Raptor migration across South America

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A decade has passed since a trio of thrilling *Neotropical Birding* articles about raptor-watching in the Neotropics. Time then, for a review of what has been learnt since then – from the author of two of those seminal pieces.

1 Swainson's Hawks *Buteo swainsoni* arriving on wintering grounds in central Argentina. If the winds are westerly or southerly in the eastern pampas of Punta Rasa, on the coast of Buenos Aires, it is possible to tally thousands of these hawks in a single day, most of which (at this site) are juveniles. Punta Rasa, Buenos Aires, November 2007 (Gabriel Battaglia).

More than 80 years ago, John Zimmer (1938) wrote: "It is not uncommon… to hear the statement made that South American birds do not migrate… A few writers [such as Dabbene (1910), de Azara (1802–05), Hudson (1918) and Wetmore (1926)] have noted the disappearance or reappearance of certain species at certain places and seasons, but there has been little evidence to show where the period of absence has been spent." Nowadays there is increasing recognition in South America of how birds move in space and time, which enables a thorough understanding of their evolution, ecomorphology, behaviour and ecology, and of how birds adjust their annual movement to our fast-changing world (Chesser 1994; Joseph 1997; Chesser & Levey 1998; Bildstein 2004; Jahn *et al.* 2004, 2006, 2020, 2021; Jahn & Cueto 2012; Dodge *et al*. 2014; Graña Grilli *et al.* 2017). Despite such efforts to comprehend the evolutionary drivers that shape migratory behaviour on the continent, doing so represents quite a challenge since migratory patterns have been described for only a handful of South American migratory birds (e.g., Tuero *et al.* 2019) and many remain unknown and undescribed. However, it is currently known that bird migration in South America is a complex phenomenon, with masses of birds moving on several axes during a given season – latitudinal, altitudinal and longitudinal – and that given this complexity, there is still much to learn (Jahn *et al.* 2020).

Diurnal raptors (hereafter simply 'raptors'), including New World vultures, hawks and eagles, and caracaras and falcons, constitute an excellent study group to investigate bird migration in South America because 32 species are thought to migrate latitudinally and to encompass a wide range of feeding habits (Fig. 2). To date, however, we have a comprehensive understanding of movement ecology for only a handful of raptor species migrating latitudinally in South America (e.g., Graña Grilli *et al.* 2017). In contrast, altitudinal movements are largely unknown and remain fertile research ground, but are known to occur (Bildstein 2004). Moreover, longitudinal movements are undescribed in South America and such movements have rarely been recorded in raptors worldwide (but see Steenhof *et al.* 2005, Garcia-Heras *et al.* 2019).

In the Neotropics more widely, migratory raptors have been sorted into three migration systems (Bildstein 2004, Juhant 2011; Fig. 3a–d). The *Nearctic–Neotropical system* involves species that breed in the Nearctic region and overwinter in the Neotropics, reaching South America via Mesoamerica or the Caribbean Basin (Fig. 3a). The *Austral–Neotropical system* involves species that breed in the Austral Temperate Region and tend to overwinter north of their breeding range within South America; the migration flyways appear to be both slopes of the Andes, central Argentina and the Atlantic coast (Fig. 3b). Finally, the *Neotropical–Intratropical system* involves species that breed in tropical and subtropical latitudes and overwinter within the tropical belt; there is no evidence of any major flyways in this system in South America, although Phillips (2021) offers a perspective on Middle America (Fig. 3c).

Some words of caution. First, some species fit into more than one migratory system, such as Snail Kite *Rostrhamus sociabilis*, which migrates wholly within the continent (Ferguson-Lees & Christie 2001, Jensen *et al.* 2005, Juhant 2010, Jahn *et al.* 2021). Second, such categorisation might not fully describe the migration of raptors on the continent, since it relates only to latitudinal movements. Note that altitudinal and longitudinal movements concern only raptors that breed and migrate within the Neotropical region, whereas latitudinal movements are shared by Nearctic and Neotropical migrants.

In South America, partial migratory behaviour (i.e., species in which some but not all members of the population regularly migrate) is very common as it is shared across several avian groups (Chesser 1994). Within South American raptors, 15 species (56%) are thought to be partial migrants with both migratory and resident populations (Fig. 2). Within migratory populations, migration can be age- or sex-dependent, or both, or might not show any type of pattern (Bildstein 2006, Newton 2008). Moreover, with one exception, South American migratory raptors have a continuous breeding distribution from the Austral Temperate Region to the equator, which means that breeding and overwintering areas overlaps (Ferguson-Lees & Christie 2001). The exception is the White-throated Hawk *Buteo albigula*, which has a widely disjunct distribution between its breeding and overwintering areas, and it is the only complete migrant of the Austral Temperate Region (Ferguson-Lees & Christie 2001).

In this context, complex movements (latitudinal and altitudinal, and perhaps even longitudinal), species belonging to three migratory systems encompassing a wide range of feeding habits, partial migratory behaviour, and overlapping breeding and overwintering areas currently represent challenges to properly assess raptor migration in South America. To address these conundrums – and doing so approximately a decade after a trio of articles in *Neotropical Birding* that introduced readers to raptor migration in the Neotropics (Juhant 2011, 2012a; Taylor 2011) – I use this article to: (1) summarise and update the migratory characteristics of raptors migrating along a latitudinal axis in South America; (2) update the raptor migration 'watchsites' found on the continent; (3) describe issues that affect the understanding of raptor migration on the continent; and (4) put forward research needs to collect data from direct observation in order to identify key areas for raptor conservation in South America.

Overview of raptor migration within South America

Migratory raptors are sorted into three migration categories, dependent on whether all members of the population leave the breeding grounds and whether they exhibit regular or irregular seasonal movements. Of the 32 species thought to migrate latitudinally in South America, Fig. 2 shows that five are *complete migrants* (species in which all or almost all members of the population regularly migrate), 16 are *partial migrants* (as defined above) and 11 are *irregular migrants* (species in which the extent of movement varies annually, typically due to between-year shifts in prey abundance). These migratory raptors also encompass a wide range of feeding habits: 16 species (50%) are generalist predators feeding on one or more of mammals, birds, reptiles and amphibians; five (16%) eat insects; four (13%) are obligate scavengers; three (9%) eat snails; two (6%) are facultative scavengers (i.e., can vary their diet); and two (6%) eat fish (Fig. 2).

