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RESEARCH

Large-scale spatiotemporal patterns in abundance and age structure of the white-tailed hawks in South America

Matías A. Juhant[1] · **Juan I. Areta**[2]

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Abstract
The white-tailed hawk (*Geranoaetus albicaudatus*), found across the Americas, is well-suited for studying spatiotemporal patterns due to its conspicuous soaring behavior, preference for open areas, partial migratory habits, and delayed plumage maturation (five age classes). Here, we investigate overall abundance and seasonal shifts in age class abundance across the Gran Chaco/Espinal and the Cerrado. We also examine single-season abundance and age class distribution in the Amazon Basin and Guianan Savanna. Our analysis is based on systematic surveys spanning 692 h and 20,755 km in 138 roads (193 h, 5,840 km in 42 roads during the austral winter, and 499 h, 14,915 km in 96 roads during the austral summer). We found that: (1) overall abundance increased during the austral summer, with a 3.7-fold increase in the Gran Chaco/Espinal and a 1.6-fold increase in the Cerrado compared to the austral winter; (2) in the Gran Chaco/Espinal, age class distribution shifted from left-skewed (oldest class most abundant) in the austral winter to a slightly right-skewed, more even pattern (younger classes more abundant) in the austral summer, while in the Cerrado it remained left-skewed in both seasons; and (3) the Amazon Basin and the Guianan Savanna, surveyed in a single-season, exhibited a left-skewed distribution during the austral summer, similar to that of the Cerrado. This study establishes a crucial baseline for understanding spatiotemporal patterns at the age-specific level across South America, emphasizing the need for further research into age class distribution and its relation to the breeding phenology in the white-tailed hawk.

Keywords Age class · Delayed plumage maturation · *Geranoaetus albicaudatus* · Road survey · Seasonal variation

Introduction

Assessing spatiotemporal patterns in raptor species is challenging due to their naturally low abundances (Newton 1979). These challenges are further compounded by anthropogenic transformations of natural habitats, which drive changes in raptor abundance and distribution patterns worldwide, potentially increasing or decreasing their numbers and expanding or contracting their ranges (e.g., James et al. 1987; Thiollay 2007a; Eakle 2008; Buij et al. 2013; Cherkaoui et al. 2013; Leveau 2021). Large-scale road surveys have proven essential for understanding spatiotemporal patterns of conspicuous and soaring raptors inhabiting both natural and altered open areas in the Neotropical region (e.g., Bildstein et al. 2007; Jensen et al. 2005; Zillio et al. 2014; Juhant 2022; Juhant et al. 2022). However, empirical data on these patterns are still lacking in most open biogeographical regions of South America, presenting significant opportunities for research (Juhant 2022).

Most migratory raptors in South America are partial migrants, many of which exhibit delayed plumage maturation and demonstrate age-dependent patterns in their regular annual migrations (Juhant 2022; Juhant et al. 2022; Juhant and Saggese 2026). Therefore, assigning age classes to these partial migrants is crucial to understanding their spatiotemporal patterns across the annual cycle. The three species in the genus *Geranoaetus* exemplify these ecological traits, acquiring their Definitive Basic Plumage after going through four annual molt cycles (Seipke 2007; Juhant 2026a; Juhant unpubl. data). They are ideal for assessing distribution patterns through road surveys,

✉ Matías A. Juhant
juhant@hawkmountain.org

[1] Acopian Center for Conservation Learning, Hawk Mountain Sanctuary, Orwigsburg, PA, USA

[2] Laboratorio de Ecología, Comportamiento y Sonidos Naturales (ECOSON), Instituto de Bio y Geociencias del Noroeste Argentino (IBIGEO-CONICET), Salta, Argentina

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given their conspicuous and soaring behavior over both natural and altered open habitats (Juhant 2022; Juhant et al. 2022). The white-tailed hawk (*Geranoaetus albicaudatus*) is becoming increasingly common in anthropogenic agroecosystems, and the expansion of these altered habitats is influencing its abundance and distribution across the Americas, as it regularly gathers in fields that are being burned, plowed, or harvested (Stevenson and Meitzen 1946; Tewes 1984; Wheeler 2003; Hilty 2010).

Information on the spatiotemporal patterns of the white-tailed hawk across its range—from the southern United States to central Argentina—remains limited (Vous 1968; Zilio et al. 2014; Juhant 2022; Farquhar 2020). In South America, the earliest observations of white-tailed hawks migrating in the eastern Pampas of Argentina (Hudson 1920) and the lowlands east of the Andes in Bolivia (Olivo 2003) have been questioned by Bildstein (2004) and Farquhar (2020). They suggest that the observed individuals may actually correspond to Swainson's hawks (*Buteo swainsoni*) misidentified as white-tailed hawks, as these areas are major flight paths for this long-distance migratory species, casting doubt on whether white-tailed hawks exhibit seasonal movements within the continent. However, these authors overlooked Giai (1952-1953) observations that white-tailed hawks in Argentina migrate north in austral autumn (after Swainson's hawks have left) and are absent during the austral winter, as well as Vous (1968) proposal that the Guiana Shield may serve as an overwintering area for individuals breeding elsewhere, such as south of the Amazon Basin or in northern South America.

Further evidence gathered over the past 15 years has reinforced the idea of seasonal movements of white-tailed hawks across South America. Road surveys revealed differences in overall abundance in the Llanos of Venezuela between the wet (April-November) and dry (December-March) seasons, and in the Pampas of Uruguay and southern Brazil between austral spring/summer compared to austral autumn/winter (Jensen et al. 2005; Zilio et al. 2014). Additionally, single individuals and small flocks were recorded migrating at various sites in Argentina and Bolivia (Juhant 2010, 2011, 2012; Pagano et al. 2012). These compelling pieces of evidence, along with the austral winter surveys presented in this study, form the basis for considering the white-tailed hawk a partial migratory species in South America by Juhant (2011, 2022). Despite all the evidence, a recent frequency distribution map derived from eBird data has treated the white-tailed hawk as a year-round resident (Fink et al. 2024). Ultimately, these differing perspectives highlight a need for further research to better understand the migratory behavior of this species.

