TEMPORAL FLUCTUATIONS IN RAPTOR ABUNDANCES IN GRASSLANDS OF SOUTHEASTERN SOUTH AMERICA

Felipe Zilio¹

PPG Animal Biology, Department of Zoology, Federal University of Rio Grande do Sul (UFRGS), Porto Alegre, Rio Grande do Sul, Brazil

LAURA VERRASTRO AND MÁRCIO BORGES-MARTINS

Department of Zoology, Federal University of Rio Grande do Sul (UFRGS), Porto Alegre, Rio Grande do Sul, Brazil

ABSTRACT.—We conducted 44 roadside surveys on grasslands landscapes of southern Brazil and Uruguay to study temporal changes in raptor abundance. Each route was surveyed twice in fall/winter and twice in spring/summer. Raptor abundance was higher during summer than winter, but did not differ between years. Thirteen of the 33 species recorded showed temporal changes in abundance, or are known to be migrants in the region. White-tailed Kite (Elanus leucurus), Yellow-headed Caracara (Milvago chimachima) and Southern Caracara (Caracara plancus) had higher abundance during fall/winter than spring/summer, which might be attributed to nomadic movements in agricultural landscapes. Changes in abundance of Savanna Hawk (Buteogallus meridionalis) and American Kestrel (Falco sparverius) suggest irruptive or nomadic movements. Turkey Vulture (Cathartes aura), Snail Kite (Rostrhamus sociabilis) and White-tailed Hawk (Geranoaetus albicaudatus) were more abundant in spring/summer than fall/winter, and our results suggest that they are partial migrants in the region. Variations in temperature, water level, and land use in agro-environment as well as dispersion, recruitment, and ephemeral concentration of food resources probably are the causes of fluctuation observed. Our results provide a starting point to better understand raptor temporal fluctuations and abundance in southeastern South America, but further investigations are required.

Key Words: abundance, Araucaria moist forest; Brazil; partial migration; raptor; seasonal fluctuations; survey; Uruguay; Uruguayan savanna.

FLUCTUACIONES TEMPORALES EN LAS ABUNDANCIAS DE RAPACES EN PASTIZALES DEL SURESTE DE AMÉRICA DEL SUR

RESUMEN.—Realizamos 44 censos a lo largo de caminos ubicados en paisajes de pastizales del sur de Brasil y Uruguay para estudiar los cambios temporales en las abundancias de rapaces. Cada ruta fue censada dos veces en otoño/invierno y dos veces en primavera/verano. La abundancia de rapaces fue mayor durante el verano que en el invierno, pero no difirió entre años. Trece de las 33 especies registradas evidenciaron cambios temporales en sus abundancias, o es sabido que son migrantes en la región. Elanus leucurus, Milvago chimachima y Caracara plancus tuvieron una mayor abundancia durante otoño/invierno que en primavera/verano, lo que puede ser atribuido a movimientos nómades en los paisajes agrícolas. Los cambios en la abundancia de Buteogallus meridionalis y Falco sparverius sugieren movimientos nómades o de irrupción. Cathartes aura, Rostrhamus sociabilis y Geranoaetus albicaudatus fueron más abundantes en primavera/verano que en otoño/invierno y nuestros resultados sugieren que son migrantes parciales en la región. Las variaciones en la temperatura, el nivel del agua y el uso del suelo en ambientes agrícolas, así como también la dispersión, el reclutamiento y la concentración transitoria de fuentes de alimento son probablemente las causas de la fluctuación observada. Nuestros resultados proporcionan un punto de partida para entender mejor las fluctuaciones temporales de las rapaces y sus abundancias en el sureste de América del Sur; sin embargo, se requieren mayores investigaciones.

[Traducción del equipo editorial]

Temporal fluctuations in species richness and abundance are common in bird assemblages due to

movements associated with changes in food resources or in habitat. Even in short periods (seasonally or annually), species abundances and assemblage composition can change substantially (Maron et al. 2005,

¹ Email address: fzilio@msn.com

Accordi and Hartz 2006, Kutt et al. 2012). In raptor assemblages, movements are usually trigged by changes in food resources, which often covary with temperature or floodplain water level (Newton 1979, Bildstein 2006). There are several kinds of bird movements that can explain variation in bird numbers: natal dispersal, migration, regular local movements, irruptions (invasive migrations), and nomadism (Newton 1979). Natal dispersal is the movement by juveniles from the natal territory (Newton 1979). Migration is the regular movement undertaken by an organism between its breeding and nonbreeding grounds, recurring seasonally and alternating in direction (Bildstein 2006). Regular local (e.g., altitudinal), irregular (or irruptive), and nomadic movements are kinds of partial migration, in which only part of the population migrates (Bildstein 2006).