In South America, the migratory behaviour of raptors is known from sporadic and systematic migration counts, individuals tracked, ringing/banding recoveries, and surveys of wintering congregations and comparative seasonal abundances. However, knowledge of the three migration systems is uneven: the Nearctic–Neotropical system is the best known, followed by the Austral–Neotropical, then the Neotropical–Intratropical.

In the **Nearctic–Neotropical system,** migrants reach South America via two pathways: Mesoamerica involving at least 3 million individuals of nine species (given that number pass through Panama; Taylor 2011), while four species traverse the Caribbean Basin, making landfall on the coast of Colombia or Venezuela (Fig. 3a). At least 10,000 individuals are involved in the latter, as migration counts in eastern Cuba involve almost that number of Ospreys *Pandion haliaetus* alone (Rodriguez-Santana *et al.* 2003, 2014).

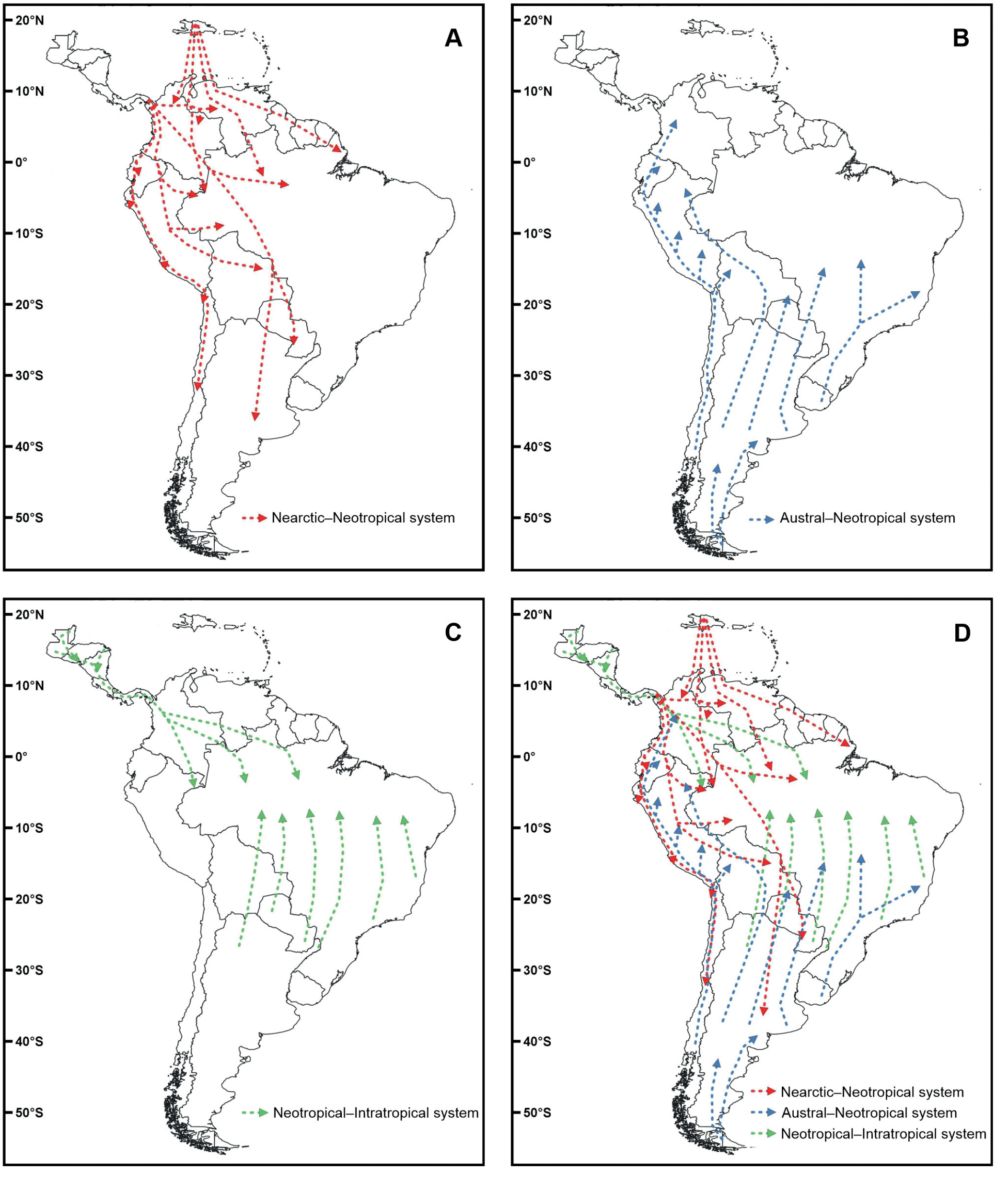
Once raptors reach South America, four species overwinter in specific locations. For example, Turkey Vultures *Cathartes aura* and American Kestrels *Falco sparverius* overwinter in the Llanos of Venezuela (Kirk & Currall 1994, Kirk & Gosler 1994, Jensen *et al.* 2005, Hedlin *et al.* 2013), Mississippi Kites *Ictinia mississippiensis* in the Gran Chaco (Juhant & Areta 2013) and Swainson's Hawks *B. swainsoni* in the Pampas (Sarasola *et al.* 2008, Kochert *et al.* 2011). In contrast, the remaining six species – Osprey, Swallow-tailed Kite *Elanoides forficatus*, Broad-winged Hawk *B. platypterus*, Merlin *F. columbarius* and Peregrine Falcon *F. peregrinus* – overwinter in a widespread manner across the continent (Clark 1985; Fuller *et al.* 1998; Martell *et al.* 2001, 2004, 2014; Haines *et al.* 2003; Zimmerman 2004; Beingolea & Arcilla 2020; McCabe *et al.* 2020; Cuadros *et al.* 2021; arcinst.org).

The landfall and departure points of raptors migrating via the Caribbean Basin in northern South America remain little studied so are a fertile topic for research. However, tracking of Ospreys and Peregrine Falcons shows that they migrate from the Greater Antilles to South America and do not continue to Puerto Rico or towards the Lesser Antilles (Fuller *et al.* 1998; Holroyd & Duxbury 1999; Martell *et al.* 2001, 2004, 2014; Juhant 2012a). The migration timing of birds heading south – landfall – occurs between August and November, while departure occurs between January and April (Martell *et al.* 2001, 2004, 2014). Landfall and departure lie across 500 km between Santa Marta (Colombia) and Paraguaná (a Venezuelan peninsula), with the main areas being across the Golfo de Venezuela between Paraguaná and Guajira peninsulas. American Kestrels and Merlins might migrate across the Greater and Lesser Antilles, making landfall around Venezuela's Golfo de Paria, although no records of departures are known in this region (Juhant 2012a).