Comprehending the annual cycle of the white-tailed hawk in South America, including its breeding phenology, is essential for understanding its spatiotemporal patterns throughout the year. However, the complexity of its breeding phenology—characterized by wide geographic variation across the continent—and a dataset of primarily anecdotal observations leads to a currently limited understanding. In the southern biogeographical regions, including the Pampas, Espinal, and Gran Chaco, as well as adjacent tropical areas like the Cerrado and the Atlantic Forest, the breeding phenology follows the typical seasons of the southern hemisphere, with breeding primarily occurring from late August to early January (Ferguson-Lees and Christie 2001). Egg-laying typically occurs between August and October, with fledglings appearing from November to January (Ferguson-Lees and Christie 2001; Di Giacomo and Krapovickas 2005; Motta-Junior et al. 2010; Maurício et al. 2013). In contrast, assessing breeding phenology in other regions of South America, such as the Amazon Basin and tropical savannas, is more complex, as breeding seems not to be closely tied to the wet and dry seasons (Mader 1981; Hilty 2010). Furthermore, large regions like the Amazon Basin experience variations in the timing of these seasons across their range, leading to considerable differences in breeding seasons within the region. For example, in the western Amazon Basin of Peru, breeding may occur from June to October, with egg-laying presumably taking place in June and July and fledging occurring in September and October (Rivas-Fuenzalida et al. 2022). In contrast, in the eastern Amazon Basin of Suriname, egg-laying occurs in February, with fledglings appearing in April (Brown and Amadon 1968). As a result of the geographically variable breeding phenology, fresh juvenile individuals can be found across the continent throughout the year.

This study aims to assess the abundance and age class distribution patterns of the white-tailed hawk based on a large-scale survey across five biogeographical regions of South America (see Fig. 1 for details). Specifically, here we: (a) compare variation in overall abundance between seasons in the Gran Chaco/Espinal and the Cerrado; (b) compare the overall abundance at the tropical regions (Cerrado, Amazon Basin, and Guianan Savanna) during the austral summer; (c) analyze the age class distribution patterns within season for each biogeographical region; and (d) identify local areas of high abundance, where over 50% of individuals were recorded in each season and biogeographical region, despite comparatively reduced field effort. The results provide valuable insights into distribution patterns by age class, emphasizing the importance of including age class assignments in species with delayed plumage maturation to enhance our understanding of their annual cycle and create more accurate distribution maps.

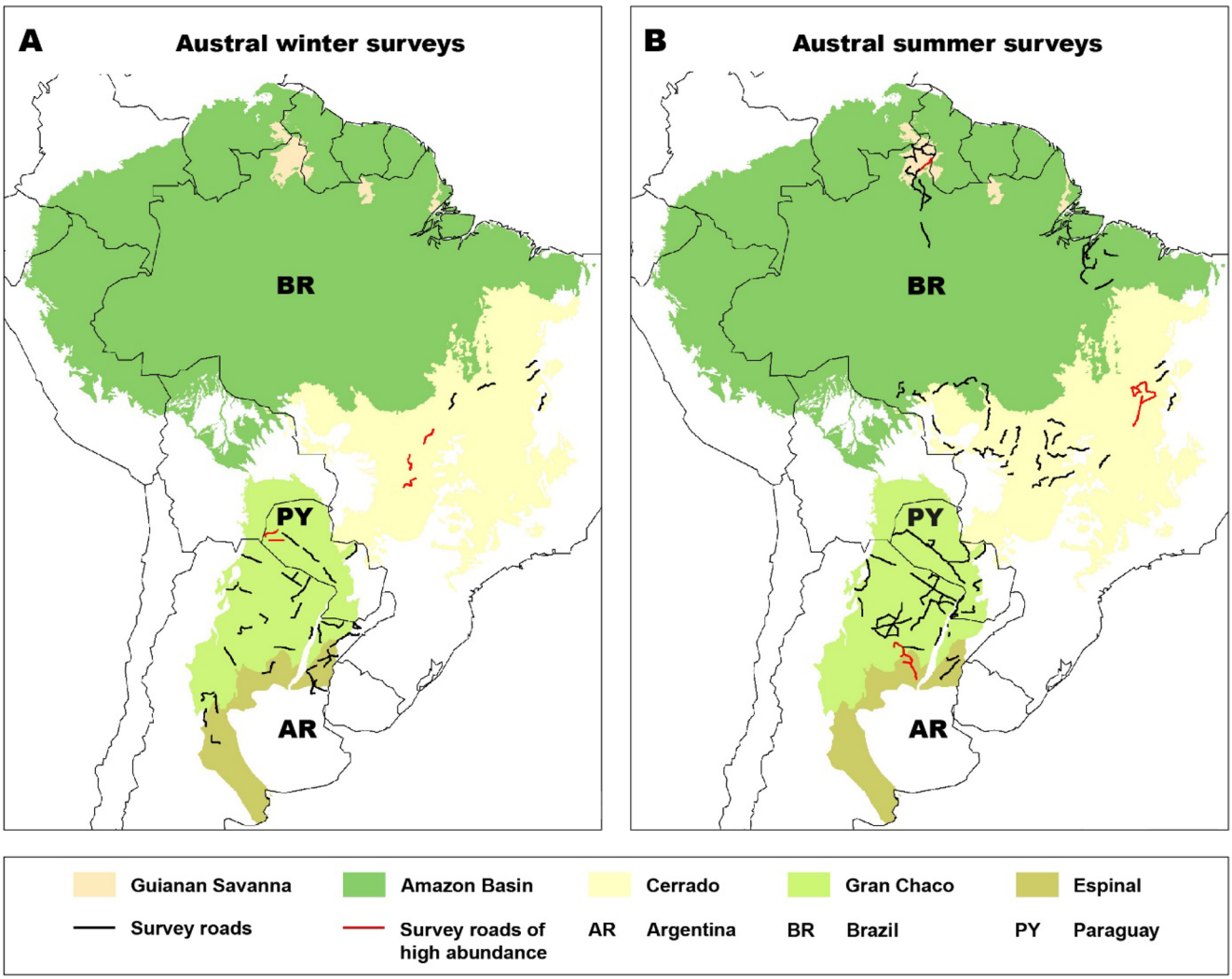


Fig. 1 Road surveys to count white-tailed hawks (*Geranoaetus albicaudatus*) were conducted over two austral winters (late May to late July) in 2018- 2019 across the Gran Chaco/Espinal and Cerrado regions, and over three austral summers (mid January to mid March) in 2022-2024 across the same biogeographical regions as well as the Amazon Basin and Guianan Savanna. (**a**) Austral winter surveys involved a field effort of 193 h and covered 5,840 km across 42 road surveys. (**b**) Austral summer surveys involved a field effort of 499 h and covered 14,915 km across 96 road surveys

