy forests where they were more likely to go undetected due to lower densities of *meridionalis*. To test these predictions, we compared (1) the use of different land cover types by tagged individuals of *ruficollis* during the period when *meridionalis* were present, versus when the latter were absent; (2) the apparent survival of *ruficollis* when migrants were present, versus when migrants were absent; and (3) whether changes occurred in the movements of tracked *ruficollis*, including home range shifts or use of different land cover types within their home ranges.

Methods

Study area

Turkey Vultures were monitored at the Fundo Pecuario Masaguaral Biological Reserve and Research Station, in Guárico State, within the Llanos of central Venezuela (08°34′N, 67°35′W) between 1984 and 1987. The area consisted of a mosaic of land cover types; on the east side of the San Fernando-Calabozo highway there was a closed-canopy gallery forest and other forest bordering the Rio Guárico and Caño Caracol, while on the west side there were open savannas with grasslands and scattered patches of large trees, marshes (esteros), and deciduous shrub woodland (Troth 1979, Delgado 2017). The dry season (period of sympatry with *meridionalis*) occurs from December to March, followed by a wet season (period of allopatry with *meridionalis*) from May to October; April and November are transitional months. Over a 20-month period, the first author made 3 separate visits to Masaguaral: 17 November 1984 to 10 July 1985, 28 November 1985 to 21 June 1986, and 6 October 1986 to 27 March 1987. Fieldwork was conducted on most days, with the exception of 4 short periods of absence (~7 d in Jun 1985, Feb–Mar 1986, Dec 1986, and Mar 1987).

Capture and telemetry

Turkey Vultures were mainly captured using walk-in funnel cage traps (dimensions 2.5 × 2.5 × 2.5 m) constructed of either weldmesh or wire-netting (Bloom 1987). Most vultures were marked with permanent, yellow cattle tags bearing black numerals (Allflex Livestock Intelligence, Rahway, New Jersey, USA) fixed to the patagium. Some individuals at the beginning of the study were marked with Darvic tags engraved with alphanumeric codes. The *ruficollis* vultures were fitted with radio-transmitters (SB2 transmitters, Holohil Systems Ltd., Carp, Ontario, Canada) between late March and early April prior to northward migration of *meridionalis* and were radio-tracked with a 3-element yagi antenna and an AVM LA12 receiver between 0830 and 1800 h, when most vultures were actively foraging. Triangulated fixes were then overlaid on land cover maps to determine land cover use and home range size (see Supplementary Materials for details on trapping and radio-telemetry).

Determining land cover use in patagially-tagged and radio-tagged vultures

To investigate seasonal movements and land cover use of *ruficollis* vultures, all subsequent sighting locations of patagially-tagged vultures were precisely recorded. Sightings of marked birds were recorded using 3 different techniques: (1) while searching for carcasses, (2) on transects between sites used for point counts (Kirk and Currall 1994), and (3) during behavioral observations at carcasses (Kirk and Houston 1995). A potential bias was that visibility was excellent in open savannah but was restricted in gallery forest areas and thus might affect methods (1) and (2). Radio-tagged vultures were located by tracking them from observation towers of 20 m height or tall wind pumps to increase reception range. Positions of vultures were determined by triangulation, taking bearings as close to 90° as possible (see Supplementary Materials for details).

We determined seasonal geographic and environmental space-use by *ruficollis* vultures. Geographic space, in the form of home range, was calculated using error-informed autocorrelated kernel density estimator (Fleming et al. 2015) with default parameter settings in the *ctmm* package (Fleming et al. 2021) in R (R Core Development Team 2016) to calculate utilization distribution while accounting for autocorrelation of locations. We quantified the home range of patagially-marked and radio-tagged birds exhibiting home-ranging behavior ($n = 6$). We compared space-use of *ruficollis* Turkey Vultures during the period of sympatry versus allopatry with *meridionalis* Turkey Vultures using the population-level analysis of home range areas developed by Fleming et al. (2022). Further, we used MODIS/Terra Vegetation Continuous Fields at a spatial resolution of 250 m (Dimiceli et al. 2015) to calculate the percent of tree cover (forest vegetation) and non-tree cover (open and semi-open vegetation) within these home ranges.

