ORNITOLOGIA NEOTROPICAL 15 (Suppl.): 83–99, 2004

RAPTOR MIGRATION IN THE NEOTROPICS: PATTERNS, PROCESSES, AND CONSEQUENCES

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Resumen. – Migración de rapaces en el Neotrópico: patrones, procesos y consecuencias. – El Neotrópico alberga poblaciones reproductivas y no reproductivas de 104 de las 109 especies de rapaces del Nuevo Mundo (i.e., miembros del suborden Falconides y de la subfamilia Cathartinae), incluyendo 4 migrantes obligatorios, 36 migrantes parciales, 28 migrantes irregulares o locales, y 36 especies que se presume que no migran. Conteos estandarizados de migración visible iniciados en la década de los 1990, junto con una recopilación de literatura, nos proveen con una idea general de la migración de rapaces en la región. Aquí describo los movimientos de las principales especies migratorias y detallo la geografía de la migración en el Neotrópico. El Corredor Terrestre Mesoamericano es la ruta de migración mas utilizada en la región. Tres especies que se reproducen en el Neártico, el Elanio Colinegro (*Ictina mississippiensis*), el Gavilán Aludo (*Buteo platypterus*) y el Gavilán de Swainson (*B. swainsoni*), de los cuales todos son migrantes obligatorios, junto con las poblaciones norteamericanas del Zopilote Cabecirrojo (*Cathartes aura*), dominan numéricamente este vuelo norteño o "boreal". Cantidades mucho menores de Aguilas Pescadoras (*Pandion haliaetus*), Elanios Tijereta (*Elanoides forficatus*), Esmerejónes (*Falco columbarius*) y Halcones Peregrinos (*Falco peregrinus*), ingresan y abandonan el Neotrópico rutinariamente utilizando rutas que atraviesan el Mar Caribe y el Golfo de México. Los movimientos sureños o "australes" e intra-tropicales, incluyendo la dispersión y la colonización en respuesta a cambios en el hábitat, son conocidos pero permanecen relativamente poco estudiados. Habiendo detallado los patrones y procesos de la migración de rapaces en la región, discuto lo que se conoce sobre las consecuencias ecológicas de estos movimientos, incluyendo las interacciones competitivas entre especies migratorias y residentes. Luego exploro como la migración de larga distancia ha moldeado la distribución y abundancia de los rapaces en el Neotrópico. Concluyo proponiendo que la configuración de las masas continentales en forma de reloj de arena y la orientación norte-sur de las cordilleras del Nuevo Mundo, no sólo facilitan la migración terrestre de larga distancia de rapaces en esta región, sino que también aumentan la diversidad regional de rapaces por medio de un proceso de especiación llamado "dosis de migración" (migration dosing). El proceso de "dosis de migración" involucra una serie de eventos en los cuales ciertas "dosis" de migrantes de larga distancia se desvían y (1) llegan a áreas que son tangencialeso que están más allá de sus principales rutas de migración, (2) en vez de regresar a sus áreas reproductivas tradicionales permanecen ahí durante el siguiente período reproductivo y (3) eventualmente divergen de la linea parental, aislados geográficamente. Ejemplos probables de "dosis de migración" se presentan de dos géneros ricos en especies y casi cosmopolitas, *Accipiter* y *Buteo.*

Abstract. – The Neotropics host breeding or non-breeding populations of 104 of the 109 species of New World raptors (i.e., members of the suborder Falconides and the subfamily Cathartinae), including 4 complete migrants, 36 partial migrants, 28 irregular or local migrants, and 36 presumed non-migrants. Standardized counts of visible migration initiated in the 1990s, together with a focused literature search provide an emerging picture of raptor migration in the region. Here I describe the movements of the principal species of migrants, and detail migration geography in the Neotropics. The Mesoamerican Land Corridor is by far the most concentrated migration flyway in the region. Three species of Nearctic breeders, the Mississippi Kite (*Ictinia mississippiensis*), the Broad-winged Hawk (*Buteo platypterus*), and the Swainson's Hawk (*B. swainsoni*), all of which are complete migrants, together with western North American populations of Turkey Vultures (*Cathartes aura*), numerically dominate this northern or "boreal" flight. Much smaller numbers of Ospreys (*Pandion haliaetus*), Swallow-tailed Kites (*Elanoides forficatus*), Merlins (*Falco columbarius*), and Peregrine Falcons (*F. peregrinus*), routinely enter and leave the Neotropics via trans-Caribbean and trans-Gulf of Mexico routes. Southern or "austral" and intratropical movements, including dispersal and colonization in response to habitat change, are known but remain relatively little studied. Having detailed the patterns and processes of raptor migration in the region, I discuss what is known about the ecological consequences of these movements, including competitive interactions between migrant and resident species. I then go on to explore the role that long-distance migration has played in shaping raptor species distributions and abundances in the Neotropics. I conclude by proposing that the hourglass configuration of continental landmasses and the north-south orientation of mountain ranges in the New World, not only facilitate long-distance land-based raptor migration in the region, but also enhance regional raptor diversity via a speciation process called "migration dosing." The process of migration dosing involves a series of events in which "doses" of diverted long-distance migrants (1) arrive in areas tangential to or beyond their major migration flyways, (2) remain there the following breeding season rather than returning to traditional breeding areas, and (3) eventually diverge from parental stock in geographic isolation. Likely examples of migration dosing are presented from two species-rich near-cosmopolitan genera, *Accipiter* and *Buteo*. *Accepted 13 December 2003.*

Key words: Raptors, Falconiformes, migration, Neotropics, patterns, processes, consequences.