Long distance migratory raptors can contribute substantially to changes in abundance. The arrival of migrant Turkey Vultures (*Cathartes aura*) to Venezuela, for instance, drastically increases the abundance of vultures in the Llanos, changing the scavenger assemblage dynamics (Kirk and Currall 1994). In the same way, in their wintering grounds in Argentina, the large flocks of Swainson's Hawks (*Buteo swainsoni*) could not go unnoticed (Sarasola et al. 2008). However, local movements such as irruptive migration or even regular partial migration, although perhaps in a more subtle way, can also temporarily change raptor abundance.

In South America, many species developed partial migration as a strategy to deal with seasonal fluctuation in resources (Jahn et al. 2004). Although similar at first glance, patterns of migration in Nearctic and Neotropical have important differences, resulting from continental features and regional species evolution (Jahn et al. 2004). North America has a large proportion of its landmass in temperate latitudes, which become unsuitable for many species during winter. Hence, complete migration evolved in many of these species, which migrate to warmer zones in Central and South America during boreal winter (Jahn et al. 2004). In South America, narrow climatic variation (i.e., more land area in tropical than in temperate latitudes) and the lack of geographical barriers along the continent favored the evolution of partial migration in several species and hence greater overlap between their breeding and nonbreeding grounds (Chesser 1994, Jahn et al. 2004). Hence, migration in South America is more complex, creating challenges to identifying the

main routes, patterns, and features of the migration (Jahn et al. 2004).

Despite the recent increase in knowledge about bird migration in South America (Chesser 1994, Joseph 1997, Jahn et al. 2004, 2012, Alves 2007), raptor migration and temporal fluctuations in abundances are still poorly known (especially in southern South America), except by few transequatorial migrants that breed in North and Central America (e.g., Swainson's Hawk, Bildstein 2006). Temporal fluctuations in abundance of some raptors have been reported, but without a clear pattern or explanation (Hayes 1991, Baumgarten 1998, 2007, Granzinolli 2009). We surveyed raptors in grasslands of southern Brazil and Uruguay during two years to detect temporal changes in species abundance. Raptor distribution, abundance, and movements are poorly known in the region, and most of the knowledge about raptor assemblage is derived from the data compiled by Belton (1984) and Arballo and Cravino (1999). The region is the southern or northern border of the distributional range of several raptors, and its position in an intermediate climatic zone between the South American Temperate-Tropical Migration Systems (SATT) and South American Cool, Tropical Migration Systems (SACT) system borders (Joseph 1997) suggests the occurrence of partial migration and the overlap of breeding and wintering populations of species of both systems (Hayes et al. 1994). Furthermore, we expected to record local or irregular migration, because these are common strategies in raptors that breed close to their species' distribution borders (Bildstein 2004). Hence, these movements would affect local raptor abundances, inducing seasonal changes due to the arrival or departure of migrant individuals.

METHODS

Study Area. We conducted road surveys in 11 areas along grasslands in the Uruguayan Savanna and Araucaria Moist Forest ecoregions (Olson et al. 2001; Fig. 1). The Uruguayan Savanna (US) covers 355 750 km² of southern Brazil (Rio Grande do Sul), Uruguay, and a small portion of northeastern Argentina (Entre Rios province; World Wildlife Fund 2001). Topography is relatively flat (altitudes range from sea-level to 500 masl), with mean annual temperatures (16°C–19°C) and rainfall (1000–1300 mm) increasing in a south-to-north gradient. This large ecoregion comprises a wide variety of habitats. Grass vegetation types prevail, with herb, shrub,

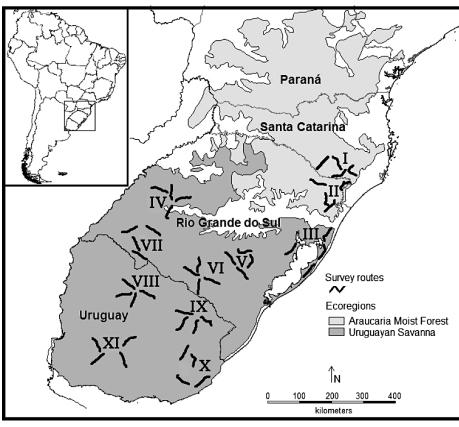


Figure 1. Study area and survey routes (black lines) in the altitudinal grasslands (Araucaria Moist Forest ecoregion; I and II) and in the Uruguayan Savanna (III to XI) in grasslands of southeastern South America (southern Brazil and Uruguay).