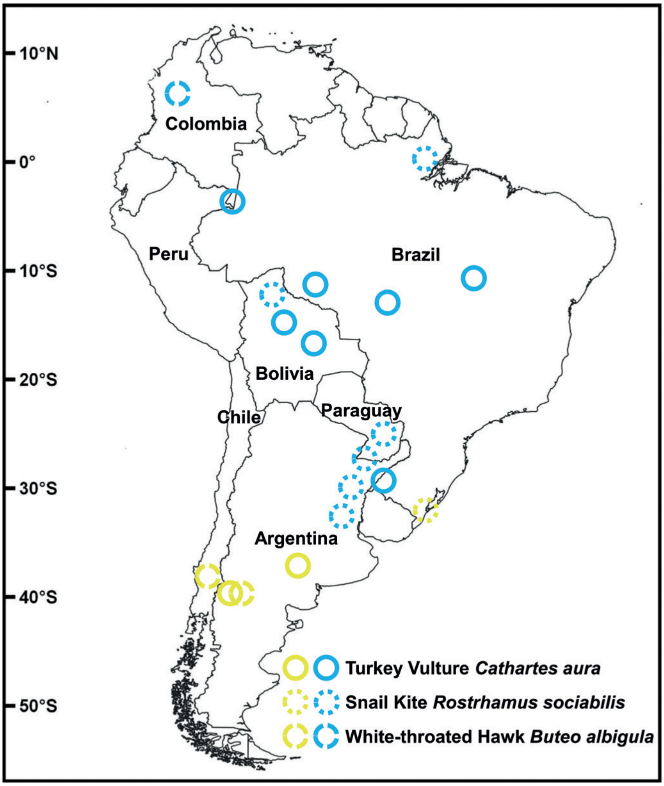
The **Austral–Neotropical system** involves those migratory raptors that breed within the Austral Temperate Region. That said, some species breeding in the northern part of this region (e.g., Plumbeous Kite *Ictinia plumbea* and Swallow-tailed Kite; see details below) are not addressed within this system because their main area of distribution lies within the tropical belt. On the other hand, some species that breed from the Austral Temperate Region continuously toward the tropical belt (e.g., Snail Kite) undertake seasonal movements throughout their distribution and thereby justifiably belong to the two South American migratory systems (Austral–Neotropical and Neotropical–Intratropical).

	Migration systems			Feeding habits
	Nearctic–Neotropical	Neotropical–Intratropical	Austral–Neotropical	
Complete migrants (5 species)				
Osprey *Pandion haliaetus*				Fish-eating
Mississippi Kite *Ictinia mississippiensis*				Insect-eating
Broad-winged Hawk *Buteo platypterus*				Generalist predator
Swainson's Hawk *B. swainsoni*				Insect-eating
White-throated Hawk *B. albigula*				Generalist predator
Subtotal	**4**	**0**	**1**	
Partial migrants (16 species)				
Turkey Vulture *Cathartes aura*				Obligate scavenger
Hook-billed Kite *Chondrohierax uncinatus*				Snail-eating
Swallow-tailed Kite *Elanoides forficatus*				Insect-eating
Snail Kite *Rostrhamus sociabilis*				Snail-eating
Rufous-thighed Kite *Harpagus diodon*				Insect-eating
Plumbeous Kite *I. plumbea*				Insect-eating
Cinereous Harrier *Circus cinereous*				Generalist predator
White-tailed Hawk *Geranoaetus albicaudatus*				Generalist predator
Variable Hawk *G. polyosoma*				Generalist predator
Black-chested Buzzard-Eagle *G. melanoleucus*				Generalist predator
Southern Crested Caracara *Caracara plancus*				Facultative scavenger
Chimango Caracara *Milvago chimango*				Facultative scavenger
American Kestrel *Falco sparverius*				Generalist predator
Aplomado Falcon *F. femoralis*				Generalist predator
Merlin *F. columbarius*				Generalist predator
Peregrine Falcon *F. peregrinus*				Generalist predator
Subtotal	**5**	**9 (2?)**	**11 (2?)**	
Irregular migrants (11 species)				
Lesser Yellow-headed Vulture *Cathartes burrovianus*				Obligate scavenger
Greater Yellow-headed Vulture *C. melambrotus*				Obligate scavenger
King Vulture *Sarcoramphus papa*				Obligate scavenger
White-tailed Kite *Elanus leucurus*				Generalist predator
Slender-billed Kite *Helicolestes hamatus*				Snail-eating
Long-winged Harrier *Circus buffoni*				Generalist predator
Rufous-thighed Hawk *Accipiter erythronemius*				Generalist predator
Savanna Hawk *Buteogallus meridionalis*				Generalist predator
Great Black Hawk *B. urubitinga*				Generalist predator
Black-collared Hawk *Busarellus nigricollis*				Fish-eating
Zone-tailed Hawk *Busarellus albonotatus*				Generalist predator
Subtotal	**0**	**9 (8?)**	**6 (5?)**	
TOTAL	**9**	**18 (10?)**	**18 (7?)**	

2 Summary accounts of the 32 species thought to migrate latitudinally in South America, sorted into three migration systems and with feeding habits identified. This species account is based on sporadic and systematic migration counts, individuals tracked, ringing/banding recoveries, surveys of wintering congregations, and comparative seasonal abundances. Complete migrants are species in which all or almost all members of the population regularly migrate; partial migrants are species in which some but not all members of the population regularly migrate; irregular migrants are species in which the extent of movement varies annually, typically due to between year shifts in prey abundance. As the migration status are largely unknown for most species, regular migrants are highlighted in green and those of uncertain status in yellow. Generalist predators feed either on one or more of mammals, birds, reptiles and amphibians.