INTRODUCTION

Diurnal birds of prey or raptors (suborder Falconides and the subfamily Cathartinae) are a diverse group of approximately 300 species of hawks, eagles, falcons, vultures, and their close relatives, one third of which occur in the Neotropics (del Hoyo *et al.* 1994). Found on many oceanic islands and on all continents except for Antarctica, the group includes several of the most broadly distributed and most mobile of all species of birds. Each year well over five million raptors migrate into and within the Neotropics. Unlike many of the region's migrants that travel principally at night, birds of prey migrate almost entirely by day, often along well-established flyways. Most are relatively large-bodied, lightly wing-loaded species, and many depend upon soaring to complete their long-distance journeys (Bildstein & Zalles 1998, 2001; Zalles & Bildstein 2000, Ferguson-Lees & Christie 2001).

Zalles & Bildstein (2000) summarize known migration choreography in the region. Overall, raptor movements are far better studied in Central America than in South America, and far more is known about the long-distance "northern" movements of North American breeders than about migrants that both breed and "overwinter" in the region. The limited information available indicates that raptor migration in the Neotropics is both complex and confusing (Bildstein & Zalles 1998).

At least 40 of 104 raptors in the region are complete or partial migrants, 28 others are irregular or local migrants. Long-distance movements, the overwhelming majority of which are made by latitudinal migrants, are numerically dominated by the influx of North American breeders in boreal autumn. The Mesoamerican Land Corridor, which is part of the larger Transamerican Flyway, is by far the most heavily used migration pathway in the Neotropics (Fig. 1). Lesser numbers of North American breeders travel into and out of Central and South America via the Gulf of Mexico and the Caribbean Sea. At least 22

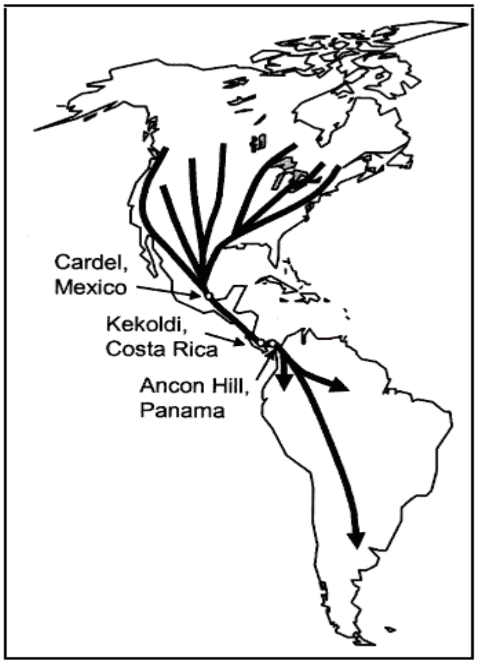

FIG. 1. The Transamerican Flyway is used by 5-10 million outbound raptor migrants each autumn. Cardel, Mexico, Kekoldi, Costa Rica, and Ancon Hill, Panama, are three important migration watchsites along the Mesoamerican Land Corridor portion of this flyway. Both the geography of the flyway and the timing of the flight, are far better understood in North America and Central America than in South America.

species of Neotropical raptors are intratropical migrants, 23 are southern or "austral" migrants, and at least 16 are altitudinal migrants (Table 1) (Zalles & Bildstein 2000). Northern or boreal migrations are far better understood and appreciated than are intratropical, austral, and altitudinal movements.

Here I (1) summarize and update the migratory characteristics of Neotropical raptors, (2) describe the geography, timing, and magnitude of long-distance raptor migration in the region, (3) assess the forces responsible, (4) detail ecological consequences of the movements, and (5) describe how raptor migration has affected species distributions and raptor diversity in the region. I conclude by detailing priority areas for future research.

METHODS

Definitions. In this analysis, raptors include the 307 species that belong to the suborder Falconides and the subfamily Cathartinae (*sensu* Sibley & Ahlquist 1990). Species taxonomy and nomenclature follow del Hoyo *et al.* 1994, as updated by more recent findings. Neotropical raptors are the 104 species known to breed within or to regularly visit the Neotropical Realm (*sensu* Darlington 1957). Migration is defined as directed and generally long-distance, recurring movements that alternate in direction and that are temporally and spatially predictable. Geographically, migration "flyways" are hemispheric networks of regional "corridors" and local "routes" along which raptors concentrate while migrating. Complete migrants are species in which $\geq$ 90% of all individuals leave their breeding range during the non-breeding season. Partial migrants are species in which < 90% of all individuals migrate. Irregular migrants are species in which the extent of migratory movements varies annually, typically in response to among-year shifts in prey abundance. Local migrants include species in which most populations, except for those at the latitudinal perimeters of the range, do not migrate, or nomadic species in which individuals tend to wander during the non-breeding season.

RESULTS

The raptors

Faunal comparisons. With 34% (104) of the world's 307 species of raptors and 46% (37) of its 81 genera, the Neotropical Realm is arguably the most raptor-diverse biogeographical realm on earth. The region's 18 endemic genera make it one of the most distinctive raptor

TABLE 1. Migratory tendencies and the tropical extent of breeding and wintering range of 104 Neotropical raptors.