and small tree species co-occurring within the grass matrix (Overbeck et al. 2007). Forest habitats include gallery forests, usually along stream and rivers, and submontane forests and palm savannas scattered throughout the ecoregion (World Wildlife Fund 2001). The two areas surveyed in the Araucaria Moist Forest ecoregion (Fig. 1, areas I and II) were restricted to the altitudinal grassland (AG), an area covering 13740 km² in the South Brazilian Plateau, mostly in the Brazilian states of Rio Grande do Sul and Santa Catarina (Overbeck et al. 2007). This region is characterized by the highest altitudes of southern Brazil (up to 1800 masl) in addition to a subtropical climate, with warm summers, cold winters (with the formation of frost) and absence of a dry season (mean annual rainfall 2000-2300 mm). Grassland dominates the highest elevations, on hilltops, forming mosaics with the Araucaria forest, which is patchily

distributed, whereas forest habitats predominate on hillsides and near rivers. The economy is based on cattle ranching, agriculture, and forestry (with nonnative species), activities that have severely altered the original habitat, both in altitudinal grasslands and in Uruguayan Savanna (WWF 2001, Overbeck et al. 2007). The east coast and northwestern Rio Grande do Sul (areas III and IV), as well as southwestern Uruguay (area XI), are highly agricultural. More than 40% of the landscape there is composed of crops, primarily soybeans and rice (F. Zilio unpubl. data). The eastern portion, along the coast (Fig. 1, areas III and X), is a complex of several water bodies mixed with humid grassland (pioneer species, with <20% native vegetation remaining in area III) and forest patches (restinga and gallery forests). Grasslands are the main habitat in all the other regions, although with different degrees of degradation due to cattle ranching. Most of the Uruguayan

Savanna has been degraded by the replacement of native grassland and wetlands with agriculture and reforestation areas, as well as by intensive grazing and the introduction of nonnative species (e.g., South African lovegrass [Eragrostis plana]; Bilenca and Miñarro 2004).

Raptor Surveys. We surveyed raptors in four transects along roads in each of 11 sample areas (Fig. 1). We surveyed each transect four times during 2009, 2010, and 2011, in fall/winter (late April to early September) and spring/summer (November to February), for a total of 176 transect surveys. Roads were chosen using the following criteria: (1) length of at least 70 km; (2) minimum distance of 10 km from any settlement of more than 20000 people; and (3) low traffic flow. Each transect consisted of 10 point counts at assigned locations along a road, with at least 5 km between adjacent count locations (mean distance = 5.4 km, range = 5-10.7 km). Each transect started 2 hr after local sunrise, and lasted for about 7.1 hr. One experienced observer (FZ) conducted each point count, which consisted of counting raptors for 30 min (thus, survey effort = 5 hr per transect). We recorded all raptors seen or heard within a 1-km radius (sampled area = 3.14 km²). In order to avoid double counting, we divided the sampled area into eight sections and plotted all raptors observed on a sketch. Furthermore, we recorded time, behavior (e.g., hunting, perched, soaring), sex, age, color morph, and molt patterns. We only recorded a second individual of a species at a point after confirming that double counting could not have occurred (e.g., if two individuals could be distinguished from one another). We also took behavior into consideration to assume that more than one individual was present at the point. For example, if an individual was recorded flying north and, 1-2 min later, another one was seen perched in the south, we assumed that two individuals were present. For any other conditions, we assumed that individuals had previously been recorded. For gregarious raptors (e.g., New World vultures), we assumed that the maximum number of individuals recorded at the same time (in one or more flocks) was the minimum number of individuals at the sample point. We conducted surveys on sunny days with cloud cover <60% and wind speed <20 km/hr. We did not perform surveys in rainy or foggy periods. We used binoculars (10×42) , a 20–60× spotting scope and a 7× laser rangefinder during surveys.

Statistical Analysis. We evaluated seasonal (spring/summer vs. fall/winter) and annual (2009–2010 vs.

2010-2011) changes in raptor abundance using randomized analysis of variance (ANOVA/MAN-OVA), performed with the program MULTIV (http://ecoqua.ecologia.ufrgs.br/ecoqua/MULTIV. html). This method performs a sum of squares test (Qb) based on the dissimilarity between groups, including a test of multiple contrasts (Pillar and Orlóci 1996). We created the dissimilarity matrix of chord distance and performed 9999 random permutations restricted to each sample area (block designed analysis) to calculate the sum of squares as well as the probability $P(Qb_0 \ge Qb_A)$. The probability P is a proportion of the sum of squares calculated in each iteration (Qb₀) that is higher than or equal to the sum of squares calculated to the sample (Qb_A). We chose a block design analysis because the raptor assemblage differed among sampled areas (Zilio 2012). Data are presented as mean ± standard deviation.

Five species (Osprey [Pandion haliaetus], Swallowtailed Kite [Elanoides forficatus], Plumbeous Kite [Ictinia plumbea], Swainson's Hawk and Peregrine Falcon [Falco peregrinus]) are obligate migrants in southern Brazil and Uruguay, present only during austral spring/summer (Belton 1984, Arballo and Cravino 1999, Bencke 2001). Hence, we performed analyses both including and excluding those species to separate the effects of their abundance on the overall pattern.

RESULTS

We recorded a total of 18 392 observations of raptors of 33 species (Table 1). Raptor abundance was higher in spring/summer (113.9 \pm 44.3 raptors/transect) than fall/winter (95.1 \pm 42.9 raptors/transect; P < 0.01; Table 1), but did not differ between years (P = 0.34). Excluding obligate migrants from the analyses did not change the results ($P_{season} < 0.01$; $P_{year} = 0.34$).