Additionally, we estimated environmental space-use by performing a third-order resource selection analysis in a use–availability design approach (Johnson 1980, Manly et al. 2002). We tested whether patagially-marked and radio-tagged *ruficollis* vultures shifted their habitat use during the period of sympatry versus allopatry with *meridionalis* vultures. We implemented a step-selection function (SSF) and fitted an SSF model with the package *amt* (Thurfjell et al. 2014, Signer et al. 2019) in R. The effect of putative competition on resource selection was modeled with an interaction term between the occurrence of *meridionalis* (presence/absence) and the proportion of tree and non-tree cover at locations available to *ruficollis* vultures. We standardized all continuous variables and fitted this model separately to each individual, as suggested by Fieberg et al. (2010). To perform the SSF model, we used 30 available points for each used point; available points were sampled using step-lengths and turning angles of the used locations following a Gamma and a von Mises distribution, respectively (Signer et al. 2019). Selection coefficients that varied by individual allowed us to examine if there was evidence for a functional response (e.g., the variation in selection strength with habitat availability) in habitat selection during the period of sympatry versus allopatry.

Apparent survival

We further examined the effects of putative competition by comparing apparent survival of *ruficollis* when migrants were present versus when migrants

were absent. Differences in apparent survival, as a measure of residence time, would suggest that *ruficollis* Turkey Vultures would be responding to the presence of *meridionalis* Turkey Vultures by increased mortality or emigration. We estimated apparent survival using Cormack-Jolly-Seber live-recapture models (Powell and Gale 2015), implemented in the *RMark* package (Laake 2013) in R. To estimate apparent survival, we created encounter histories beginning the recapture period at the first month of each field season (Oct/Nov of each year) until the end of each season in each year (Mar, Jun, Jul). Each month was treated as a recapture (resighting) event within each individual encounter history. We fitted a univariate model to explore the occurrence of *meridionalis* as a factor explaining variation in seasonal resighting probability (ρ) and apparent survival (φ) of *ruficollis*. Note that in this analysis we included 26 individuals randomly selected in the dry season and the 26 individuals from the wet season to balance sample sizes (n = 52 birds, 24 individuals resighted).

Results

In total, 71 adult *ruficollis* and 133 adult *meridionalis* Turkey Vultures, 146 adult Black Vultures, and 4 adult Lesser Yellow-headed Vultures (*Cathartes burrovianus*) were patagially marked. Six individuals of the *ruficollis* subspecies were fitted with radio-transmitters but only 3 provided sufficient data for analysis. Further, 6 individuals were radio-tagged in late October and early November, but disappeared from the study area, following transmitter attachment (only 1 was relocated, 40 km north of the study area).

Geographic space-use by *ruficollis* vultures

Our population-level analysis of home range areas included 5 radio-tagged and 1 patagially-marked individuals. We found significant differences in home range size between periods of sympatry and allopatry (Fig. 1). Population-level home ranges during the period of sympatry were smaller (22.9 km^2, 95% CI: 16.7–30.1) when compared to the period of allopatry (236.9 km^2, 95% CI: 166.7–319.4). The *ruficollis* Turkey Vultures demonstrated a shift in the proportional use of forest and semi-open land cover types within their home range from 88.3% to 41.4% during sympatry and allopatry, respectively. Conversely, they used more open savannas during periods of allopatry (58.7%) than in sympatry (11.6%).

Of the 6 individuals originally tagged with radio-transmitters, 2 (bird IDs 24 and 60) provided data from pre- and post-departure of *meridionalis*. Both birds demonstrated range expansion between the dry and wet season (bird ID 24: 27.30 km^2 [CI 17.44–39.35] to 159.05 km^2 [CI 110.23–216.69] and bird ID 60: 34.46 km^2 [CI 21.98–49.71] to 102.31 km^2 [CI 57.67–159.54]). Bird ID 24 demonstrated a shift in the proportional use of forest and semi-open land cover types within its home range (sympatry 98%; allopatry 48%) to open land cover types (sympatry 2%; allopatry 52%) between seasons (Supplemental Fig. S1 and S2a). However, this was not apparent for bird ID 60, which showed little difference in the proportional use of forest and semi-open land cover (sympatry 67%; allopatry 57%) and open savanna (sympatry 33%; allopatry 44%) between seasons within its home range (Supplemental Fig. S1 and S2b). A third individual (bird ID 58), with insufficient data to compare land cover use between seasons, demonstrated extensive use of open savanna (70% proportional use) during the period of allopatry (Supplemental Fig. S1 and S2c). The dispersion of locations for all (6) individuals (including the 3 used in radiotelemetry analyses) is shown in Supplemental Fig. S3.