Methods

Age class assignment

The white-tailed hawk reaches its Definitive Basic Plumage after undergoing four annual molt cycles (Juhant unpubl. data). Individuals were assigned to age classes primarily based on the molt patterns of flight feathers (especially primaries) and secondarily on the overall coloration of the underparts, following the nomenclature established by Howell et al. (2003) for species with delayed plumage maturation (see Table 1 for details). Furthermore, each age class can be associated with a timescale based on the onset of primary molt, which begins when individuals are around nine months of age (though some may start at ten months).

Table 1 Age class nomenclature for white-tailed hawks (*Geranoaetus albicaudatus*) based on the annual molt cycle of flight feathers. Each age class corresponds to an approximate absolute time scale, as primaries begin to molt at around nine months of age and new molt cycles begin every 12 months thereafter

Age class nomenclature	Age in months	Annual molt cycle
Basic I (juvenile)	≤8	None
Basic II (second year)	9-20	One
Basic III (third year)	21-32	Two
Basic IV (fourth year)	33-44	Three
Basic V (adult)	≥45	Four or more

The primary molt lasts about eight months and recurs every twelve months thereafter, starting from the onset of the first primary molt (Table 1; Juhant unpubl. data). In the Espinal, Gran Chaco, and Cerrado (see details below for each

area), the white-tailed hawk molts from September to April. This means that individuals observed during the austral winter surveys were in the non-molting season, while those observed in the austral summer were in the middle of the molting season, indicating that the individuals observed were born between late austral spring and early austral summer. However, in the northern Amazon region and Guianan Savanna (see details below for the area), individuals were observed both at the onset and the cessation of the annual molt cycle, indicating that the individuals observed were born at different times of the year.

In *Geranoaetus*, new and old flight feathers can be reliably distinguished by their wear and color pattern (older feathers are lighter and more abraded than newer ones) and shape (the flight feathers of Basic I plumage are shorter, narrower, and more pointed at the tip than those of more advanced age classes resulting in a ragged trailing edge to the wing which is noticeable in flight) (Juhant et al. 2022; Juhant and Saggese 2026).

In Accipitriformes, the molt pattern in primaries is the most accurate method for assigning individuals to a given age class, as a new molt wave begins at primary 1 at the start of each annual molt cycle, regardless of whether all primaries were replaced in the previous cycle (Clark 2004; Juhant 2026b). Therefore, Basic I (≤8 months; juvenile age class) shows a single generation of primary feathers and no molt waves. Basic II (9-20 months; second year) shows two generations of primaries and one molt wave. Basic III (21-32 months; third year) shows three generations and two molt waves. Basic IV (33-44 months; fourth year) shows two generations and three molt waves. Finally, Basic V (≥45 months; adult) includes individuals that begin the four annual cycle to acquire the Definitive Basic Plumage, as well as those with five or more annual molt cycles, since by this stage all primaries have been replaced at least once, making it no longer possible to accurately age individuals based on their flight feather molt (see Table 1 for details).

Biogeographical region surveys

The majority of the Gran Chaco (800,000 km^2) and the entire Espinal (100,000 km^2) are located within the Austral Temperate Region and experience the four distinct seasons typical of temperate regions. The Gran Chaco is characterized by a humid eastern section and a primarily dry western section, while the Espinal stretches as an irregular arch, forming a transitional region between the Gran Chaco and the Pampas. Due to limited field research in the Espinal, these two regions were combined and labeled as Gran Chaco/Espinal. In contrast, the Cerrado (2,000,000 km^2), Amazon Basin (7,000,000 km^2), and the Guianan Savanna (100,000 km^2) are distinctly tropical biogeographical regions, with the Cerrado and Amazon Basin encompassing the largest areas within the tropical belt of South America. Due to the variations in latitude and longitude, the wet and dry seasons differ significantly both within and among these regions. The Cerrado features a mix of grasslands, shrubs, and scattered trees, with distinct wet (October-April) and dry (May-September) seasons. The Amazon Basin is generally flat, with interspersed low hills covered by dense canopy forests, and experiences one or two wet seasons annually, which vary considerably across the region. Finally, the Guianan Savanna spans from 1°N to 5°N, is predominantly flat with low hills, plateaus, and patches of woodland, and has distinct wet (December-July) and dry (August-November) seasons. The biogeographical and climatic patterns summarized here follow the regional framework proposed by Cabrera and Willink (1973).

Field effort, survey protocols, and survey area selection

The total field effort during the austral winter included 193 h and 5,840 km across 42 road surveys, whereas in the austral summer it totaled 499 h and 14,915 km across 96 road surveys (Table 2, Appendix A). These surveys were conducted using methods commonly employed in similar large-scale road surveys (e.g., Sánchez-Zapata et al. 2003; Bildstein et al. 2007; Garbett et al. 2018):

1. Surveys were conducted by MAJ (first author) and an assistant (the driver, who remained the same throughout all surveys). This two-person setup is widely used worldwide (e.g., Jensen et al. 2005; Thiollay 2006; Carrete et al. 2009; Garbett et al. 2018), though some surveys have employed one- or three-observer setups (e.g., Wuczyński 2003; Baltag et al. 2013); yet, to our knowledge, no research has specifically examined or controlled for the effects of observer setup variation (McClure et al., 2021).
2. Each survey covered a considerable distance (100–250 km) on low-traffic roads, which allowed the driver to simultaneously assist in searching for individuals while maintaining focus on the road.
3. Surveys were conducted between 08:00 and 17:00, with lunch break generally between 12:00 and 13:00 (the break lasted from half an hour to one hour).
4. Coordinates were taken at the start and the end of each survey, and details on the itinerary followed were tracked with a GPS device.
5. Travel speed was 25–50 km per hour.
6. Surveys were carried out in good climatic conditions.
7. Individuals were recorded at a maximum distance of 700 m from each side of the road, covering a combined