The abundances of ten species were too low (n < 10 individuals) to perform statistical analyses. For twelve of the 23 species analyzed, abundances changed significantly seasonally or annually (Table 1).

Cathartiformes. Among the four vulture species recorded, the Turkey Vulture was the only one which showed significant differences in abundance. Its abundance was higher during spring/summer than fall/winter (P < 0.01), in both years (P > 0.50; Table 1).

Accipitriformes. Black-and-white Hawk-Eagle (*Spizaetus melanoleucus*, n = 1), Ornate Hawk-Eagle (*Spizaetus ornatus*, n = 3), Gray-headed Kite (*Leptodon*

Table 1. Mean raptor abundance per transect (±SD) recorded in southern Brazil and Uruguay grasslands between fall 2009 and summer 2011. Taxonomy follows Remsen et al. (2013).

Species	ABUNDANCE (MEAN NO. OF RAPTORS/TRANSECT)			
	SEASON		YEAR	
	FALL/WINTER	SPRING/SUMMER	2009–2010	2010–2011
Cathartiformes				
Cathartes aura	$23.17 \pm 18.59*$	$34.26 \pm 24.26*$	28.03 ± 21.88	29.40 ± 22.73
Cathartes burrovianus	3.08 ± 4.12	2.5 ± 3.16	2.76 ± 3.77	2.82 ± 3.86
Coragyps atratus	19.89 ± 33.12	17.24 ± 28.23	16.12 ± 26.79	21.00 ± 34.18
Sarcoramphus papa ¹	0	0.03 ± 0.18	0.02 ± 0.15	0.01 ± 0.11
Accipitriformes				
Elanus leucurus	$0.20 \pm 0.57*$	$0.06 \pm 0.23*$	0.11 ± 0.35	0.15 ± 0.52
Leptodon cayanensis ¹	0	0.02 ± 0.21	0	0.02 ± 0.21
Elanoides forficatus	0.00*	$0.67 \pm 2.56*$	0.27 ± 1.40	0.40 ± 2.19
Spizaetus melanoleucus ¹	0	0.01 ± 0.11	0.01 ± 0.11	0
Spizaetus ornatus ¹	0.01 ± 0.11	0.02 ± 0.15	0.01 ± 0.11	0.02 ± 0.15
Rostrhamus sociabilis	$0.57 \pm 2.70*$	$4.51 \pm 10.73*$	2.57 ± 7.77	2.51 ± 8.37
Harpagus diodon ¹	0	0.05 ± 0.26	0	0.05 ± 0.26
Ictinia plumbea	0*	$0.18 \pm 0.64*$	0.10 ± 0.50	0.08 ± 0.41
Circus cinereus	0.05 ± 0.21	0.09 ± 0.33	0.06 ± 0.23	0.08 ± 0.31
Circus buffoni	0.66 ± 1.38	0.81 ± 1.52	0.69 ± 1.38	0.77 ± 1.52
Accipiter striatus	0.16 ± 0.48	0.13 ± 0.50	0.16 ± 0.60	0.13 ± 0.33
Accipiter bicolor ¹	0	0.04 ± 0.26	0.05 ± 0.26	0
Geranospiza caerulescens ¹	0.02 ± 0.15	0.05 ± 0.21	0.01 ± 0.11	0.06 ± 0.23
Buteogallus meridionalis ²	3.03 ± 4.12	4.09 ± 3.67	3.22 ± 3.61	3.91 ± 4.21
Buteogallus urubitinga	0.10 ± 0.40	0.07 ± 0.33	0.07 ± 0.33	0.10 ± 0.40
Buteogallus coronatus	0.10 ± 0.68	0.03 ± 0.24	0.08 ± 0.57	0.06 ± 0.44
Rupornis magnirostris	3.94 ± 3.22	3.62 ± 3.01	3.45 ± 2.99	4.11 ± 3.21
Parabuteo unicinctus ¹	0.06 ± 0.35	0.01 ± 0.11	0.01 ± 0.11	0.06 ± 0.35
Parabuteo leucorrhous ¹	0	0.01 ± 0.11	0	0.01 ± 0.11
Geranoaetus albicaudatus	$0.39 \pm 0.93*$	$5.98 \pm 10.48*$	3.28 ± 8.82	3.08 ± 6.97
Geranoaetus melanoleucus	1.01 ± 1.50	0.99 ± 1.56	0.95 ± 1.44	1.05 ± 1.61
Buteo brachyurus	0.11 ± 0.44	0.08 ± 0.27	$0.02 \pm 0.15*$	$0.17 \pm 0.48*$
Buteo swainsoni	0*	$6.11 \pm 31.26*$	3.05 ± 21.74	3.07 ± 22.88
Falconiformes				
Caracara plancus	$14.10 \pm 9.89*$	$10.92 \pm 8.18*$	$10.89 \pm 8.45*$	$14.13 \pm 9.65*$
Milvago chimachima	$2.20 \pm 3.37*$	$1.62 \pm 2.55*$	1.74 ± 2.70	2.01 ± 3.26
Milvago chimango	9.87 ± 12.42	8.75 ± 9.86	8.76 ± 11.84	9.86 ± 10.55
Falco sparverius ²	11.98 ± 8.16	10.61 ± 6.18	9.75 ± 6.47	12.84 ± 7.69
Falco femoralis	0.38 ± 0.90	0.31 ± 0.79	0.23 ± 0.71	0.45 ± 0.96
Falco peregrinus ¹	0	0.02 ± 0.15	0.02 ± 0.15	0
Гotal	95.09 ± 42.86	113.91 ± 44.26		