Species	Long-distance migrants[a]	Trans-equatorial migrants[b]	Altitudinal migrants[c]	Water crossing behavior[d]	Maximum flock size[e]	Tropical species[f]
Complete migrants						
Pandion haliaetus	Yes	Yes		Long	> 50	Mainly
Ictinia mississippiensis	Yes	Yes			> 100*	
Buteo platypterus	Yes	Yes		Short	> 1000*	Mainly
Buteo swainsoni	Yes	Yes		Short	> 1000*	
Partial migrants						
Cathartes aura	Yes	Yes		Short	> 1000*	Mainly
Coragyps atratus			Yes		> 10*	Mainly
Elanoides forficatus	Yes	Yes	Yes	Moderate	> 100*	Mainly
Elanus leucurus						Mainly
Rostrhamus sociabilis					> 10*	Mainly
Ictinia plumbea					> 100*	Mainly
Haliaeetus leucocephalus				Moderate	< 10	
Circus buffoni						Mainly
Circus cyaneus	Yes			Long	< 10	
Circus cinereus			Yes	Short		
Accipiter poliogaster						Mainly
Accipiter striatus	Yes		Yes	Short	< 10	
Accipiter cooperii			Yes	Short	< 10	
Accipiter bicolor			Yes			Mainly
Accipiter chilensis						
Accipiter gentilis			Yes	Short		
Buteogallus anthracinus						Mainly
Buteogallus meridionalis						Mainly
Parabuteo unicinctus						Mainly
Geranoaetus melanoleucus						Mainly
Buteo nitidus						Mainly
Buteo lineatus				Short	< 10	
Buteo brachyurus					< 10	Mainly
Buteo albigula			Yes			Mainly
Buteo albicaudatus					< 10	Mainly
Buteo polyosoma						
Buteo albonotatus					< 10	Mainly
Buteo jamaicensis				Short	> 10	
Buteo regalis					< 10	
Aquila chrysaetos	Yes			Moderate		
Milvago chimango				Short		
Falco sparverius				Moderate	< 10	
Falco femoralis			Yes	Short		Mainly
Falco columbarius	Yes		Yes	Long	< 10	
Falco mexicanus			Yes			
Falco peregrinus	Yes	Yes		Long		

TABLE 1. Continuation.

Species	Long-distance migrants[a]	Trans-equatorial migrants[b]	Altitudinal migrants[c]	Water crossing behavior[d]	Maximum flock size[e]	Tropical species[f]
Irregular or local migrants						
Cathartes burrovianus						Mainly
Cathartes melambrotus						Wholly
Sarcoramphus papa						Mainly
Vultur gryphus						
Chondrohierax uncinatus			Yes			Mainly
Harpagus bidentatus						Mainly
Harpagus diodon						Mainly
Geranospiza caerulescens						Mainly
Leucopternis lacernulata						Wholly
Leucopternis polionota						Mainly
Buteogallus urubitinga						Mainly
Busarellus nigricollis						Mainly
Harpyhaliaetus solitarius						Mainly
Harpyhaliaetus coronatus						Mainly
Buteo magnirostris						Mainly
Buteo leucorrhous						Mainly
Buteo poecilochrous			Yes			Mainly
Buteo ventralis			Yes			
Harpia harpyja						Mainly
Spizaetus tyrannus						Mainly
Spizaetus ornatus			Yes			Mainly
Phalcoboenus carunculatus						Mainly
Phalcoboenus megalopterus						Wholly
Phalcoboenus australis						
Polyborus plancus						Mainly
Milvago chimachima						Mainly
Falco rufigularis						Mainly
Falco deiroleucus						Mainly
Nonmigrants						
Leptodon cayanensis			Yes			Mainly
Leptodon forbesi						Wholly
Gampsonyx swainsonii						Mainly
Rostrhamus hamatus						Mainly
Accipiter superciliosus						Mainly
Accipiter collaris						Wholly
Accipiter chionogaster			Yes			Wholly
Accipiter ventralis						Wholly
Accipiter erythronemius						Mainly
Accipiter gundlachi						Wholly
Leucopternis plumbea						Wholly
Leucopternis schistacea						Wholly
Leucopternis princeps						Wholly

TABLE 1. Continuation.

Species	Long-distance migrants[a]	Trans-equatorial migrants[b]	Altitudinal migrants[c]	Water crossing behavior[d]	Maximum flock size[e]	Tropical species[f]
Leucopternis melanops						Wholly
Leucopternis kuhli						Wholly
Leucopternis semiplumbea						Wholly
Leucopternis albicollis						Wholly
Leucopternis occidentalis						Wholly
Buteogallus aequinoctialis						Mainly
Buteogallus subtilis						Wholly
Buteo ridgwayi						Wholly
Buteo galapagoensis						Wholly
Morphnus guianensis						Mainly
Spizastur melanoleucus						Mainly
Oroaetus isidori						Mainly
Daptrius ater						Wholly
Daptrius americanus						Mainly
Phalcoboenus albogularis						
Herpetotheres cachinnans						Mainly
Micrastur ruficollis						Mainly
Micrastur plumbeus						Wholly
Micrastur gilvicollis						Wholly
Micrastur mirandollei						Wholly
Micrastur semitorquatus						Mainly
Micrastur buckleyi						Wholly
Spiziapteryx circumcinctus						

[a]Complete or partial migrants, ≥ 20% of whose populations (sometimes entire subspecies) regularly migrate > 1500 kms.
[b]Long-distance migrants, ≥ 20% of whose populations (sometimes entire subspecies) regularly migrate across the Equator.
[c]Species in which at least some populations are known or suspected to migrate altitudinally.
[d]Short, species that regularly cross water barriers of < 25 km; moderate, 25–100 km; long, > 100 km.
[e]Species whose maximum flock sizes are marked with an asterisk (*) regularly migrate in flocks, all others with maximum flock sizes listed flock occasionally.
[f]Species in which at least 50% (mainly) or all (wholly) of the range falls within the Tropics of Cancer and Capricorn.

faunas as well. In addition, the Neotropics is the center of generic diversity in the family Falconidae (del Hoyo *et al.* 1994), as well as the ancestral home of the genus *Buteo* (Amadon 1982, Voous & deVries 1978, Riesing *et al.* 2003).

Seventy-nine percent of the Neotropics lies between 30º S and N, and most raptors in the region are wholly (23%) or mainly (53%) tropical species, many of which are non-migratory (Table 1) (Bildstein *et al.* 1998). Indeed, there are only 4 species of complete migrants and 7 species of long-distance, trans-equatorial migrants in the region, compared with 11 and 14, respectively, in the Afrotropical Realm. And overall, the Neotropical raptor community is less migratory than that of any other continental region excepting Indomalaysia and Australasia (Bildstein *et al.* 1998, Zalles & Bildstein 2000).