Environmental space-use by *ruficollis* vultures

A plot of all resightings of all marked *ruficollis* and *meridionalis* individuals demonstrated differential land cover use by the 2 subspecies (Fig. 2). Using data from a subset of 13 *ruficollis* individuals, we found evidence of a functional response in habitat selection during the period of sympatry versus allopatry. As predicted, we found that *ruficollis* strongly selected areas with higher proportional tree cover (forest) when *meridionalis* was present ($\beta = 4.632$, 95% CI: −0.324 to 14.018; Fig. 3a) than when migrants were absent ($\beta = 1.713$, 95% CI: −0.267 to 4.470; Fig. 3a). Similarly, we also found that *ruficollis* strongly selected areas with lower proportional non-tree cover (open and semi-open) during periods of sympatry with *meridionalis* ($\beta = 3.667$, 95% CI: −1.214 to 12.372; Fig. 3b)

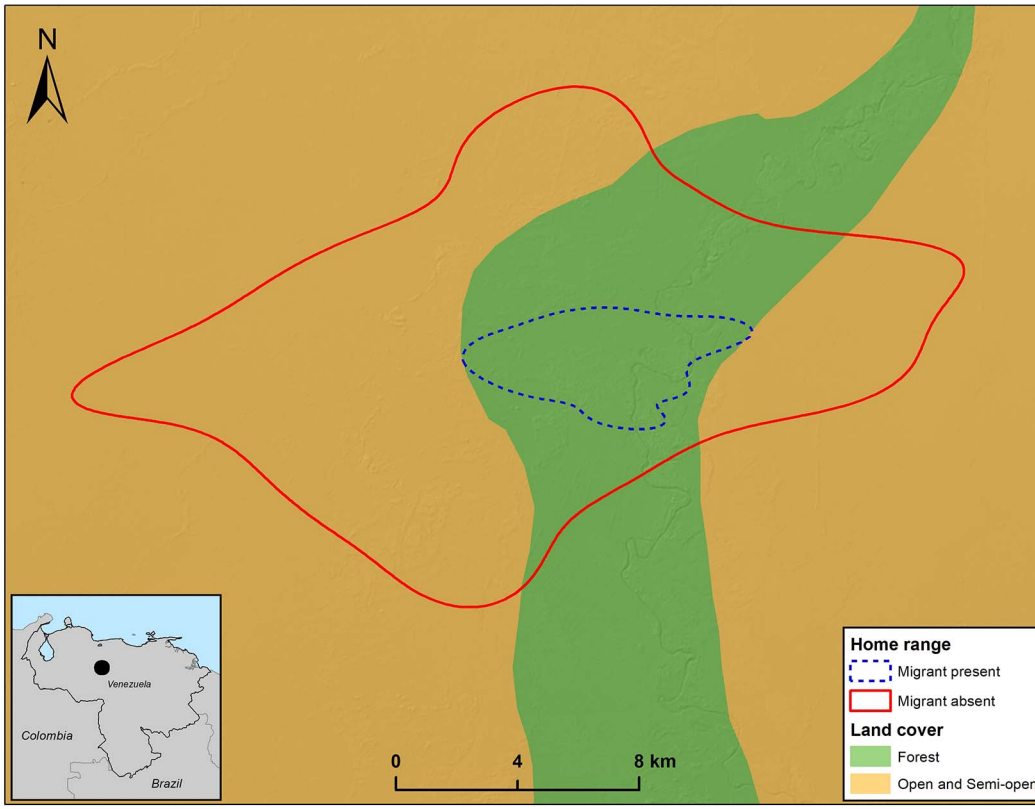

Figure 1. Population-level home range shifts between seasons (solid line = wet season, dashed line = dry season) of Turkey Vultures (*C. a. ruficollis*; $n = 6$) in relation to open, semi-open, and forested land cover in Guárico State, central Venezuela.

versus periods of allopatry ($\beta = 1.321$, 95% CI: −0.691 to 4.12; Fig. 3b).