^{*} P < 0.05.

cayanensis, n=2), Rufous-thighed Kite (Harpagus diodon, n=4), Bicolored Hawk (Accipiter bicolor, n=4), Crane Hawk (Geranospiza caerulescens, n=6), Harris's Hawk (Parabuteo unicinctus, n=6), and White-rumped Hawk (Parabuteo leucorrhous, n=1)

were rarely recorded. Swallow-tailed Kite and Plumbeous Kite were recorded only during spring/summer, and were significantly more abundant during these seasons (P < 0.01) in both years (P > 0.50). All records of these species, except for one (a Plumbeous

¹ Species with abundance too low for statistical analysis.

² Significant interaction between the predictor variables: year and season (P < 0.05).

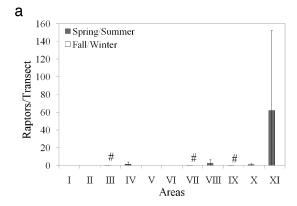
Kite observed on the coast of southern Brazil), were in northern Rio Grande do Sul and southern Santa Catarina (sampled areas I, II, and IV).

Swainson's Hawks were recorded during the spring/summer through most of the study area (in seven sampled areas; Fig. 2a). Its abundance was higher during these seasons (P < 0.01) in both years (P = 0.99). Observations of solitary individuals, pairs or small flocks (fewer than six raptors) were common, but flocks greater than 50 raptors (up to hundreds) were observed in western Uruguay. In Florida and Flores provinces (area XI), up to 117 Swainson's Hawks per point count were counted, totaling 92.6% (n = 498) of all individuals recorded. Once, more than 300 Swainson's Hawks were observed near the road. Flocks consisted of both juveniles and adults, which were usually foraging near the road (flying or perched on fences, trees, or on the ground).

Short-tailed Hawk (*Buteo brachyurus*) showed significantly higher abundance during 2010–2011 (P > 0.01), but did not change seasonally (P > 0.50). This species was recorded mainly in northern areas (areas I, II, IV, with the exception of three records in areas III and V), always in low abundance (mean = 0.1 individuals/transect).

Changes in the abundance of Savanna Hawk (Buteogallus meridionalis) showed an interaction between year and season ($P_{year\ x\ season} = 0.01$). In general, abundances (A) were similar across both years and seasons (Table 1). However, in spring/summer of 2009-2010, Savanna Hawk was almost twice as abundant as in fall/winter ($A_{\text{spring/summer}} = 4.3 \pm 3.9$ individuals/transect; $A_{fall/winter} = 2.2 \pm 2.9$ individuals/transect). In fall/winter of 2010-2011, Savanna Hawk abundance was higher than in the previous fall/winter, in contrast to the decline in abundance in spring/summer, resulting in similar abundances between seasons ($A_{\text{fall/winter}} = 3.9 \pm 4.9$ individuals/transect; $A_{spring/summer} = 3.9 \pm 3.4$ individuals/transect). Savanna Hawk was fairly common on Brazil's southern coast (area III), where it showed the highest seasonality ($A_{\text{spring-summer/2009-2010}} = 11.0$ \pm 1.4 individuals/transect; $A_{fall\text{-winter}/2009-2010} = 4.3$ \pm 3.3 individuals/transect).

White-tailed Kite (*Elanus leucurus*) abundance was higher in fall/winter than spring/summer (P = 0.036) and did not change annually (P > 0.50; Table 1). On the other hand, Snail Kite (*Rostrhamus sociabilis*) and White-tailed Hawk (*Geranoaetus albicaudatus*) were both more abundant in spring/summer than in fall/winter (P = 0.04) in both years (P = 0.04) in both years (P = 0.04)



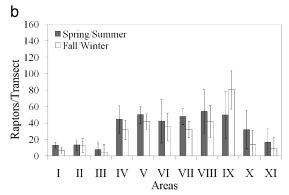
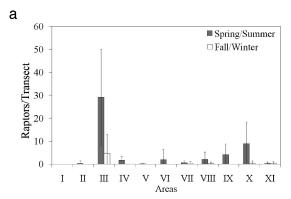


Figure 2. Mean abundance (±SD) of (a) Swainson's Hawk (*Buteo swainsoni*), and (b) Turkey Vulture (*Cathartes aura*) during spring/summer and fall/winter seasons in southern Brazil and Uruguay grasslands. In Fig. 2a, "#" indicates abundance equals 0.12 raptors/transect (areas III, VII, IX). See Fig. 1 for the sampled areas.