3 Schematic representation of post-breeding migration flyways of raptors (New World vultures, harriers and hawks, and caracaras and falcons) in South America. These flyways are based on sporadic and systematic migration counts, tracked individuals, ringing/banding recoveries, surveys of wintering congregations, and comparative seasonal abundances. **3a** The Nearctic–Neotropical system involves species that breed in the Nearctic region and overwinter in the Neotropics, reaching South America via Mesoamerica or the Caribbean Basin. **3b** The Austral–Neotropical system involves species that breed in the Austral Temperate Region and tend to overwinter north of their breeding range within South America. **2c** The Neotropical–Intratropical system involves species that breed in tropical and subtropical latitudes and overwinter within the tropical belt. **2d** Comprises the three migration systems showing the complexity of migrating raptors across South America.



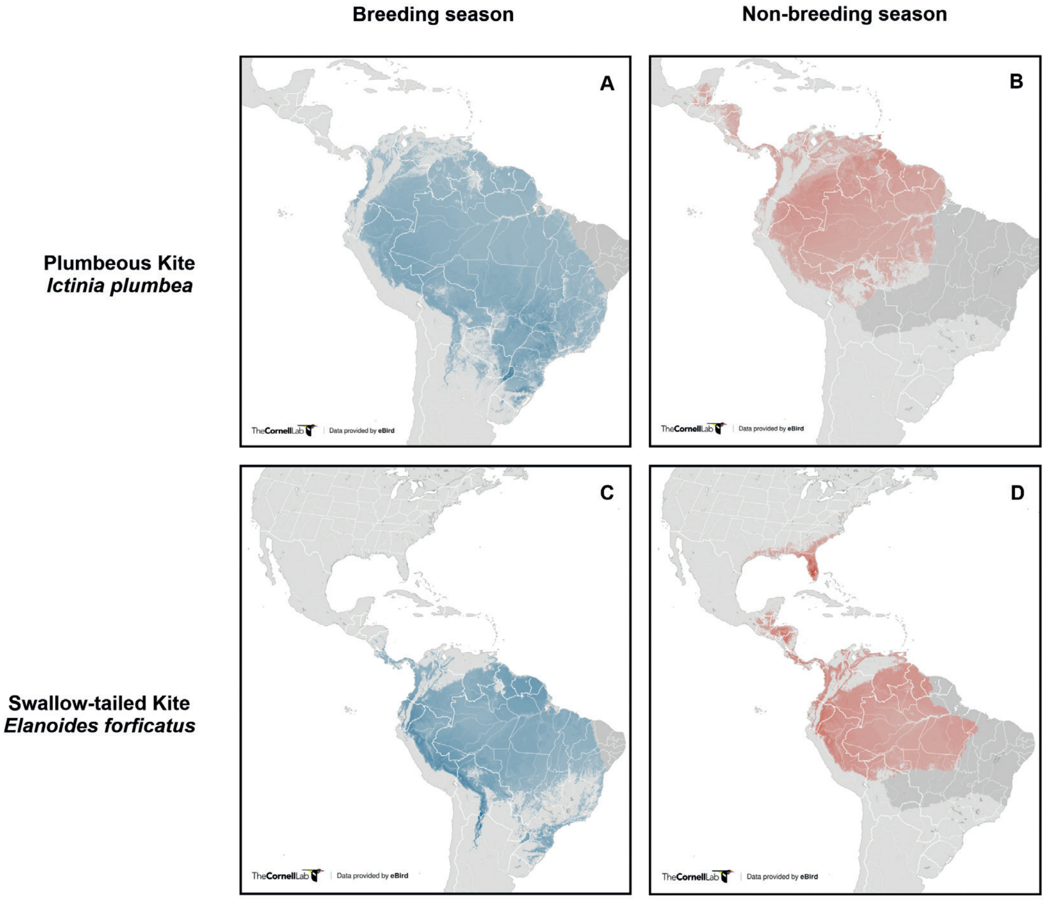
4 Schematic representation of the spatial and temporal distribution within South America of individuals of three species (Turkey Vulture *Cathartes aura*, Snail Kite *Rostrhamus sociabilis* and White-throated Hawk *Buteo albigula*) tagged with GPS devices. Austral summer distribution is coloured yellow and austral winter records are pale blue. These latitudinal movements include transequatorial migration, which has never been reported in raptor species breeding in southern Africa or Oceania. Turkey Vultures were tagged in two locations in central Argentina; the species was distributed widely during the austral winter, with most individuals overwintering in the tropical region. Snail Kites were tagged in southern Brazil, migrating to tropical and subtropical areas. White-throated Hawks were tagged in northern Patagonia (of both Argentina and Chile) and overwinter in Colombia. These data are based on Bechard *et al.* (2010), Dodge *et al.* (2014), Graña Grilli *et al.* (2017), Fundación Ñankulafkén (2021), Jahn *et al.* (2021) and movebank.org/cms/movebank-main

In recent years, three species – Turkey Vulture, Snail Kite and White-throated Hawk – have been tracked with GPS devices, which have revealed clear latitudinal movements (both short and long distance), including transequatorial migrations, the like of which has never been reported in any raptor breeding in southern Africa or Oceania (Bechard *et al.* 2010, Dodge *et al.* 2014, Graña Grilli *et al.* 2017, Fundación Ñankulafkén 2021, Jahn *et al.* 2021; Fig. 4). Additionally, data from those tracked individuals and direct observations indicate that the migration flyways comprise the western and eastern slopes of the Andes, central Argentina and the Atlantic coast (Fig. 3b).

The **Neotropical–Intratropical system** involves those migratory raptors that breed in northern or southern subtropical and tropical latitudes, and migrate towards the equator (Fig. 3c). This poorly understood system promises novel insights into how much variation in migratory strategies exists across species as rainfall in tropical latitudes is more unpredictable between years than is temperature, and this affects the spatio-temporal abundance of prey species such as insects, and land and freshwater snails (see Phillips 2021 for the Middle American perspective). For example, as annual rainfall is not equally distributed across the Amazon Basin, the abundance of Swallow-tailed Kite, Plumbeous Kite, Hook-billed Kite *Chondrohierax uncinatus*, Snail Kite and Slender-billed Kite *Helicolestes hamatus* might vary considerably across space and time, with individuals recorded around the equator hailing from three different populations (individuals from north or south plus sedentary individuals from the equatorial region itself). The details of this system remain a mystery, mainly due to the impracticality of fieldwork in many parts of the Amazon Basin plus the lack of GPS-tracking data for species mentioned. However, the citizen science initiative eBird is providing key information on the spatio-temporal movements of species such as Swallow-tailed Kite and Plumbeous Kite within the Neotropical region (Fink *et al.* 2020; Fig. 5).