Survival of *ruficollis* Turkey Vultures in presence and absence of migrants

Our results demonstrated that *ruficollis* Turkey Vultures ($n = 52$, 24 resighted) had lower seasonal survival when migrants were present (φ: 0.83, 95% CI: 0.62–0.94) than when they were absent (φ: 1, 95% CI: 1–1; Fig. 4). We did not find significant differences in resighting probability when migrants were absent (ρ: 0.12, 95% CI: 0.07–0.20) than when they were present (ρ: 0.15, 95% CI: 0.09–0.24).

Discussion

Our results suggested that *ruficollis* adjusted their foraging movements to avoid land cover types with high densities of *meridionalis* and reduce interference competition from the larger migratory subspecies. When *meridionalis* migrants were absent, marked *ruficollis* foraged in both savanna and forest, but during the dry season when there were large numbers of *meridionalis* in the area, they foraged almost exclusively in forest and semi-open land cover types. Although our sample size was limited, the combination of patagial-tag and radio-tracking data together with robust methods for analyzing animal movements with small sample sizes (e.g., Fleming et al. 2022) partially confirmed a shift in use of land cover types by *ruficollis*.

We also found evidence that some *ruficollis* individuals made local or regional movements, perhaps in response to high densities of *meridionalis*. The best evidence for this came from 6 *ruficollis* individuals, radio-tagged just 3 weeks prior to the arrival of large numbers of *meridionalis*, which may possibly have left the study area (Kirk 1988), and from our

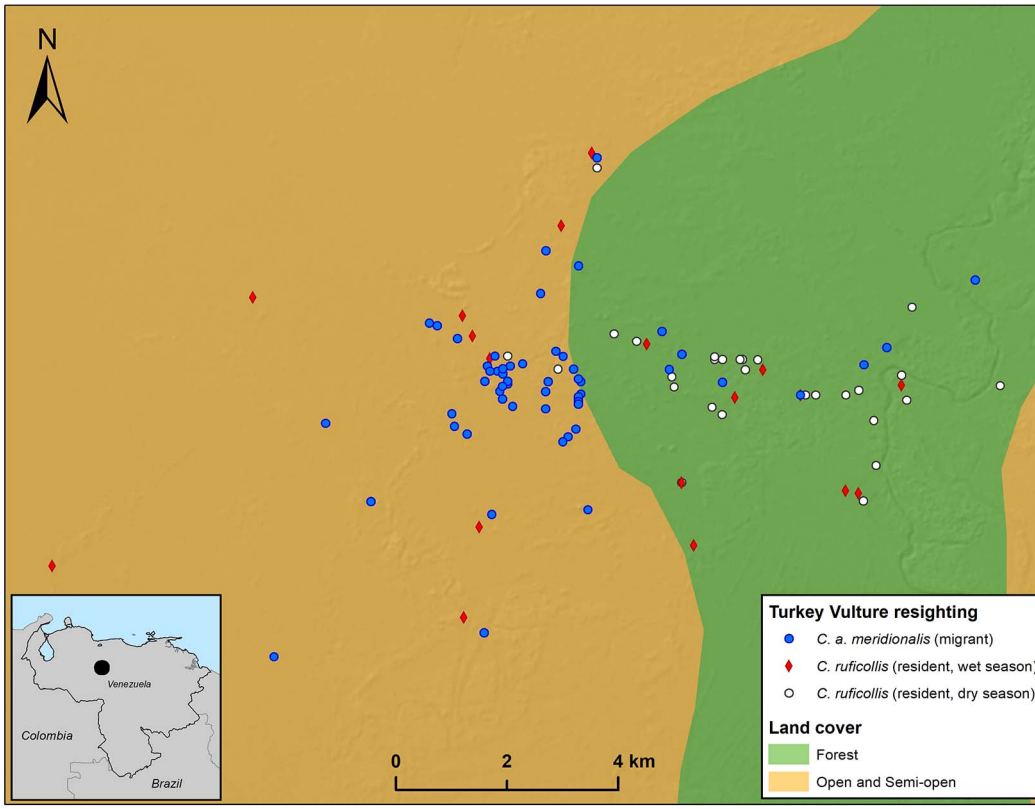

Figure 2. Seasonal distribution of resightings of patagially-tagged migrant (*C. a. meridionalis*; $n = 21$ individuals) and resident (*C. a. ruficollis*; $n = 24$ individuals) Turkey Vultures in open, semi-open, and forested land cover in Guárico State, central Venezuela.