> 0.50; Table 1). The highest abundances of Snail Kite were recorded in the wetlands of Brazil's southern coast and Uruguay's coast (areas III and X), and in the humedáles (wetlands) in Uruguay (area IX; Fig. 3a). Although recorded throughout all sampled areas, White-tailed Hawk was more abundant in northwestern Uruguay (area VIII), where it showed substantial seasonal variation (A_{fall/winter} = 0 individuals/ transect; $A_{spring/summer} = 31.9 \pm 17.5$ individuals/ transect; Fig. 3b). In this area, up to 14 individuals (juveniles, adults, pale and dark morphs) were observed foraging in same point count. The observations of White-tailed Hawk in the rest of the study area consisted of single raptors or pairs (84.8% of the records), with a few exceptions in Uruguay (areas IX, X, XI) and western Rio Grande do Sul (area VII), where small flocks of three to seven raptors were recorded (n = 12 flocks).



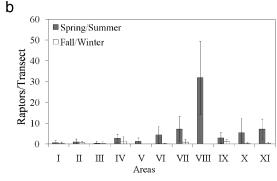


Figure 3. Mean abundance (±SD) of (a) Snail Kite (Rostrhamus sociabilis) and (b) White-tailed Hawk (Geranoaetus albicaudatus) during spring/summer and fall/winter seasons in southern Brazil and Uruguay grasslands. See Fig. 1 for the sampled areas.

Falconiformes. We recorded six species (Table 1). Peregrine Falcon was rare, recorded only twice: during spring/summer, on the coast of southern Brazil (area III) and in southeastern Uruguay (area XI). Abundances of Chimango Caracara (Milvago chimango) and Aplomado Falcon (Falco femoralis) did not change seasonally or yearly (P > 0.50); Table 1). However, Southern Caracara (Caracara plancus) showed both seasonal and annual variations in abundance (P < 0.01). Southern Caracara abundance was higher in fall/winter than spring/ summer ($A_{fall/winter} = 14.1 \pm 9.9$ individuals/transect; $A_{spring/summer} = 10.9 \pm 8.2$ individuals/transect) and in 2010–2011 than 2009–2010 ($A_{2010-11}$ = 14.1 ± 9.3 individuals/transect; $A_{2009-10} = 10.9 \pm$ 8.5 individuals/transect; Table 1). Yellow-headed Caracara (Milvago chimachima) was more abundant in fall/winter than spring/summer in both years (Table 1), whereas American Kestrel (Falco sparverius) abundance showed a significant interaction between year and season (Table 1). American Kestrel abundance did not change seasonally in 2009–2010 ($A_{\rm fall/winter} = 9.2 \pm 6.2$ individuals/transect; $A_{\rm spring/summer} = 10.3 \pm 6.8$ individuals/transect), but increased substantially by the next fall/winter ($A_{\rm fall/winter} = 14.8 \pm 9.0$ individuals/transect; $A_{\rm spring/summer} = 10.9 \pm 5.6$ individuals/transect).

DISCUSSION

The seasonal changes in raptor abundance observed in the southeastern South America grassland were expected based on the presence of migratory species that winter in the region during austral spring/summer but are absent in fall/winter. However, the variations in abundance observed for resident species suggest that some of these species are at least partial migrants; and the status assumed may be mistaken. About 50% of the species recorded can be classified, following Bildstein's (2004) definitions, as complete or partial migrants, as well as local migrants or nomads in the region.

Swainson's Hawk was the only complete migrant recorded, with complete migrants defined as "species in which ≥90% of all individuals leave their breeding range during the non-breeding season." (Bildstein 2004). Nevertheless, at least three partial migrant raptors (Bildstein 2004), which do not occur year-round in the region (Belton 1984, Arballo and Cravino 1999, Bencke 2001), could be defined as complete migrants in this region: Peregrine Falcon, Swallow-tailed Kite, and Plumbeous Kite. There are no records of Swallow-tailed and Plumbeous kite outside the spring/summer seasons in southern Brazil and Uruguay. However, Peregrine Falcon has two distinct migrant populations recorded in the region, from North America (trans-equatorial migrants) and Patagonia (austral migrants; Ferguson-Lees and Christie 2001). Our records were all in spring/summer, suggesting that these raptors were North American migrants. The higher abundance of Swainson's Hawk in western Uruguay was not surprising because this region is inside the main wintering area of the species (Sarasola et al. 2008, Kochert et al. 2011). Our records of single raptors and small aggregations in central and eastern Uruguay and Rio Grande do Sul probably represent vagrant individuals. As expected for a complete migrant species, Swainson's Hawks can cover long distances quickly, and assume a vagrant behavior in the wintering area, joining flocks that follow locally abundant food resources (Jaramillo 1993, Kochert et al. 2011).