Table 2 Field effort and counts of white-tailed hawks (*Geranoaetus albicaudatus*) by age across five biogeographical regions of South America during the austral winter and summer. See Table 1 for the definition of age classes and Table 3 for a summary of survey timing in relation to phenology

Field effort	Gran Chaco/Espinal		Cerrado		Amazon Basin	Guianan savanna	Total
	Austral winter	Austral summer	Austral winter	Austral summer	Austral summer	Austral summer	
Road surveys	34	39	8	28	22	7	138
Hours	154	213	39	135	114	37	692
Km	4,710	6,735	1,130	4,205	3,005	970	20,755
Km/hour	30.8 (±4.2 SD)	32.2 (±5.2 SD)	29.3 (±4.5 SD)	31.6 (±7.6 SD)	26.4 (±4.4 SD)	26.3 (±3.6 SD)	30.3 (±5.7 SD)
Individuals counted							
Basic I	1	41	0	11	3	4	60
Basic II	1	31	1	2	1	17	53
Basic III	3	30	3	8	4	29	77
Basic IV	5	16	8	41	13	17	100
Basic V	19	31	11	67	26	51	205
Subtotal	29	149	23	129			
Total	178		152		47	118	495

width of 1,400 m. This distance was based on visual estimation in the field and represents the maximum observable range under open conditions. Actual visibility and detection distance varied among sites depending on topography and vegetation cover, and in some areas, the effective detection distance was less than 700 m.

8. Each individual detected was recorded to the nearest tenth of a kilometer using the car odometer, and its GPS coordinates were taken.
9. Each individual was assigned to one of the five age classes, using the nomenclature established by Howell et al., (2003).
10. Stops were allowed to photograph the individuals detected using a Canon EOS 7D Mark II with a Canon EF 400 mm f/4.0 L lens; during these stops, only those individuals detected at the moment of the stop were counted (i.e., individuals detected after the stop due to wider angles of view or increased distance of observation were excluded). For some individuals, the age class was validated by carefully assessing the photographs obtained, in addition to direct observations. Further details on itineraries followed within the five biogeographical regions are provided in Appendix B.

The areas surveyed across these five biogeographical regions (Fig. 1) were selected based on the mainstream literature (e.g., Ferguson-Lees and Christie 2001) and from maps generated by Citizen Science Initiatives (e.g., eBird and WikiAves Brasil), both of which identify the white-tailed hawk as a common breeder in these regions. This area selection approach is widely accepted, especially for species with well-documented distribution patterns, as it allows for the assessment of spatiotemporal variation in abundance (e.g., Bildstein et al. 2007). By concentrating efforts in regions with the highest likelihood of white-tailed hawk presence, this approach enhances survey efficiency and provides a more reliable understanding of the spatiotemporal abundance.

Survey timing in relation to phenology

Surveys were conducted during the non-breeding season (overwintering) and immediately after the breeding season (fledgling dispersal period) in the Gran Chaco/Espinal and the Cerrado (Ferguson-Lees and Christie 2001; Di Giacomo and Krapovickas 2005; Motta-Junior et al. 2010; Maurício et al. 2013). In addition to these two-season surveys, single-season surveys were carried out in the Amazon Basin and the Guianan Savanna. These regions were further divided into subregions due to variations in breeding phenology across the areas. Based on published information on regional breeding phenology, we infer that surveys in the southern Amazon were conducted immediately after the breeding season (fledgling dispersal period) (Rivas-Fuenzalida et al. 2022). In the eastern Amazon, surveys likely coincided with the middle of the breeding season (Brown and Amadon 1968). Finally, in the northern Amazon and the Guianan Savanna, surveys likely occurred during the non-breeding season (overwintering) (Mader 1981; Hilty 2010). See Table 3 for a summary of survey timing in relation to phenology.

Data analysis

We used the ratio of the total number of individuals observed per season and biogeographical region to the

Table 3 Summary of our preliminary understanding of the annual cycle phenology of the white-tailed hawk (*Geranoaetus albicaudatus*) in the five biogeographical regions surveyed in South America

Biogeographical regions	Survey timing	Southern hemisphere seasons	Phenology	Survey itinerary
Gran Chaco/Espinal and Cerrado	late-May to mid-July	Austral winter	Non-breeding season (overwintering)	Appendix B.1-3
	January to early-March	Austral summer	Immediately after the breeding season (fledging dispersal period)	Appendix B.1-3
Southern Amazon	January	Austral summer	Immediately after the breeding season (fledging dispersal period)	Appendix B.4
Eastern Amazon	March	Austral summer	Middle of the breeding season	Appendix B.5
Northern Amazon and Guianan Savanna	late-January to mid-February	Austral summer	Non-breeding season (overwintering)	Appendix B.6-7

total hours of observation per season and biogeographical region as an index of the overall abundance (combining the five age classes). This standardization facilitates direct comparisons, as field effort varied among seasons and regions. Calculating individuals per hour of observation, rather than individuals per kilometer, highlights the proportion of observed individuals more clearly.

Additionally, to evaluate age class distribution patterns across seasons and biogeographical areas, we used the relative abundance of each age class. After calculating the number of individuals per hour for each age class, the abundance of each class was divided by the overall abundance for a given season and region to generate a relative abundance index. This approach allows for direct comparison of age class distributions (proportions) across seasons and regions, irrespective of differences in total counts or effort (e.g., low counts in the Amazon Basin with large sampling effort compared to high counts in the Guianan Savanna with comparatively reduced sampling effort; see Table 2 for details). Using relative abundance provides a clearer understanding of the population's age structure and offers a more accurate reflection of age class distribution patterns.