Raptor migration watchsites

A global directory of raptor migration watchsites published two decades ago (Zalles & Bildstein 2000) provided the first complete overview of raptor migration in South America, describing 20 potential watchsites across the continent for the establishment of long-term monitoring programmes. A decade later, 35 watchsites had

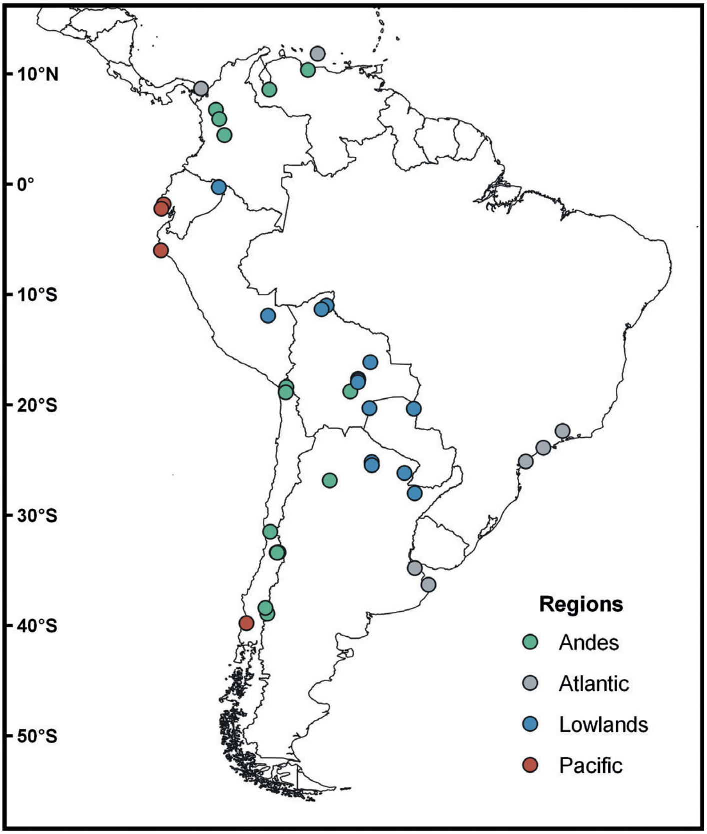


5 Relative abundance of Plumbeous Kite *Ictinia plumbea* and Swallow-tailed Kite *Elanoides forficatus* during the breeding and non-breeding seasons are represented from the southern hemisphere perspective, based on data from eBird (eBird Status and Trends Project, reproduced with permission). For Plumbeous Kite, the breeding season (in the austral summer) is defined as December–January and for Swallow-tailed Kite, November–January. For both species, the non-breeding season (in the austral winter) is defined as April–July. The relative abundance (i.e., the estimated number of individuals detected by an eBirder during a travelling count at the optimal time of day) depicted follows a colour gradient: light shades indicate lower relative abundance and dark shades a higher relative abundance. This material uses data from the eBird Status and Trends Project at the Cornell Lab of Ornithology (https://ebird.org/science/status-and-trends). Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author and do not necessarily reflect the views of the Cornell Lab of Ornithology.

been described and allocated to one of four main regions in order to assess species composition of migrants across the continent (Juhant 2011). The 'Pacific' region covers the entire Pacific coast; the 'Andes' region covers the Andean mountains; the 'Lowland' region encompasses lowlands east of the Andes; and the 'Atlantic' region incorporates the entire Atlantic coast, including islands off the continent's north coast (Fig. 6).

On the heel of these two publications, attention began to focus on raptor migration counts as six new sites were found in the last decade. For example, a new migration watchsite has been found in the Colombian Darién, with nine species recorded (Bayly *et al.* 2014). Here an average of *c.*370,000 individuals were counted in two boreal autumns and *c.*32,000 individuals in a single boreal spring (Bayly *et al.* 2014). Also new were two watchsites in the desert plateau of Chile, where two species were recorded and *c.*750 individuals counted in a single austral autumn (Hidalgo *et al.* 2018).

More recently, three new migration watchsites have been found across the northern Andes in Ibagué and Cañasgordas, Colombia, and Mérida, Venezuela. At Ibagué ten species of migrating

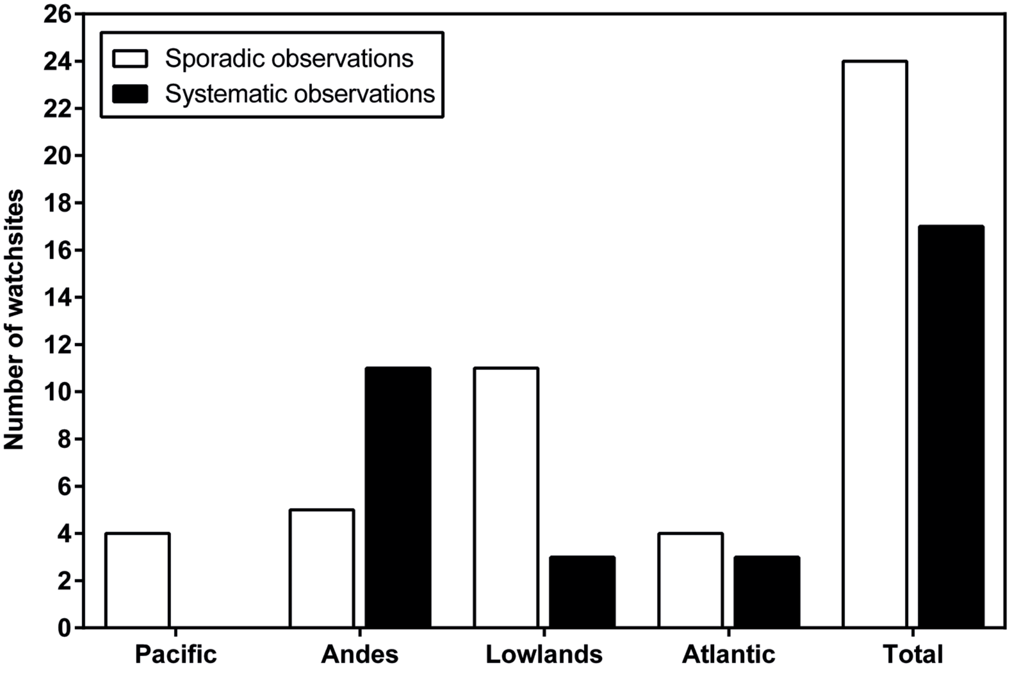


6 The 41 watchsites proposed across South America, each allocated to one of four main regions: the 'Pacific' region (four watchsites) covers the entire Pacific coast; the 'Andes' region (16) covers the Andean mountains; the 'Lowland' region (14) encompasses lowlands east of the Andes; and the 'Atlantic' region (seven) incorporates the entire Atlantic coast, including islands off the continent's north coast. Note that large areas of South America, such as central Argentina, southern Patagonia and the northeast of South America, lack any information on migration counts and could be potential areas to search for raptor migration bottlenecks.