Patterns of Turkey Vulture migration in South America are little known. Although some of the North American populations (C. a. meridionalis) are trans-equatorial migrants, the South American populations (C. a. ruficollis) are assumed to be residents across the continent, except for Patagonian populations (C. a. jota), which probably are at least partial austral migrants (Ferguson-Lees and Christie 2001). Although our results do not challenge the resident status of Turkey Vulture in southern Brazil and Uruguay (Belton 1984, Arballo and Cravino 1999, Bencke 2001), they do suggest a partial migrant status in the region. The significantly higher abundance of this species in spring/summer than in fall/winter in 90% of the sampled area in both years (Fig. 2b) suggests migration, not local movements or sampling bias, because those would probably also result in annual variation or no spatial pattern. Moreover, raptor migration counts in Bolivia (Olivo 2005) and Argentina (Juhant 2010) suggest migration of Turkey Vulture in these countries, and, more recently, satellite-tracking data (Bildstein and Barber 2013, www.movebank.org) confirmed migration between northern Argentina and southern Bolivia. These data support the hypothesis of partial migration by vultures in Uruguay and southern Brazil; however, the numbers of individuals and the migration routes remain unknown.

Based on our observations and previous reports (Olivo 2003), we suggest that intracontinental migration occurs in White-tailed Hawk in South America. Despite the assumption that this species is a resident throughout its distributional range (Ferguson-Lees and Christie 2001), our results suggest partial migration, as in Uruguay (Arballo and Cravino 1999). The White-tailed Hawk breeds in the tropical savanna (cerrado) biome (Baumgarten 1998, 2007, Granzinolli 2009), and also in southern Brazil (Maurício et al. 2013). Moreover, no significant seasonal fluctuations have been reported for grasslands in the center of Brazil (Baumgarten 1998, 2007, Granzinolli 2009). This supports the hypothesis of partial migration, through the transamerican flyway (sensu Bildstein 2004), through central South America. There are a few reports suggesting migration in the White-tailed Hawk in South America; all were assumed to be resident hawks that joined flocks with Swainson's Hawks or simply misidentified birds (see Bildstein 2004). However, it is possible that those records were truly migratory raptors that migrate in the same way as Swainson's Hawks (although not necessarily the North American individuals),

and winter in the same regions in southern South America. Also, our observations are quite different from previous reports. We recorded single hawks foraging, close to each other, but we did not record flocks moving through the point counts. This pattern was constant along the survey routes, reducing the probability that the observed hawks were resident raptors. In addition, the species abundance changes seasonally, and, as with Turkey Vulture, the pattern does not suggest local movements or sampling bias. Although our data suggest intracontinental migration in South America, in the absence of more robust data (e.g., satellite tracking, genetic studies), we can only suggest a pattern of migration for the White-tailed Hawk in South America. We cannot exclude the possibility of a more complex pattern of migration that involves more than one migration system (SATT and SACT systems, sensu Joseph 1997) and overlapping of these migrant individuals with resident ones. More data are needed, especially to investigate a possible austral migration.

Although previously assumed to be resident in southern Brazil (Bencke 2001) and Uruguay (Arballo and Cravino 1999), the Snail Kite is a partial migrant in most of South America (Bildstein 2004). Feeding mainly upon the freshwater snail of genus Pomacea, Snail Kites have movements that are probably related to the seasonal changes in water level in the wetlands of the Paraguay River basin (Hayes 1991, Antas 1994, Hayes et al. 1994, Olivo 2005), on the coast of southern Brazil (Albuquerque et al. 1986) and Argentina (Capllonch 2004, Juhant 2010). Our results support Albuquerque et al.'s (1986) assertion of partial migration in the Snail Kite in southern Brazil, although Belton (1984) and Bencke (2001) assumed the species is resident. The pattern we observed of higher abundance in coastal and inland wetlands (Fig. 3a) was repeated in both years, despite the occurrence of an ENSO (El Niño Southern Oscillation) in 2009-2010 (source: http://enos.cptec.inpe.br), and suggested partial migration rather than irregular or nomadic movements by Snail Kite in the region.

Three species that were more abundant during fall/winter, White-tailed Kite, Southern Caracara, and Yellow-headed Caracara, are assumed to be partial, local, or irregular migrants (Bildstein 2004). Data from Bolivia (Olivo 2005) suggest austral migration in White-tailed Kite. However, in that case, we would expect higher abundance during spring/summer. The absence of seasonal and spatial patterns observed in the region (Fig. 4) suggests irregular

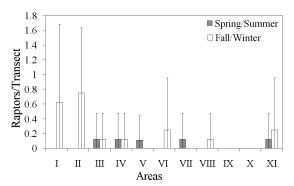


Figure 4. Mean abundance (±SD) of White-tailed Kite (*Elanus leucurus*) during spring/summer and fall/winter in southern Brazil and Uruguay grasslands. See Fig. 1 for the sampled areas.

movements. The White-tailed Kite was usually recorded foraging in harvested croplands and our records may simply reflect opportunistic use of such habitat.