Finally, local areas of high abundance within a given season and biogeographical region were defined as such when more than 50% of the total individuals observed were recorded with comparatively reduced field effort, accounting for less than 50% of the total hours of observation and distance surveyed. This arbitrary 50% threshold was chosen as an objective aid to identify sites where individuals were aggregated relative to sampling effort, thereby reflecting seasonal congregation patterns rather than uniform spatial distributions.

Surveys conducted in the Gran Chaco/Espinal were not entirely paired across seasons. A total of 2,060 km was repeated in both seasons, accounting for 44% of the total km surveyed during the austral winter and 31% during the austral summer. These repeated surveys included paired surveys, incomplete pairs, and surveys conducted in opposite directions (see Appendix A.1 for details). In contrast, in the Cerrado, 800 km were surveyed in pairs, accounting for 71% of the total km surveyed during the austral winter and 19% during the austral summer (see Appendix A.1 for details). Despite the different sampling regimes in the seasonal surveys, the overall field effort within each season and region was comparable to that employed in similar large-scale roadside raptor surveys (Sánchez-Zapata et al. 2003; Bildstein et al. 2007; Garbett et al. 2018). This is because the non-repeated road surveys or segments of road surveys were generally located near those surveyed in the complementary season (Fig. 1 and Appendix B.1-3 for details). This comprehensive field effort ensures that the dataset is highly representative and reliable for direct seasonal comparisons (Bildstein et al. 2007).

The three regions of the Amazon Basin (southern, eastern, and northern) were analyzed together despite differences in breeding phenology across these distant sites (Table 3). Each region, considered separately, had limited field effort (see Appendix A.3 for details); therefore, to assess the overall abundance and age class distribution in the Amazon Basin, the regions had to be combined. This approach allowed for a cursory analysis of the basin as a whole.

Given the nature of the data, we used descriptive statistics to compare overall abundance across biogeographical regions, examine seasonal shifts in overall abundance within the Gran Chaco/Espinal and Cerrado, and identify local areas of high abundance within each season and region. To assess patterns in age class distribution, we performed Chi-square tests of independence (with significance set at $P<0.05$) to evaluate (1) seasonal shifts in age class distribution within the Gran Chaco/Espinal and Cerrado and (2) differences in age class distribution among the three tropical regions (Cerrado, Amazon Basin, and Guianan Savanna) during the austral summer. All statistical analyses were conducted using GraphPad Prism version 6.01 (GraphPad Software, San Diego, CA, USA).

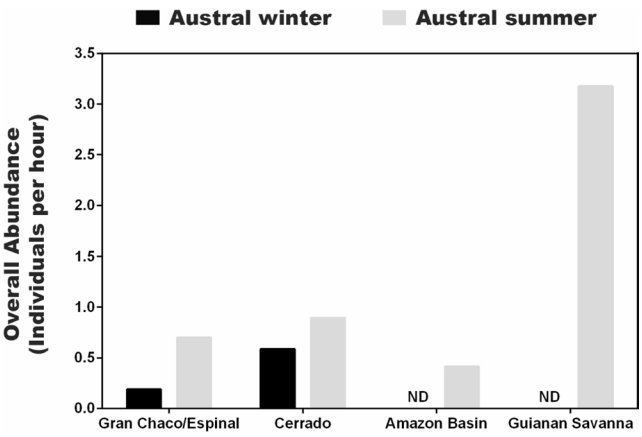


Fig. 2 Overall abundance (total number of individuals observed per season and region divided by the total hours of observation per season and region) of the five age classes combined for the white-tailed hawk (*Geranoaetus albicaudatus*) during the austral winter and summer across five biogeographical regions of South America

Results

Individuals counted

A total of 495 white-tailed hawks were counted over 692 h and 20,755 km in 138 road surveys (Table 2). Of these, 178 individuals (36%) were recorded in the Gran Chaco/Espinal, 152 individuals (31%) in the Cerrado, 47 individuals (9%) in the Amazon Basin, and 118 individuals (24%) in the Guianan Savanna (Table 2). Seasonally, in the Gran Chaco/Espinal, 29 individuals (16%) were counted in the austral winter, compared to 149 individuals (84%) in the austral summer. A similar pattern was found in the Cerrado, with 23 individuals (15%) counted in austral winter, compared to 129 individuals (85%) in austral summer (Table 2).

Overall abundance and seasonal shifts

The abundance of white-tailed hawks varied considerably across latitudes both within and among seasons (Fig. 2). Seasonally, the Gran Chaco/Espinal exhibited the greatest difference in the overall abundance between austral winter and summer, with a 3.7-fold increase in abundance during the austral summer (Fig. 2), while the Cerrado showed only a 1.6-fold increase in abundance during the austral summer (Fig. 2). In the single-season surveys within tropical latitudes, the overall abundance varied notably across the three regions (Fig. 2). The Guianan Savanna exhibited 3.3 and 7.7 times more individuals than the Cerrado and the Amazon Basin, respectively (Fig. 2).

Age class structure and seasonal patterns

In the Gran Chaco/Espinal, the age class distribution during the austral winter was left-skewed, with the oldest age class (Basic V) being the most abundant (Fig. 3a). In contrast, during the austral summer, the distribution shifted to a slightly right-skewed more even pattern, with the youngest age classes (Basic I-III) becoming the most prevalent (Fig. 3a). This seasonal shift showed significant differences ($\chi^2 = 29.43$, df=4, $P<0.0001$), indicating a marked difference in age class distribution between seasons.