Complete migrants. Four species of complete migrants occur in the Neotropics (Table 1). Adult Osprey (*Pandion haliaetus*) breed in small numbers and over-winter in large numbers in the region, and North American juveniles over-summer there as well (Poole *et al.* 2002). North American (i.e., world) breeding populations of Mississippi Kite (*Ictinia mississippiensis*), Broad-winged Hawk (*Buteo platypterus*), and Swainson's Hawk (*B. swainsoni*) overwinter in the region, and all three species typically travel to, within, and out of the region in large, multi-thousand bird migratory flocks (Zalles & Bildstein 2000).

Partial migrants. Thirty-six partial migrants occur in the region (Table 1). They include 13 species that breed largely in North America and that over-winter mostly or entirely in Central America, 12 species that breed mainly in the Neotropics and that over-winter there, and 11 species that breed and over-winter wholly within the Neotropics. North American breeding populations of Turkey Vulture (*Cathartes aura meridionalis*) are by far the most numerous partial migrant. Other partial migrants whose movements involve > 10,000 birds include Swallow-tailed Kite (*Elanoides forficatus*), Plumbeous Kite (*Ictinea plumbea*), and Snail Kite (*Rostrhamus sociabilis*). Populations of nine species, Turkey Vulture, Cinereous Harrier (*Circus cinereus*), Bicolored Hawk (*Accipiter bicolor*), Red-backed Hawk (*Buteo polyosoma*), Rufous-tailed Hawk (*B. ventralis*), Striated Caracara (*Phalcoebanus australis*), American Kestrel (*Falco sparverius*), Aplomado Falcon (*F. femoralis*), and Peregrine Falcon (*F. peregrinus*) evacuate Tierra del Fuego (53º–56ºS) for mainland South America in austral winter (Humphrey *et al.* 1970). Concentrated movements of hundreds of White-throated Hawks (*Buteo albigula*) are reported for the mountains of central Chile (33º–34º S) (Pavez 2000, Zalles & Bildstein 2000).

Irregular and local migrants. Twenty-eight irregular and local migrants occur in the region (Table 1). They include 22 mainly and 3 wholly tropical species, and 3 species whose distributions fall mainly within the non-tropical "southern cone" of South America. Most of these species are best characterized as local migrants with relatively small "latitudinally peripheral" migratory or partially migratory populations, either north or south of the tropics or both. Examples include Hook-billed Kite (*Chondrohierax uncinatus*) in Mexico (E. Ruelas pers. com.) which are at the northern limits of their range, and the Rufous-thighed Kite (*Harpagus diodon*) which is migratory in temperate South America at the southern limits of its range (Hayes *et al.* 1994, Ridgely & Greenfield 2001). Nomadic species include the regionally migratory Savanna Vulture (*C. burrovianus*) in Brazil and Panama (Sick 1993), and Snail Kite in many parts of its extensive range (Angehr 1999, Ferguson-Lees & Christie 2001).

Recent unconfirmed sightings of southbound flocks of as many as several hundred White-tailed Hawks (*B. albicaudatus*) near Santa Cruz, Bolivia, in mid-November raise the possibility of significant regional movements in this species as well (Olivo 2003). However, as previous reports of migration in this species [e.g., Hudson (1920) in Argentina, and Wetmore (1943) in Mexico] are thought to have involved either individuals that had briefly joined flocks of true migrants, and were not themselves migrating (Farquhar 1992), or misidentified Swainson's Hawks (Bildstein & Zalles 2001), and because Bolivia falls along a major flightline for Swainson's Hawks, these recent sightings require careful confirmation.

Truly irruptive migrants include the White-tailed Kite (*Elanus leucurus*), a species that in Buenos Aires Province, Argentina, tracks rodent cycles (Ferguson-Lees & Christie 2001). Nomadic migrants include the Snail Kite, a species that feeds almost exclusively upon apple snails, and which established a breeding population at Lake Gatun, Panama, from populations at least 350 km away, fewer than 10 years after apple snails were introduced to the lake (Angehr 1999).

Altitudinal migrants. At least 16 species are altitudinal migrants in the region (Table 1). They include Andean Condors (*Vultur gryphus*), Hook-billed Kites, White-throated Hawks, Puna Hawks (*Buteo poecilochrous*), and Aplomado Falcons, populations of which breed in the high Andes and migrate to lower elevations at other times of the year (Fjeldså & Krabbe 1990, Ferguson-Lees & Christie 2001). Condors, for example, regularly travel both to near and distant lowland feeding sites on a seasonal basis, including as far as Mato Grosso, southwestern Brazil, which requires a roundtrip journey of several thousand kilometers (Sick 1993). A recent analysis that indicates low genetic variability in this species (Hendrickson 2003), despite its partially disjunct distribution, indicates the likelihood of long-distance intra-Andean movements as well. The Rufous-tailed Hawk also may be an altitudinal migrant (Ferguson-Lees & Christie 2001).

Migration geography in the Neotropics

Transamerican Flyway. The Transamerican Flyway, the southern two thirds of which stretches from northwestern Mexico to the temperate southern cone of South America (Fig. 1), far and away is the most numerically important raptor migration flyway in the region. Thirty-two species, including three accipiters, eight buteos, and five falcons travel along the flyway's central 4000-km Mesoamerican Land Corridor that extends from southern Texas through eastern Panama. Numerically significant migrants using the corridor include Turkey Vultures [2,000,000 (minimal estimate of number of birds based on autumn-watchsite counts), Osprey (5000), Swallow-tailed Kite (1000), Plumbeous Kite (1000), Mississippi Kite (200,000), Northern Harrier (*Circus cyaneus*; 1000), Sharp-shinned Hawk (*Accipiter striatus*; 5000, northern part only), Cooper's Hawk (*A. cooperii*; 2000, northern part only), Broad-winged Hawk (1.5 million), Swainson's Hawk (800,000), American Kestrel (3000, northern part only), Merlin (*Falco columbarius*; 1000), and Peregrine Falcon (5000).