apparent survival estimation. If *ruficollis* used gallery forest exclusively during the dry season to avoid competition from *meridionalis*, then some individuals might also leave the study area to forage over gallery forest bordering the large rivers when *meridionalis* numbers peak in November and December (Kirk and Currall 1994). This is consistent with our lower apparent survival estimate during the dry season (when migrants were present), which likely suggests that *ruficollis* may be emigrating from the study area as a result of competition with *meridionalis*. Thus, our results support the hypothesis that *ruficollis* are reciprocal migrants in response to the arrival of *meridionalis*; Bildstein et al. (2007) demonstrated that local movements of *ruficollis* and *aura* vultures occurred in response to the arrival of large numbers of *meridionalis* migrants. Substantial seasonal shifts have been documented elsewhere in the tropics for both Turkey and Black vultures. For example, while no seasonal differences in Turkey Vulture numbers were found during road surveys in Costa Rica and western Panama between winter (Dec–Feb) and summer (Jun–Jul) periods, numbers increased by >500% during the boreal winter in central Panama (Bildstein et al. 2007).

These findings validated the results of point counts (Kirk 1988, Kirk and Currall 1994) and road surveys (Bildstein et al. 2007). At our study site, *meridionalis* outnumbered *ruficollis* by 7:1, and foraged primarily in open savanna vegetation types where carrion is probably most abundant (Kirk and Currall 1994, Kirk and Houston 1995). Point counts in the study area demonstrated that densities of *Cathartes* vultures followed a bell-shaped curve—increasing from 0.5 individuals/km^2 in October, peaking at 5.5/km^2 in mid-December, and decreasing to <0.5/km^2 at the end of April when migrants departed. Following this, there was

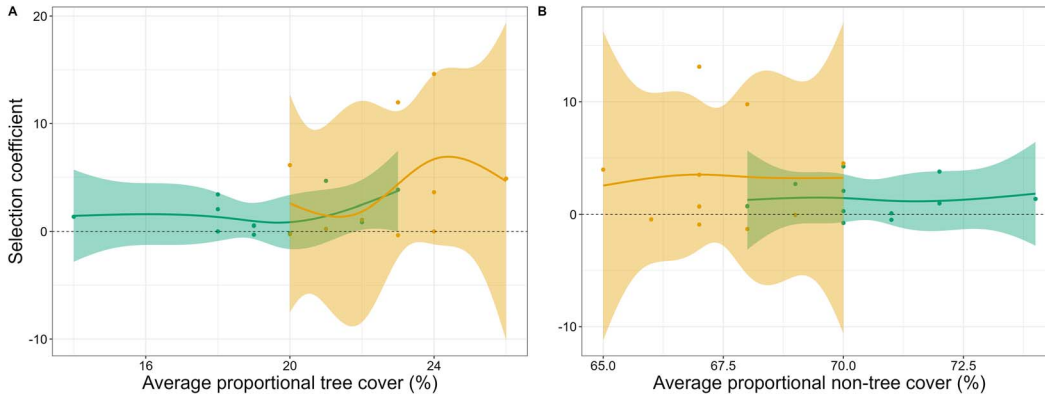

Figure 3. Functional responses in habitat selection by *ruficollis* Turkey Vultures during periods of sympatry and allopatry with *meridionalis* Turkey Vultures in Guárico State, central Venezuela. Panel A: Tree (Forest) cover, Panel B: Non-tree (Open and Semi-open) cover. Dark gray color (turquoise in online version of this paper) corresponds to periods of allopatry (migrants absent), light gray color (mustard in online version of this paper) represents periods of sympatry (migrants present).

a slight increase in densities accounted for by *ruficollis* and some *C. a. burrovianus* vultures (Kirk and Currall 1994).

Our results documenting lower resighting probability during the wet season, when *meridionalis* are absent, suggested that *ruficollis* can perform unrestricted displacement across the study area during this time of the year. Conversely, during the dry season when *meridionalis* occurred in the study area, resident *ruficollis* Turkey Vultures were confined to forest and semi-open areas, which increased their resighting probability.