In the Cerrado, the age class distribution during both seasons was left-skewed, with Basic IV and Basic V being the

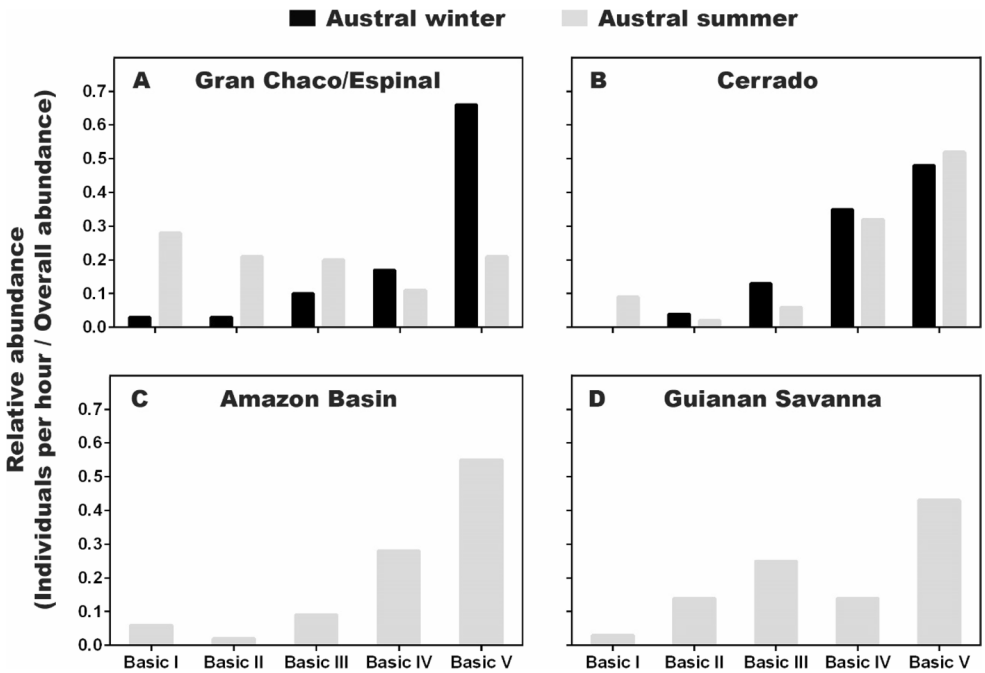


Fig. 3 Relative abundance of white-tailed hawk (*Geranoaetus albicaudatus*) by age class and season (total number of individuals observed per hour for each age class divided by the corresponding seasonal and regional overall abundance) observed across five biogeographical regions of South America. (**a**) Gran Chaco/Espinal. (**b**) Cerrado. (**c**) Amazon Basin. (**d**) Guianan Savanna. See Table 1 for the definition of age classes

most abundant (Fig. 3b). This lack of a pronounced seasonal shift showed no significant differences (χ^2 = 4.117, df=4, P=0391), indicating minimal variation in age class distribution between seasons. However, the distribution among the youngest age classes (Basic I-III) differed most notably for Basic I: no Basic I individuals were observed during the austral winter, while this was the most frequently recorded youngest age class during the austral summer (Fig. 3b). However, it is important to note that our austral winter sample is approximately one-third the size of the austral summer sample (Table 2).

In the Amazon Basin, the age class distribution was left-skewed, with the oldest age class (Basic V) being the most abundant (Fig. 3c). Similarly, the Guianan Savanna exhibited a left-skewed pattern, although Basic II and Basic IV displayed the same level of abundance (Fig. 3d). Despite this overall left-skewed distribution across the three tropical regions (Cerrado, Amazon Basin, and Guianan Savanna) during the austral summer, their age class distributions showed significant differences when compared across these three regions (χ^2 = 44.94, df=8, P<0.0001).

Local areas of high-abundance

These areas were defined as those where over 50% of all individuals were detected with less than 50% of the sampling effort. Two areas of high abundance—one in the Gran Chaco and one in the Cerrado—were found during the austral winter (Fig. 1a). In contrast, three areas of high abundance—the Gran Chaco/Espinal, the Cerrado, and the Guianan Savanna—were found during the austral summer (Fig. 1b). Notably, no area of high abundance was found in the Amazon Basin, as the observed individuals were more evenly distributed across the surveys (Fig. 1b and Appendix B.4-6).

During the austral winter, the first area within the Gran Chaco, Paraguay (21°S), harbored 16 individuals (55%) found over 8 h (5%) and 230 km (4%) (Fig. 1a, Appendix B.2 road labels #32-33AW). The second area situated in the Cerrado, Brazil (15-18°S), included 19 individuals (83%) found over 17 h (44%) and 450 km (40%) (Fig. 1a, Appendix B.3 road labels #1-3AW). Both areas were characterized by a mixture of forest patches, open livestock areas, and agroindustrial landscapes.

During the austral summer, the first area, which includes the Gran Chaco/Espinal, Argentina (27-31°S), contained 80 individuals (54%) counted over 40 h (19%) and 1,280 km (19%) (Fig. 1b, Appendix B.1 road labels #12-13AS, #18-20AS, #23AS, and #25AS). In the second area situated in the Cerrado, Brazil (11-13°S), 73 individuals (58%) were recorded in 25 h (18%) and 890 km (22%) (Fig. 1b, Appendix B.3 road labels #7-10AS). The third area in the Guianan Savanna, Brazil (3°N), had 65 individuals (55%) counted over 5 h (7%) and 115 km (6%) (Fig. 1b, Appendix B.7 road label #6AS). The first two areas were characterized by large-scale agroindustrial landscapes, while the third one was predominantly a natural grassland with interspersed agricultural fields. In these areas,white-tailed hawks were observed, with up to two individuals perched together on consecutive electricity towers and light poles next to the road, especially in the Cerrado (Appendix B.3 road labels #7-10AS), or in small flocks catching insects, mainly in the Gran Chaco (Appendix B.1 road labels #12-13AS, #18-20AS, #23AS, and #25AS). In the Guianan Savanna, two flocks were spotted: one with 44 individuals during plowing and another with 19 individuals during a fire event (Appendix B.7 road label #6AS).

Discussion

Based on large-scale surveys conducted across five biogeographical regions of South America, we found the following regarding the abundance of white-tailed hawks: (1) the highest overall abundance was found in the Guianan Savanna, followed by the Cerrado, Gran Chaco/Espinal, and Amazon Basin; (2) clear seasonal patterns emerged in the Gran Chaco/Espinal, with a dramatic increase in abundance in the austral summer compared to winter, while the Cerrado also exhibited a modest increase in the same season; (3) with the exception of the Gran Chaco/Espinal during the austral summer, the remaining seasons and biogeographical regions showed a left-skewed distribution in age classes, with the oldest age class being the most abundant; and (4) five distinct areas of high abundance were identified during both seasons across the Gran Chaco/Espinal and Cerrado, and in a single-season in the Guianan Savanna, while the Amazon Basin exhibited even abundance, lacking any high-abundance area.