During outbound migration in boreal autumn, flight lines of the four numerically dominant migrants using the corridor converge in coastal Veracruz, Mexico, before splitting west of the Isthmus of Tehuantepec. Although the bulk of the flight crosses to the Pacific slope at this point, a substantial portion and perhaps most of the broadwing flight, continues east along the Caribbean slope into eastern Guatemala and northwestern Honduras.

Visual counts of migrants have been sporadic in El Salvador, Honduras, and Nicaragua, and the geography of the migration corridor is less well understood there than elsewhere in Mesoamerica. Satellite trackings of outbound Broad-winged Hawks (Haines *et al.* in press), and Swainson's Hawks (Fuller *et al.* 1998), suggest that large numbers of broadwings travel along the Caribbean slope of the continental divide, as well as along the near-coastal Pacific slope, as far south as the Gulf of Fonseca, where the flight again coalesces on the Pacific side, whereas the vast majority of Swainson's Hawks migrate along the coastal Pacific slope throughout this portion of the route. Observations in the western coastal plain of Chiapas, southern Mexico, suggest that the bulk of the Turkey Vulture flight also follows the Pacific slope in this region (Tilly *et al.* 1990).

Farther south the principal flightline enters the lowlands of northwestern Costa Rica where it largely tracks the foothills of the Atlantic slope southeast into Panama. In Panama, most of the flight crosses to the Pacific slope east of Volcan Baru, before entering northwestern Colombia via the Darien. Falcons migrating coastally through Mesoamerica apparently join the flight whenever it passes within several kilometers of the coast.

Once the birds reach South America, the flightline turns south, where many and perhaps most of the migrants follow the Magdalena Valley south into Tolima in central Colombia, before entering the Amazon lowlands en route to east-central Bolivia and, from there, the Pampas of northeastern Argentina. At least some of the flight, including large numbers of Swallow-tailed Kites, pass through Colombia along the Pacific slope of the Andes, before crossing the mountains to the east near the border with Ecuador (K. Meyer pers. com.).

Broadwings begin to drop out of the flight in large numbers and into wintering areas at least as far north as El Salvador, and most have left the main flightline before southern Colombia, as have most Turkey Vultures. Large numbers of Mississippi Kites continue at least as far south as central Bolivia, and most Swainson's Hawks remain on the flightline into Argentina (Zalles & Bildstein 2000, M. Bechard, C. Marquez, & K. Meyer pers. com.).

So far as is known, in spring, the less studied return flightline largely retraces the outbound flightline, excepting that proportionately more birds travel along the Atlantic slope while crossing the Panama Canal in central Panama (Smith 1985), and the Pacific slope in southeastern Costa Rica (Skutch 1945) than occurs in autumn, presumably because of seasonal differences in the weather.

Austral flyways. Austral or South American migration system migrants (*sensu* Joseph 1997) are species that breed in the temperate, southern cone area of South America and that migrate north toward the Equator in austral winter (Chesser 1994, Joseph 1997). Austral movements are particularly pronounced along the southern Andes and in wetlands associated with the Paraguay River, where notable migrants include White-throated Hawk and Snail and Plumbeous kites, respectively (Pavez 2000, Hayes *et al.* 1994). Diversion lines and migration bottlenecks are lacking in the region, however, and details regarding the magnitude of such movements, as well as the origins and destinations of most of the migrants involved remain uncertain.

Hayes *et al.* (1994) recognized two types of austral migrants, northern and southern, coinciding with Joseph's (1997) temperate-tropical and cool, temperate South American migrants, respectively. Regional populations of at least 23 species of raptors (18 partial migrants and 5 irruptive or local migrants) have been characterized as northern or southern austral migrants, or both. They include the Turkey Vulture, four species of kites, two harriers, two accipiters, two buteos, and three falcons, all but four of which are wholly or largely Neotropical species (Chesser 1994, Hayes *et al.* 1994, Zalles & Bildstein 2000). Much remains to be learned about austral raptor migration, and careful observations of these movements offer the promise of substantial new information.

Intratropical flyways. Because many are local, regional, irruptive, or are mixtures of all three types of movements, and because the numbers of individual migrants involved apparently are relatively few, intratropical movements are decidedly less well understood than is either northern or austral migration. The situation in the eastern lowlands of Bolivia, a region that falls along an important north-bound route for populations of North American Swallow-tailed Kite, Mississippi Kite, and Swainson's Hawk, as well as Neotropical populations of Snail Kite, Plumbeous Kite, and, possibly, Swallow-tailed Kite (Zalles & Bildstein 2000) typifies the challenges involved. Although the North American origins of Mississippi Kites and Swainson's Hawks in Bolivia is certain based on their breeding distributions, and whereas satellite telemetry substantiates the North American origins of at least some of the Swallow-tailed Kites traveling through the country (K. Meyer pers. com.), the origins and destinations of thousands of Plumbeous Kites and hundreds of Snail Kites migrating in the area are largely unknown.