Competition for food with *meridionalis* is only one explanation for changes in the habitat use or movements of *ruficollis*. Two other factors that might affect foraging habitat use are stage of breeding and seasonal changes in the dispersion of carrion. Increased energetic demands, when incubating or feeding large, dependent young, could induce the foraging habitat shifts we observed. However,

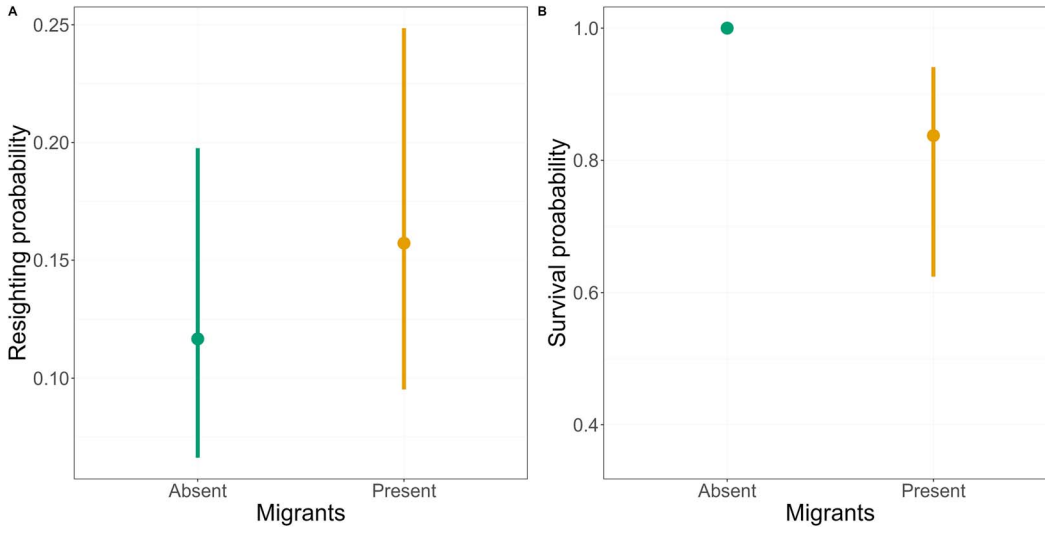

Figure 4. Survival and resighting probability of *ruficollis* Turkey Vultures in the presence and absence of migrants based on Cormack-Jolly-Seber live-recapture analyses ($n = 52$ birds, 24 individuals resighted) in Guárico State, central Venezuela.

although 2 Black Vulture nests were found, we did not find any nests of *ruficollis* and the breeding season for *ruficollis* is uncertain. Only 1 juvenile *ruficollis* was captured during our study and there is only 1 observation of a juvenile bird in August at Masaguaral (Thomas 1979).

Marsh Harriers (*Circus aeruginosus*), like Turkey Vultures, have populations with differing degrees of migratory behavior (Cardador et al. 2015). In this species, numerically dominant and larger-sized migrant birds from northern Europe overwinter in Spain, where they are spatially segregated from smaller, resident birds (Cardador et al. 2015). Increasing numbers of migrants with burgeoning populations in northern Europe have led to declines in resident birds. Thus, the range expansion and possible population increases in North American Turkey Vultures (Kirk et al. forthcoming) could possibly have similar repercussions on *ruficollis*. Coupled with climatically induced changes in the vegetation of the Llanos over the last 25 years—notably an increase in shrub encroachment in grassland and a concomitant decline in species diversity (Delgado 2017)—this could alter competitive strategies among vulture taxa. Such vegetation shifts and species' responses to them could have widespread implications for other species with resident and migrant populations and the potential for niche segregation to be achieved by avoidance of competition through differential habitat use. Over the decades since our original study was carried out, there has been increasing awareness of the magnitude and diversity of migration patterns among Neotropical avifauna (Jahn et al. 2020). Indeed, at that time *ruficollis* was referred to as the "resident" Turkey Vulture in South American lowlands (Kirk 1988) because the subset of birds that were in fact resident masked influxes and effluxes of migrants. Analogous to northern races of Turkey Vulture, the *ruficollis* subspecies has complex migration patterns spanning residency to partial migration (Kirk et al. forthcoming). It differs in being either a Neotropical–Austral or intra-tropical migrant and the distances moved are believed to be hundreds, rather than thousands, of kilometers. Further study of *ruficollis* and *meridionalis* using GPS transmitters (e.g., Hedlin et al. 2013, Dodge et al. 2014) not available at the time of our research would elucidate movement patterns and habitat shifts in response to changing movements of northern migrants. In addition, investigations of seasonal changes in food availability could uncover further aspects of resource separation between *ruficollis* and *meridionalis* Turkey Vultures.

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