Overall abundance, age class distribution patterns, and seasonal shifts

A notable pattern emerged in the overall abundance across age classes of the white-tailed hawk, with Basic I individuals (≤8 months old) representing only 12% of all individuals recorded, whereas Basic V (≥45 months old) accounted for 41% (Table 2). Since the white-tailed hawk typically lays two eggs (Ferguson-Lees and Christie 2001), we would expect a more balanced age class ratio than the observed 1:3 (Basic I: Basic V). This low abundance cannot be attributed to survey timing, as the surveys were conducted at various points across the annual cycle (Table 3). Despite the low abundance of Basic I individuals, the three youngest age

classes (≤32 months old) together accounted for 38% of the total, resulting in a left-skewed age class distribution (Table 2). This age class distribution pattern, however, does not consistently apply within each season across the biogeographical regions.

The observed seasonal variation in both overall abundance and age class distribution—particularly in the Gran Chaco/Espinal—is consistent with the expected patterns for partial migrants in temperate regions, where winter abundance is low and largely composed of adults that remain year-round, while younger individuals undertake wider seasonal movements (Bildstein 2006). Although surveys in these regions were not perfectly matched across seasons, the extensive field effort provides robust evidence of seasonal movements, consistent with the seasonal shift in abundance (spring-summer vs. autumn-winter) reported further south in the Pampas by Zillio et al. (2014). In contrast, the Cerrado exhibited an atypical pattern, as the overall abundance increased during the austral summer, but the age class distribution remained similar in both seasons, with a notably low abundance of the youngest age classes compared to the two oldest. Despite this, the highest abundance of Basic I individuals (recently fledged) in the austral summer, compared to Basic II and Basic III, matches the observations from the Gran Chaco/Espinal; notably, no Basic I individuals were found during the austral winter. This age class distribution pattern suggests that populations breeding within the Cerrado may not follow the biannual movement patterns seen in the Austral Temperate Region. Instead, the youngest age classes might not return to the breeding grounds and may remain in their wintering grounds somewhere within the tropical belt until their first breeding attempts. If this hypothesis holds, it provides a novel perspective on the complexity of the Neotropical-Intratropical migration system (see, for instance, Areta and Juhant 2019; Juhant 2025 for analyses of seasonal abundance patterns of the rufous-thighed kite *Harpagus diodon* within the tropical and subtropical belts). Potential overwintering and oversummering areas for individuals not returning to the Cerrado include the Llanos of Venezuela and Colombia, as well as the Savannas within the Guiana Shield, including the Guianan Savanna, the Sipaliwini savanna in Suriname, and the Paru-savanna in Brazil.

Alternative explanations for the age class distribution observed during the austral winter and summer in the Cerrado could involve anthropogenic processes, such as increased mortality or breeding failure of younger age classes. Although such factors could theoretically explain the low proportion of Basic I individuals, they seem unlikely given the absence of documented threats to the white-tailed hawk or other large raptors in these regions. Instead, similar age class distributions observed in the Amazon Basin and the Guianan Savanna suggest that the pattern arises from ecological factors that remain to be identified (see above). These results highlight the need for further research into the mechanisms underlying the spatiotemporal variation in abundance and age class distribution of the white-tailed hawk across tropical South America.

In the Guianan Savanna, the observed variation in molt patterns of flight feathers—seen both at the onset and cessation of the annual molt cycle—suggests two plausible explanations. First, fledging may occur year-round without a specific breeding season, as described by Mader (1981) in the Llanos of Venezuela, which may result in the absence of a distinct molting season. Second, this variation might arise from the presence of individuals from different breeding populations, as proposed for the Guiana Shield in Suriname (Vous 1968). Aside from the Llanos of Venezuela (Jensen et al. 2005), empirical data on seasonal abundance in tropical South America are scarce. Therefore, this lack of information makes it challenging to provide an ecological interpretation of the observed age class distribution patterns within the tropical belt.

Within the Amazon Basin, the expansion of anthropogenic activities such as agriculture and livestock farming is creating open areas interspersed with forest patches that are emerging as new breeding habitats for white-tailed hawks, as documented across the Americas (Stevenson and Meitzen 1946; Tewes 1984; Wheeler 2003; Hilty 2010). Despite the availability of these new suitable habitats, our surveys revealed the lowest abundance of white-tailed hawk among all biogeographical regions, indicating that it remains a relatively uncommon avian predator. These findings imply that while altered habitats may facilitate breeding opportunities, the overall population of white-tailed hawks is still low. To better understand how habitat transformation influences their abundance and range expansion, annual monitoring through surveys will be crucial. Such efforts can provide valuable insights into the dynamics of this species in the ever-changing landscape of the Amazon Basin.

Local areas of high abundance and feeding ecology

Local areas of high abundance of white-tailed hawks identified across the Gran Chaco/Espinal, Cerrado, and Guianan Savanna were associated with heterogeneous landscapes composed of forest patches, open livestock areas, and large-scale agroindustrial fields. Such mosaics likely favor the species by providing abundant foraging opportunities and suitable hunting conditions for strategies such as sit-and-wait and hovering, particularly in areas undergoing active disturbance from ploughing, burning, or harvesting (Stevenson and Meitzen 1946; Tewes 1984; Wheeler 2003; Hilty 2010). The recurrent presence of both large and small aggregations in actively disturbed agroecosystems (e.g.,

during ploughing and fire events), as observed in the Gran Chaco and Cerrado during both seasons, and in the Guianan Savanna during the austral summer, reinforces the species' tendency to exploit natural or human-generated transient resource peaks. Accordingly, during the austral summer surveys, local areas of high abundance in the Gran Chaco were linked to large-scale soybean plantations and cornfields, whereas in the Cerrado, they were associated exclusively with large-scale soybean plantations.

Taken together, these findings confirm that local peaks in abundance are not anomalies, but ecologically meaningful responses of white-tailed hawks. Although such aggregation behavior introduces some heterogeneity into the dataset, excluding these observations would obscure critical aspects of the species' behavioral ecology in South America. Instead, these data reflect genuine ecological patterns and highlight the importance of interpreting local areas of high abundance within a broader ecological and spatial context.