Consequences of raptor migration

Competition between long-distance migratory and sedentary raptors. Competition between migratory and resident Neotropical raptors is little studied. However, the numbers of migrants involved (i.e., 5-6 million birds), similarities in ecology between many of the migratory and sedentary species, and a detailed study of interactions between migratory and resident Turkey Vultures in Venezuela, all suggest the likelihood of significant, widespread competition. Consider, for example, the situation in Costa Rica involving the closely related Broad-winged Hawk and Roadside Hawk (*B. magnirostris*). Both species are abundant territorial inhabitants in lowland and mid-elevational disturbed areas and forest edges in the country, and both spend much of their time perch hunting for the same prey (i.e., large insects, reptiles, and small mammals) (Stiles & Skutch 1989, Ridgely & Gwynne 1989). Although competitive interactions between these two raptors have yet to be documented, within Talamanca, Costa Rica, the home ranges of the two often interdigitate, and it seems reasonable to assume that the two sometimes interact competitively (but see Smith 1980). Intraspecifically, in Cuba, where wintering migratory American Kestrels (*F. s. sparverius*) co-occur with the island's smaller resident form (*F. s. sparveroides*), migrants typically displace residents from preferred feeding areas (F. Rodriguez pers. com.). In the llanos of Venezuela, migratory Turkey Vultures (*C. a. meridionalis*) socially dominate smaller residents (*C. a. ruficollis*) when the two commingle at carcasses, and resident vultures withdraw from savanna feeding areas and forage almost entirely within gallery forests when the larger migrants arrive in the region. Significantly, the body condition of resident vultures declines at this time, particularly when the migrants overwinter in large numbers, whereas that of migrant vultures improves during their stay in the area (Kirk & Gosler 1994, Kirk & Houston 1995). Suggestively, in western Panama, where migrants are believed to make up 45% of the Turkey Vulture population in winter, residents begin egg-laying in February after many of the migrants have left (Smith 1980). Other potentially competitive migrant-resident pairs include Osprey and Black-collared Hawk (*Busarellus nigricollis*), Mississippi Kite and Plumbeous Kite, and Swainson's Hawk and White-tailed Hawk. Obviously, there is need for additional careful study of this phenomenon in the region.

Migration-dosing speciation. One unintended consequence of large-scale raptor movements in the Neotropics is that each year some migrants are displaced from their principal migration flyways, either by weather or by failed navigational systems, and once lost eventually wind up in areas that are geographically isolated from the species' traditional wintering grounds. The so-called "vagrants" face three potential outcomes. They can die in the new-found area without breeding, they can reorient themselves and successfully relocate their intended destinations, or they and other simultaneous vagrants can survive the winter, forego return movements the following spring, and subsequently settle and breed in isolation from their parental stock. This last scenario can result in the phenomenon of migration dosing speciation (*sensu* Bildstein & Zalles in press).

Simply put, migration dosing is orchestrated vagrancy in which viable groups of potential propagules in the form of wind drifted or otherwise navigationally challenged flocks of migrants (1) simultaneously arrive at sites tangential to or beyond their traditional wintering areas, (2) fail to return to their intended destinations, and (3) via random genetic drift, natural selection in response to the new circumstances, or both, eventually diverge from their parental stock and speciate in isolation (Bildstein & Zalles in press). Most likely, inexperienced juveniles constitute the majority of "dosed' propagules, as they often migrate together, are particularly vulnerable to wind drift (Kerlinger 1989, Thorup *et al.* 2003), and have a propensity to develop new migratory habits (Viverette *et al.* 1996).

Note that migration dosing differs from adaptive radiation, in that adaptive radiation involves "simultaneous divergence of numerous lines from much the same adaptive type into different [and] also diverging adaptive zones" (Simpson 1953), whereas migration dosing refers to changes from relatively specialized highly migratory forms into other specialized, or in some instances – especially on islands – into generalized sedentary forms.

Although migration dosing has not received widespread attention as a speciation mechanism in birds, conditions associated with it, including long-distance migration, migration in large flocks, vulnerability to wind drift, and high rates of vagrancy among migratory birds (Alerstam 1990, Newton 2003), as well as numerous examples of speciation that are most simply explained by this process, are well described in the avian literature (e.g., Snow 1978, Bildstein & Zalles in press).

Neotropical migratory raptors appear to be particularly prone to migration dosing for several reasons. Most prey on nutritionally substitutable prey rather than specific taxa, which makes it easy for them to adapt to new prey types in new areas. Many soar on migration and are particularly vulnerable to wind drift. And many, and in particular most long-distance migrants, migrate in large flocks, thereby increasing the likelihood of simultaneous vagrancy (Kerlinger 1989, Schulter 2000). The tropics are an ideal location for migration dosing speciation because of the increased likelihood of sedentary behavior there, and the subsequent greater impact of geographic barriers (Mayr 1969).

Migration dosing is most common when raptors are blown off course and onto relatively isolated islands from which return is difficult. The most dramatic raptor example of this phenomenon involves the genus *Accipiter* in the South Pacific. Nineteen species, or fully 38% of the world's 50 species of accipiters, occur on islands in Melanesia (18 species) and in Australia (3 species) east of Wallace's Line (del Hoyo *et al.* 1994). The likely origins of most of these forms appear to be tied to the seasonal long-distance over-water migrations of close to half a million Chinese Goshawks (*Accipiter soloensis*). In most years these migrants complete their outbound migrations aided by monsoonal northwesterly winds and their return movements aided by easterly trade winds. Each autumn, however, their movements carry the birds across an active tropical cyclone region in which typhoons can scatter the migrants, and in the springs of El Niño-Southern Oscillation events, strong westerly winds replace the easterly trade winds, making return migration difficult for many of the birds. Both of these potential disruptions provide the backdrop for episodic misdirected movements that place some of the migrants on islands east of Wallace's Line far beyond their normal flight line from which they are unable to return to their continental breeding areas. The "dosed' vagrants, in turn, appear to have provided the seed stock for much of the region's high level of endemism (Bildstein & Zalles in press).