raptors were recorded during the boreal springs of 2020 and 2021, totalling *c.*403,000 and *c.*626,000 individuals respectively (Vallejo 2021, E. Vallejo pers. comm.). At Cañasgordas, *c.*624,000 individuals of 14 migratory raptor species were recorded during the boreal autumn of 2020 (E. Vallejo pers. comm.). These two Andean watchsites and the other site located in the lowlands of the Colombian Darién represent the most significant bottlenecks found within South America. On the other hand, in Mérida, counts started in the boreal autumn of 2020 and will only be focused on that season (L. Saavedra pers. comm.) Unlike the two Colombian sites, birds passing over Mérida might comprise individuals migrating through the lowlands of the Darién and birds reaching South America via the Caribbean Basin. The goal at these sites is to conduct long-term counts during both seasons, if feasible. This initiative is a critical step in monitoring Nearctic–Neotropical migrants, which will help to better understand principal migration routes, phenology and flight dynamics in northern South America.

Forty-one migration watchsites have been proposed for South America (Fig. 6). However, most information on migration counts is from sporadic observations rather than systematic ones (Fig. 7), so an important topic for future research is to comprehend species composition and the phenology of individuals migrating at specific locations in South America. Also, large areas – such as central Argentina, southern Patagonia and the northeast of South America – lack any information on migration counts (Fig. 6).

That basic field observations are still critical and much needed means that ordinary birdwatchers (that means you!) can contribute to the study of raptor migration in South America. Taylor (2011) suggested several points to record when observing raptors on migration, namely predominant flight direction, estimated altitude and horizontal distance of migrants, the number of observers and total period of observation. Prevailing weather conditions should be measured or estimated on an hourly basis. In addition, observers should note that even records of birds identified solely to genus are valuable. Raptor researchers will value any contribution, no matter how small, that you can make on this topic.



7 The 41 watchsites proposed across South America (for details see Fig. 6) have been identified mainly thanks to sporadic rather than systematic observations (Matías Juhant). Further fieldwork is needed to comprehend species composition and the phenology of individuals migrating at specific locations across the four regions specified.

Issues that affect the understanding of raptor migration in South America

For the past decade or so (2008–19), I have been conducting fieldwork over a wide area of South America (Argentina, Bolivia, Brazil, Chile and Paraguay), collecting data from direct observation by counting raptors on migration, conducting road surveys to assess seasonal abundance, and carrying out foot surveys at specific locations to assess wintering congregations and their between-year fluctuations. Based on this field experience (comprising 2,550 hours across 440 days), I have found in the scientific literature three main issues adversely impacting our understanding of raptor migration in South America: *misidentification at the species level*, *misassignment to age-classes* and *unknown breeding/overwintering areas*.

I consider that these issues substantially and unintentionally alter conclusions, which leads to different interpretations of raptor movements in the continent. Below, I focus on each issue by providing examples of three migratory species and presenting evidence that might affect a wide range of raptors.

Misidentification at the species level: the case of White-throated Hawk

South America is home to one of the highest diversity of raptors in the world with a wide variety of plumages in terms of overall coloration and patterns (something to which I intend to dedicate a series of future *Neotropical Birding* articles). Throw in a highly diverse set of movements that covers a vast range of ecosystems (Fig. 3), and you reach a situation where it is difficult to collect data from direct observation without an appropriate field guide to identify raptors and knowledge of their migration behaviour.

White-throated Hawk is a medium-sized, forest-dwelling raptor endemic to South America, which is found across Andean temperate and humid tropical forests (Ferguson-Lees & Christie 2001). An isolated breeding population in the Austral Temperate Forest of Chile and Argentina is completely migratory, with birds moving long distances to winter in the tropical Andes from middle Bolivia to Venezuela (Ferguson-Lees & Christie 2001, Bechard e*t al.* 2010, Fundación Ñankulafkén 2021). However, single individuals are occasionally recorded in northwestern Argentina during the austral winter.

It has been proposed that, during its northbound migration, White-throated Hawk crosses the Andes from the western slope to the east somewhere south of 26°S, passing along a valley oriented south–north at Tafí del Valle, Tucumán, Argentina; and that it might use this route during southbound migration, with some individuals (immatures) probably staying year-round (Trejo *et al.* 2007). This idea is based on direct observations of several dozens of White-throated Hawks recorded during early autumn and late austral winter (Trejo *et al.* 2007).

However, based on my direct observations in the valley over ten austral winters (comprising 699 hours across 114 days and 1,417 km walked), I question these observations and further propose that the individuals observed at Tafí de Valle are actually Variable Hawk *Geranoaetus polyosoma* rather than White-throated Hawk. I do so for five reasons.

First, Variable Hawks, as well as Black-chested Buzzard-Eagles *G. melanoleucus*, use this valley as a migration route and wintering grounds, with individuals gathering at food sources (Capllonch & Ortiz 2009, Juhant unpublished data). Second, this valley is an open grassland habitat rather than a humid Andean forest in which White-throated Hawk typically overwinters (Bechard *et al.* 2010, Fundación Ñankulafkén 2021). Third, multiple White-throated Hawks have never been photographed or seen in northwestern Argentina in a single year – just sporadic observations of single individuals. Fourth, data from migration counts from southern Argentina, and from central and northern Chile show that White-throated Hawk uses the western slope of the Andes (rather than the east) as a migration flyway during both northbound and southbound migrations (Pavez 2000, Juhant & Seipke 2010, Hidalgo *et al.* 2018). Fourth, the outcome of the spatio-temporal movements using data from citizen science initiative provide critical information on the breeding and non-breeding distribution of the species across the continent and show that the non-breeding range extends from the Bolivian tropical Andes to the Colombian Andes (Fink *et al.* 2021). Finally, data from three tracked individuals with GPS devices from Argentina and Chile (Fig. 4) show a clear latitudinal movement migrating across the western slope of the Andes, including transequatorial migration (Bechard *et al.* 2010, Fundación Ñankulafkén 2021).