The higher abundance of Southern and Yellowheaded caracaras in fall/winter could be related to irregular movements while foraging. In agricultural landscapes, raptors may change foraging habitat according to seasonal changes in land use; thus, their local abundance may be affected (Leveau and Leveau 2002). Both species were observed foraging opportunistically in plowed fields (e.g., after potato harvest), sometimes forming large aggregations (especially the Southern Caracara). Changes in Yellowheaded Caracara abundance could also be related to a decrease in the detectability during the breeding period. This species inhabits ecotone-forest habitats (Belton 1984, Arballo and Cravino 1999), and was more abundant in more forested areas (areas I, II, and V), which reduces the probability of detection by the roadside survey method (Millsap and LeFranc 1988). Migration reports of Southern Caracara in South America suggest local or irregular movements (Hayes 1991). The observations reported by Olivo (2005), Juhant (2010) and Juhant and Seipke (2009) only weakly support partial migration (low abundance recorded as well as migration inferred by flying direction and behavior). Moreover, another species assumed to be an austral migrant by these authors, Chimango Caracara, did not show seasonal changes in abundance in our study, suggesting that their records of both Southern and Chimango caracaras may represent wandering raptors (irregular or local migrants), not true migrants. Another hypothesis postulated by Albuquerque et al. (1986) to explain the higher abundance of Southern Caracaras in southern Brazil was recruitment. They found a high number of juveniles during winter; however, we recorded only a slight increase in the proportion of juveniles in fall/winter (10%) relative to spring/summer (8%), a proportion that was similar in both years (3.8% and 4.9%; F. Zilio unpubl. data). Based on the above data, irregular or local movements trigged by food resources may be a plausible explanation for the seasonal changes in abundance of Southern Caracara, except perhaps in extreme southern Patagonia, where it is probably an austral migrant like other raptors in that region (Ferguson-Lees and Cristie 2001, Bildstein 2004).

Temporal changes in the abundance of the Savannah Hawk, Short-tailed Hawk, and American Kestrel could be explained by variation in the number of juveniles, or floaters, as well as in the species detectability. Because we did not focus our surveys on forest habitats, we probably underestimated the abundance of forest raptors such as the Short-tailed Hawk and Bicolored Hawk. The higher abundance of American Kestrel and Savanna Hawk recorded in fall/winter surveys in 2010 could be due to the presence of juveniles during those counts. In southern Rio Grande do Sul, Albuquerque et al. (1986) recorded higher abundances of these raptors in winter, and believed the presence of juveniles explained this increase. We have no better explanation than changes in the abundance of non-territorial individuals for our American Kestrel results. However, Savanna Hawk juveniles and subadults were more common in our counts in spring/summer (F. Zilio unpubl. data). In the Paraguay River, the Savanna Hawk abundance seems related to the changes in the river water level (Hayes 1991). Irregular or nomadic movements trigged by changes in prey availability seem likely for this generalist midsized raptor with relatively high capacity for dispersal, and hence such movements may explain the changes in abundance that we recorded.

Although Cinereous Harrier (*Circus cinereus*) was uncommon, we recorded this species year-round and found no evidence for seasonal changes in abundance, suggesting resident status for Cinereous Harrier in southern Brazil and Uruguay, as also indicated by breeding data (Maurício and Dias 1996, Arballo and Cravino 1999, Camilotti et al. 2008). However, the possibility that two overlapping populations occur in the region in fall/winter, one resident and the other austral migrants from Patagonia, remains to be evaluated. Our records of Rufous-thighed Kite all occurred

in spring/winter, agreeing with recent data that suggest migration in southeastern and southern Brazil (Cabanne and Seipke 2005, Azevedo et al. 2006).

Conclusions. The southeastern South American grassland has a high diversity of raptors, whose population dynamics indicate several different migratory strategies. Unfortunately, our study did not allow us to distinguish local or irregular migration strategies from nomadic movements. Nevertheless, our results provide a necessary starting point to better understand the poorly known intra-tropical migration in the Neotropics. Our results strongly suggest that at least three species currently classified as residents in the region, Turkey Vulture, Snail Kite, and White-tailed Hawk, are instead partial migrants, with resident and migratory populations overlapping part of the year. For these species in particular, as well as for Cinereous Harrier and Southern Caracara, further investigations are required, including studies with marking and tracking of nonbreeding individuals to identify migration routes.

Conservation efforts for migratory raptors should consider the threats in both breeding and wintering grounds, as well as throughout the migration route (Bildstein 2006). Thus, the conservation of migrant raptors in Nearctic and Neotropical habitats depends on (1) identifying each species' migratory strategy, and (2) mapping their migration routes, breeding areas, and wintering areas. Data are still far too scarce for most South American raptors. Finally, we highlight the need to amplify the raptor migration monitoring network in South America, including the establishment of fixed points to count migratory raptors, not only along the transamerican flyway, but at strategic sites in still undiscovered locations in the central and southern parts of the continent (Paraguay, Brazil, Argentina and Uruguay).

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