Neotropical examples of accipiters that most likely speciated via migration dosing include the critically endangered Cuban Gundlach's Hawk (*Accipiter gundlachi*), the Central American White-breasted Hawk (*A. chionogaster*), and the South American Plain-breasted (*A. ventralis*) and Rufous-thighed (*A. erthronemius*) hawks. The first appears to be derived from the migratory Cooper's Hawk, and the last three from the far more migratory Sharp-shinned Hawk. Intriguingly, several of the non-migratory Neotropical forms tend to be decidedly more intensely rufous ventrally, a difference that parallels that between the Palaearctic migratory Eurasian Sparrowhawk (*A. nisus*) and the Rufous-breasted Sparrowhawk (*A. rufiventris*), its non-migratory African derivative (Snow 1978). High-frequency episodic or continual gene flow between the North American migratory subspecies of the Sharp-shinned Hawk (*velox*) and the five largely Neotropical non-migratory subspecies [*suttoni* (extreme s. New Mexico south to s. Veracruz), *madrensis* (Guerro and possibly w. Oaxaca, Mexico), *striatus* (Hispaniola), *fringilloides* (Cuba), and *venator* (Puerto Rico)], all of which occur north of the three full-species forms associated with this north American migrant, apparently precludes speciation via migration dosing in these forms. Two South American partial migrants, Bicolored Hawk and Chilean Hawk (*A. chilensis*), both of which are close relatives of the Cooper's Hawk, also most likely resulted directly or indirectly from migration dosing. The origins of the region's three remaining accipiters, Grey-bellied Goshawk (*A. poliogaster*), Tiny Hawk (*A. superciliosus*) and Semi-collared Hawk (*A. collaris*) are less certain (see Wattel 1973)

There are putative *Buteo* examples of migration dosing as well. Seventeen species of buteos, or 60% of the world's 28 species, including two complete and nine partial migrants, occur in the region. Two Neotropical species, Broad-winged Hawk and Swainson's Hawk, are long-distance, transequatorial migrants that breed in the Nearctic and overwinter in the Neotropics. Both of the latter regularly "dose" the Neotropics with at least hundreds and possibly thousands of misguided individuals, and both appear to have spawned several new species via migration dosing. Two of four range-restricted endemics in the genus, Galapagos Hawk (*B. galapagoensis*) and Hawaiian Hawk (*B. solitarius*) represent examples of migration dosing via *swainsoni* (Mayr 1943, Riesing *et al.* 2003). Both of these island forms almost certainly are derived from wind-drifted flocks of Swainson's Hawks that were driven off-course, possibly by tropical cyclones, and thereafter carried westwards across the Pacific Ocean via easterly trade winds, which are known to facilitate round-the-clock soaring via large-scale sea thermals (Augstein 1980). Two recent molecular phylogenies (Fleischer & McIntosh 2001, Riesing *et al.* 2003) place *solitarius* and *galapagoensis* together with *swainsoni* and the Central and South American Short-tailed Hawk (*B. brachyurus*) and the South American White-throated Hawk. This raises the possibility that the latter two continental forms also arose via migration dosing.

Another range-restricted island endemic, the Ridgway's Hawk (*B. ridgwayi*), most likely represents a migration dosing example via the far less migratory Red-shouldered Hawk (*B. lineatus*) although its origins via *platypterus* can-not be ruled out (Riesing *et al.* 2003). The Rufous-tailed Hawk appears to be an end-of-the-migration-route continental form of the northern Red-tailed Hawk (*B. jamaicensis*). On the other hand, five insular, Caribbean basin races of the Broad-winged Hawk [e.g., *cubanenis* (Cuba), *brunnescens* (Puerto Rico), *insulicola* (Antigua), *rivierei* (Lesser Antilles), and *antillarum* (St. Vincent, Grenada, Trinidad & Tobago)], apparently are "dosed" too frequently by continental forms, or have been isolated too recently, for speciation to occur.

The origins of the remaining truly Neotropical buteos are a bit more difficult to assess. Red-backed, White-tailed, Gurney's hawks and, somewhat less so, the Gray Hawk (*B. nitidus*), appear basal to the genus. The largely non-migratory Roadside Hawk and White-rumped Hawk (*B. leucorrhous*) may be even more basal, possibly to the point of being in different genera (Riesing 2003).

Other likely migration dosed species in the region include the Orange-breasted Falcon (*F. deiroleucus*) that is probably derived from northern migratory populations of the Peregrine Falcon (*F. peregrinus anatum* or *tundrius*), or, possibly, from the Bat Falcon (*F. rufigularis*), which appears to be closely related to the highly migratory Northern Hobby (*F. subbuteo*) (Ferguson-Lees & Christie 2001).

DISCUSSION

The closing of the Central American land bridge approximately three million years ago opened the way to substantial and significant long-distance, land-based raptor migration in the Neotropics. The Mesoamerican Land Corridor, together with relatively extensive land masses north of 30º in North America and south of 30º in South America, is largely responsible for most long-distance northern and austral migration in the region. The latitudinal location (20º–25º S), north-south orientation, and seasonal nature of Paraguay River wetlands facilitate additional austral movements, and the High Andes produce the backdrop for considerable altitudinal migration in the region.

As is true of many other groups of North America migrants (see Keast & Morton 1980 and references therein), most, if not all, northern raptors overwintering in the Neotropics do so principally in (1) coastal or inland aquatic and wetland habitats (e.g., Osprey, Peregrine Falcon, Turkey Vulture), (2) grasslands and open savannas (e.g., Mississippi Kite, Swallow-tailed Kite, Swainson's Hawk), or (3) forest edges and second growth forests (Broad-winged Hawk), rather than in large, undisturbed forest tracts. Presumably most of this reflects the fact that the northern migrants inhabit similar habitats on their breeding grounds. As there is no evidence for competitive exclusion or increased predation risk for migrants inhabiting undisturbed forests, it seems likely that the habitat shifts occur because of the presence of "superabundant and/or sporadically available" prey in many open areas (Karr 1976), coupled with a lack of nest-site constraints during the non-breeding season.