Misassignment to age-classes: the case of Black-chested Buzzard-Eagle

Several migratory raptors in South America, such as the genus *Geranoaetus*, exhibit delayed plumage maturation (i.e., a sequence of transitional plumages in which the overall coloration and pattern are consistently distinct from the definitive basic adult plumage; see box, p46, for age-class nomenclature and assignment in *Geranoaetus*). In this context, using the moult pattern of the flight feathers (primaries, secondaries and rectrices) is the key to properly assign individual age-class and understand species' annual movements across their lifespan.

Black-chested Buzzard-Eagle is a large raptor endemic to South America, where it inhabits open areas (Ferguson-Lees & Christie 2001). Its delayed plumage maturation comprises five distinctive age-classes (Seipke 2007, Juhant unpublished data). Historically, Black-chested Buzzard-Eagle has been considered as a sedentary species (e.g., Ferguson-Lees & Christie 2001); however, evidence from direct observations over the past decade shows that seasonal movements occur across the Austral Temperate Region (López *et al.* 2017, Juhant *et al.* 2022, Juhant unpublished data).

During 2015–16, unusually high rainfall was recorded in central Argentina due to the El Niño Southern Oscillation. As a result, in the austral winter of 2016, a large congregation of Black-chested Buzzard-Eagles (113–126 individuals in a 30-km segment) was recorded in a semi-arid grassland in La Pampa, where they were presumably gathering at food sources (López *et al.* 2017). The bulk of individuals were assigned as 'juvenile', 'immature', 'subadult' and 'adult' based on the overall plumage coloration rather than using the moult pattern of flight feathers as an approach. This is problematic for two reasons: first, the nomenclature used to assign individuals' age-classes is arbitrary, and second, in large-sized raptors, body moult may start before the onset of flight-feather moult, and birds with advanced body moult may be wrongly aged as being much older if based on overall coloration and pattern (Pyle 2005). Within this context, providing a biological explanation for this winter irruption (i.e., an unpredictable increase in the number of individuals into a given area as a response to fluctuations in the food supply, usually dominated by one age-class, whether juvenile or adult) becomes a difficult task due to the inaccurate assignment of the age-classes (see Juhant *et al.* 2022 and below).

Variable Hawk *Geranoaetus polyosoma* and Black-chested Buzzard-Eagle *Geranoaetus melanoleucus* exhibit winter irruption in Argentina's Monte Desert (semi-arid grassland and shrubby steppes). The winter irruption is possible to assess in these two species by comparing the winter fluctuations of the extreme age-classes basic I (juveniles) versus basic V (adults). During the winter irruption, basic I outnumber basic V considerably. **8** Variable Hawk (juvenile or basic I), Isla de Chiloé, Chiloé, Chile, February 2019 (Matías Juhant); **9** Variable Hawk (adult or basic V), La Carrera, Mendoza, Argentina, July 2016 (Matías Juhant); **10** Black-chested Buzzard-Eagle (juvenile or basic I), Tafí del Valle, Tucumán, Argentina, July 2019 (Matías Juhant); **11** Black-chested Buzzard-Eagle (adult or basic V), Ushuaia, Tierra del Fuego, Argentina, August 2016 (Matías Juhant). For an explanation of 'basic' plumages, see the box on p46.

Unknown breeding/wintering ranges: the case of Rufous-thighed Kite *Harpagus diodon*

The paucity of information on the breeding and overwintering areas of South American raptors, especially in the tropics, poses a major obstacle to assessing their spatio-temporal movements. As a result, mapping the breeding and wintering ranges with caution is crucial to understanding the annual distribution of migratory raptors in the continent.

Rufous-thighed Kite is a small, forest-dependent South American kite that breeds in subtropical and tropical latitudes and overwinters in the Amazon Basin (Ferguson-Lees & Christie 2001, Areta & Juhant 2019). Recently, a spatio-temporal analysis of Rufous-thighed Kite based on citizen-science data concluded that it is a complete migrant breeding (almost) exclusively in the Atlantic Forest (thereby constituting 'hidden [biogeographical] endemism') and overwintering in the eastern Amazonian lowlands (Lees & Martin 2015). However, that study missed key data from large areas which, when investigated, resulted in a different biogeographical pattern, thereby rejecting the 'hidden endemism' hypothesis (Areta & Juhant 2019). Instead, Rufous-thighed Kite is a more widespread breeder in the Cerrado, southern Andean Yungas and the Atlantic Forest, which makes seasonal movement in those ecoregions, and further research is needed in order to consider whether it is a complete or partial migrant (Juhant 2011, Areta & Juhant 2019). Only two South American watchsites have recorded Rufous-thighed Kite on migration during the austral autumn: one in Concepción, Santa Cruz, Bolivia, and Parque Nacional Itatiaia, Rio de Janeiro, Brazil (Cabanne & Seipke 2005, Juhant 2012b).

Suggestions for future studies on raptors in South America

Future research must improve our understanding of critical details of the annual cycle of raptors in South America, such as breeding and wintering distribution, migration timing, main migration routes, bottlenecks during migration, and differences in seasonal abundance within overlapping breeding and wintering areas, among others. Constraints on baseline knowledge represent a major obstacle towards development of effective conservation actions to conserve this diverse set of species and the habitats on which they depend. Once a basic description of the annual cycle of a given migratory bird population is accomplished, further research on the mechanisms driving its migratory patterns can be attempted. The migration of most raptors in South America is likely to be highly population-specific, given that 26 species (96%) of raptors that breed and migrate within South America are thought to be partial and irregular migrants (Fig. 2). For instance, the movement of a particular age or sex of a given species or migratory population might depend on the phase of the El Niño/La Niña Southern Oscillation across the Austral Temperate Region or migration might be age- or sex-dependent without the need for extrinsic factors.

Due to the financial limitations that South American researchers confront to track the migration of raptors with GPS devices, collecting systematic data by direct observations is a starting point to understand the complex suite of drivers that shape the migratory systems. The examples provided in these topics below represent evidence that collecting systematic data by direct observations – in different timeframes (short, medium and long) – can make a difference in understanding the annual life-history strategies of migratory raptors in South America.