Seasonal shifts in foraging behavior were also observed, particularly in the Gran Chaco/Espinal, where insect-feeding activity was recorded during the austral summer but was notably absent in the austral winter. These patterns suggest that white-tailed hawks adjust their foraging strategies in response to seasonal fluctuations in prey availability. Comparable seasonal variation has been documented in resident breeding pairs in the Brazilian Cerrado, where mammal consumption increased during the dry season (May to September), coinciding with the egg-laying and incubation period, while a broader prey spectrum was observed during the wet season (October to April), corresponding to chick hatching and the presence of well-developed fledglings (Granzinolli and Motta-Junior 2007; Motta-Junior et al. 2010).

Such seasonal variation highlights the ability of the white-tailed hawk to cope with variation in food availability, making it crucial to evaluate the feeding ecology across the five age classes. Since individuals in non-Definitive Basic Plumage presumably take several years to breed, their diet may differ significantly from that of breeding Definitive Basic Plumage individuals, particularly because they do not have to feed fledglings with a broader range of food items, as has been documented in the age-related diet differences in other raptors species (e.g., Naude et al. 2019; Panter and Amar 2021). Therefore, the feeding ecology of different age classes may also be playing a relevant role in influencing the distribution of the white-tailed hawk in South America.

Data strength and coverage of this large-scale survey

Our large-scale survey provides valuable baseline data to understand the spatiotemporal abundance of the white-tailed hawk. Although there were disparities in seasonal survey coverage within the Gran Chaco/Espinal and the Cerrado, the total number of hours spent and the distances surveyed in each region are substantial. Non-repeated survey routes were generally located near those surveyed in the complementary season, except in the southern Espinal and western Cerrado, where the non-repeated routes were not close to those of the complementary season. Also, another possible source of bias is that the surveys were not conducted within the same year, potentially conflating seasonal and yearly variation. However, the Cerrado and southern Amazon, surveyed over two austral summers and sharing a similar annual phenological cycle, exhibited similar age class distribution patterns. Since the surveys were repeated over three austral summers immediately after the breeding season and across multiple areas, in the Gran Chaco/Espinal, the Cerrado, and the southern Amazon, we are confident that the observed age class distribution patterns present a realistic perspective. Lastly, although the Amazon Basin and Guianan Savanna were surveyed in a single season, our data still provide essential baseline information and contribute significantly to our understanding, given the incomplete knowledge of the abundance of the white-tailed hawk in tropical regions. Clearly, our data lacks enough power to characterize the dynamics of white-tailed hawks in biomes as a whole, but we provide a novel foundation which more extensive and more protracted route surveys can build upon.

From a broader perspective, our data on the white-tailed hawk, together with published data on the variable hawk (*G. polyosoma*) and the black- chested buzzard-eagle (*G. melanoleucus*)—all of which exhibit five age classes—provide valuable insights into age class distribution patterns (Juhant et al. 2022; Juhant and Saggese 2026). Our findings reinforce the notions put forward by Juhant et al. (2022) and Juhant and Saggese (2026), who highlight that the assignment of age classes is crucial for understanding patterns of distribution and abundance of species with delayed plumage maturation. The assignment of age classes based on biological criteria, such as molt patterns, requires long-term skill development to properly assign individuals to the correct age class, which is essential to understand the annual cycle of the white-tailed hawk. The patterns described here lay the groundwork for developing hypotheses about the seasonal movements of all age classes. In this context, learning how the migratory behavior differs across the age classes will provide insightful information on the nature of seasonal abundance and help to develop accurate spatiotemporal maps by age. For example, in the Boreal Temperate Region, individuals of some raptor species cease regular migration once they acquire their Definitive Basic Plumage and establish a mate and territory (Bloom et al. 2015; Panuccio et al. 2021). Given these dynamics, using data from multiple

seasons and areas will be essential to further understand the geographic and temporal variation in the age class distribution of white-tailed hawk in South America.

Frequency distribution map (year-round) of white-tailed hawks derived from ebird data

Recent eBird data have been used to estimate the relative abundance and distribution of the white-tailed hawk, revealing that its distribution is clustered in multiple fragments and that it is a year-round resident across the Americas (Fink et al. 2024). While the proposed eBird map (year-round) offers the most comprehensive distribution and abundance data, it has notable gaps within South America. For example, it underrepresents the species in the Guiana Shield (Vous 1968; Thiollay 1989, 2007b; O'Shea and Ramcharan 2011; Zyskowski et al. 2011), where we recorded its highest overall abundance, and in the Atlantic Forest, where it is a common breeder along the Brazilian coast (https://wikiaves.com.br/wiki/gaviao-de-rabo-branco). Furthermore, the frequenc y distribution map did not account for seasonal fluctuations by age class (Fink et al. 2024), which could lead to a misrepresentation of the true spatiotemporal distribution of the species. Thus, while this map provides the most up-to-date distribution and abundance data for the white-tailed hawk across the Americas, our results highlight the need for cautious interpretation.

Conclusion and moving forward

The lack of prior empirical data in these five biogeographical regions highlights the pioneering nature of this research. Within the tropical belt of South America, the white-tailed hawk exhibits complex and poorly understood age class distribution patterns, making it essential to assess its breeding phenology for accurate interpretation of spatiotemporal dynamics in this region. Expanding survey efforts, particularly in northern South America—such as the Llanos and Guiana Shield—will help address current data gaps. Future studies should adopt a similar approach to assigning individual age classes to deepen our understanding of the annual cycle of the white-tailed hawk. This research establishes a quantitative baseline for exploring spatiotemporal variation in abundance and age-specific distribution patterns. Furthermore, tagging individuals with GPS devices across the five age classes will provide valuable insights into their migration patterns, habitat use, and year-round distribution, ultimately enhancing our understanding of the annual cycle of white-tailed hawks on a continental scale.

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Data availability The data presented in this contribution were collected through direct observations in different regions of South America.

Declarations

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Competing interests The authors declare no competing interests.

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