Somewhat surprisingly, the region's two largest seasonal tropical freshwater wetland complexes, the 300,000-km^2 Venezuelan-Colombian llanos and 200,000-km^2 Brazilian-Bolivian-Paraguayan pantanal (Scott & Carbonell 1986), do not appear to host large numbers of long-distance migrants, although intratropical migrants are well represented there. A recent two-year survey of raptors in the central and western Venezuelan llanos, for example, indicates that North American migrants, Osprey, American Kestrel, and Peregrine Falcon, comprise only 4.2% of all raptors seen, and that when kestrels – which are both resident and migratory in the area – are eliminated from the analysis, the two remaining migrants make up only 1.2% of the community. On the other hand, numbers of several local and regional migrants either increased [Yellow-headed Caracara (*Milvago chimachima*), Savanna Hawk (*Buteogallus meridionalis*), and Crane Hawk (*Geranospiza caerulescens*)] or decreased (Snail Kite and White-tailed Hawk) during the November–April dry season (Jensen 2003). Unfortunately, the study did not survey the wetland's New World vultures, and the relative densities of migratory versus resident Turkey Vultures was not determined. A detailed study of raptor populations in the Pantanal is lacking, but there are no reports of large numbers of northern migrants over-wintering in that area either (see for example Sick 1993). Large numbers of northern migrants, including Swallow-tailed Kite, Mississippi Kite and, particularly, Swainson's Hawk, do overwinter in South America's semitropical and temperate grasslands, steppes, and savannas, however. As is so in southern Africa, northern migrants often outnumber resident species in these habitat types, presumably because of the seasonal nature of insect and small mammal abundances in these areas (see Smeenk 1974).

As a result, the open habitats of South America play host to some of the most temporally and spatially diverse raptor communities anywhere. The extent to which migrants and residents compete for resources in these circumstances is unclear. Most, if not all, of the long-distance migrants are principally nomadic during the dry season, as are most regional and local migrants. Many of the latter at least are attracted to large-scale seasonal burns where they feed upon animals along active fire lines (Sick 1993). Others, including Swainson's Hawk, track migrating swarms of dragonflies (*Aeshna bonariensis*) (Jaramillo 1993), and still others, including Swallow-tailed Kite, track populations of ephemerally swarming termite alates (Termitidae) (Bildstein pers. observ.). Many species feed at livestock carcasses that accumulate during particularly severe wet or dry seasons.

Arguably, highly diverse and apparently superabundant prey, together with a lifestyle that allows raptors to track food resources regionally, may enable migrants and residents to coexist in Neotropical open habitats with relatively little in the way of inter-species competition, particularly if intra-species competition (Kirk & Gosler 1994, Kirk & Houston 1995) and territoriality (Smith 1980) limit densities within species. Nevertheless, much remains to be learned regarding the ways in which northern migrants and Neotropical residents parse the resources available to them, and careful observations in this area are likely to provide rich sources of information regarding competition between these two groups of raptors.

So far, conservation biologists focusing on the factors responsible for the creation and maintenance of biological diversity have concentrated their efforts on the roles that geological processes, past climates, dispersal, and the current availability of local resources play in shaping current biodiversity, with little, if any, attention being paid to long-distance migration (see for example Newton 2003). My assessment of raptor movements in the Neotropics suggests that migration plays a substantial role in shaping patterns of species richness of several widespread genera of raptors in the region. Based on examples presented above, migration dosing appears to provide a plausible addition to the allopatric "refugium theory" (Haffer 1969) and parapatric speciation across vast distances (Knapp & Mallet 2003) in explaining high species diversity in the Neotropics, at least for the region's raptors.

As raptor migration is representative of that of birds in general, it seems reasonable to conclude that migration dosing as a speciation mechanism occurs in other groups of birds as well (see for example Snow 1978).

TABLE 2. Priority areas of inquiry for raptor-migration science in the Neotropics.

Why don't Broad-winged Hawks (*Buteo platypterus*) shift their flight line from the Atlantic slope to the Pacific slope at the Isthmus of Tehuantepec as do Turkey Vultures (*Cathartes aura*) and Swainson's Hawks (*B. swainsoni*)?
Where do most Turkey Vultures, Mississippi Kites (*I. mississippiensis*), Broad-winged and Swainson's hawks overwinter in the region, both geographically and in terms of habitat?
What are the migratory patterns of intratropical and austral migrants in the region?
To what extent to long-distance migrants from North America compete with wholly Neotropical migrant and resident species?
To what extent is migration dosing responsible for raptor species diversity and distribution in the region?

Thus, I strongly recommend that researchers studying avian diversity in tropical regions, including those working on molecular phylogenies, consider the possibility of migration dosing when discussing their results.

Finally, much remains to be learned about raptor migration in the Neotropics. The priority areas of inquiry listed in Table 2 offer a starting point for additional study.

ACKNOWLEDGMENTS

In addition to published sources, much of the information herein was gathered and submitted to Hawk Mountain Sanctuary by cooperators working on the Hawks Aloft Worldwide migration atlas project. I thank all of them, and in particular Jorge Aguilar, Chelina Batista, Ernesto Ruelas Inzunza, Cristian Olivo, Pablo Porras, Freddy Rodriquez Santana, Marco Saborio, Cesar Sanchez, and Julio Sanchez, for helping clarify my impressions of raptor migration in the region. My colleague and friend Jorje Zalles played a major role in introducing me to the Spanish-language literature, as well as in helping refine my thoughts on migration dosing. Jaime Jimenez and the co-organizers of the VIIth Neotropical Ornithological Congress graciously provided an appropriate forum for presenting my ideas on Neotropical raptor migration. Kyle McCarty and Pablo Porras commented on earlier drafts of the ms. This is conservation science contribution number 103 from Hawk Mountain Sanctuary.

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