AGE-CLASS NOMENCLATURE IN VARIABLE HAWK *GERANOAETUS POLYOSOMA*, WHITE-TAILED HAWK *G. ALBICAUDATUS* AND BLACK-CHESTED BUZZARD-EAGLE *G. MELANOLEUCUS*

The age-class terminology used across the main text follows Howell *et al.* (2003), based on the annual moult cycles of the flight feathers (primaries, secondaries, and rectrices). In Accipitriformes, the moult pattern in primaries is the most accurate means to assign individuals to a given age-class, since a new moult wave is initiated at primary 1 at the start of every annual moult cycle, regardless of whether all primaries were replaced or not in the previous cycle (Clark 2004). Following this criterion, individuals of the genus *Geranoaetus* can be assigned easily during the non-moulting season (late April to late September within Austral Temperate Region) to one of five age-classes: basic I shows a single generation of primary feathers and no moult waves. Basic II shows two generations of primaries and one moult wave. Basic III shows three generations and two moult waves. Basic IV shows two generations and three moult waves. Finally, basic V has acquired the definitive basic (adult) plumage and replaced all primaries at least once, meaning that it is no longer possible to precisely age individuals by assessing their moult in the flight feathers. Note that the individuals observed during the moulting season (early October to mid-April) can also be precisely assigned to a given age-class through direct observation by knowing the final product of each age-class.

12 White-tailed Hawk *Geranoaetus albicaudatus* has traditionally been considered a resident species. However, evidence in the last decades shows that seasonal abundances between austral summer and winter occur in this species in the southern part of its distribution. Adult or basic V individual, Mimoso do Oeste, Bahia, Brazil, July 2019 (Matías Juhant).

Short-term (single season): winter road-surveys

During the austral winter of 2019, I carried out an intensive road-survey throughout the humid and dry Chaco, Monte Desert, Argentine Espinal, Cerrado, Caatinga and lowland rainforests encompassing Argentina, Paraguay and Brazil, covering an area of *c.*2.65 million km^2. The field effort comprised 185 hours across 42 days, and covered 5,720 km on secondary roads at an average speed of 30 km/h. The goal was to assess the abundance and age-class structure of White-tailed Hawk *Geranoaetus albicaudatus* – a common open-area species inhabiting the lowlands east of the Andes – during the non-breeding season and across the southern part of its distribution. A total of 52 individual White-tailed Hawks were recorded with the following age-class structure (see box, p46): basic I (one individual; 2% of the total); basic II (two birds; 4%); basic III (five; 10%); basic IV (11; 21%); and basic V (33; 63%).

The low abundance recorded of this common hawk and the age-class structure provide evidence of partial migratory behaviour and differential migration by age (i.e., individuals in which different age-classes differ in their geographical distribution on wintering grounds) as the age-class structure shows a clinal increase from the youngest to the oldest age-class. These data, collected in a single austral winter, strongly support previous suggestions that White-tailed Hawk makes seasonal movements in the southern part of its distribution within South America (Voous 1968; Olivo 2003; Juhant 2010, 2011, 2012b; Zilio *et al.* 2014).

The next steps would be to conduct: (1) the same survey during the austral summer (breeding season) to compare the abundance and age-class structure between austral winter *vs.* summer; and (2) surveys across the tropical grasslands of Roraima, Brazil, plus the Llanos of Colombia and Venezuela during the austral winter, to assess whether White-tailed Hawk uses these regions as wintering grounds; this could be done by comparing the abundance of the extreme age-classes (i.e., basic I *vs.* basic V).

Medium-term (two seasons): migration count

During the austral spring of 2008, I counted migrating raptors on the Atlantic coast of Buenos Aires, Argentina, with field effort comprising 223.5 hours across 35 days. The goal of the study was to assess species composition, timing and abundance of migrating individuals. However, the most relevant discovery – supported also by sporadic observations from previous years – is how wind direction shapes raptor migration across this region. When the wind is blowing from the west and southwest, it pushes a large number of migrants to the coast, with as many as 10,000 individuals being seen in a single day (Jaramillo 1993, Juhant 2010). Collecting data across a couple of seasons would provide information on how physical features can shape the migration behaviour in a given area, a topic largely unexplored at South American raptor migration watchsites (but see Olivo 2005).

Long-term (several seasons): winter surveys at specific location

During six austral winters (2011, 2014–16 and 2018–19), I carried out intensive foot-surveys in the Andean foothills of Mendoza, Argentina, with field effort comprising 1,244 km walked in 432 hours across 66 days. The goal was to assess intra-year fluctuations of the wintering congregations and age-class structures of Variable Hawk and Black-chested Buzzard-Eagle during the non-breeding season at an overlapping breeding and overwintering area (see box, p46, for age-class nomenclature and assignment in *Geranoaetus*). I found that: both species exhibited winter irruptions; the irruptions were largely driven by a marked increase of basic I individuals (the youngest age-class), with basic V individuals (the oldest age-class) exhibiting (modestly) lowest abundance; and winter irruptions might be species-specific as the responses differed between the two *Geranoaetus* with a joint irruption event in the austral winter 2016 and a second irruptive event only recorded in Black-chested Buzzard-Eagle in the austral winter of 2018 (Juhant *et al.* in press). This study represents the first of its kind as winter irruption in the Austral Temperate Region is unheard of. The next step would be to conduct long-term, large-scale quantitative studies during the austral winter and summer to understand the fluctuations in abundance of the different age classes of Variable Hawk and Black-chested Buzzard-Eagle in relation to prey density and rainfall.

General conclusions

Data generated by individuals tracked with GPS devices, systematic fieldwork and citizen science initiatives such as eBird (an increasingly important source for scientists: e.g., Sullivan *et al.* 2009, 2017) represent the ideal framework through which to understand the annual cycle of migratory raptors in South America. For example, the model generated from eBird data on the movement of Plumbeous Kite and Swallow-tailed Kite (Fig. 5) shows for the first time how the relative abundance of these migratory kites changes in space and time across the continent (Fink *et al.* 2020). Simply put, as we move forward, it is essential that we work together with volunteer raptor-watchers and the wider conservation and scientific communities, and that we use adaptive data management, data sharing and effective collaborations to strengthen our efforts. Large areas of South America, such as central Argentina, southern Patagonia and the northeast of the continent, lack any information on migration counts and could be potential areas to search for raptor migration bottlenecks.

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