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Raptor and large soaring bird migration across the Isthmus of Tehuantepec, Mexico: distribution, seasonality, and phenology

SERGIO A. CABRERA-CRUZ, JUAN A. CERVANTES-PASQUALLI, ERNESTO RUELAS INZUNZA, TERESO HERNÁNDEZ-MORALES and RAFAEL VILLEGAS-PATRACA

Summary

We present the first study of the spatial and temporal dynamics of raptors and large soaring birds from the Isthmus of Tehuantepec, Mexico. Using systematic migration counts from multiple localities in the southern states of Oaxaca and Chiapas, as well as observations of their flight trajectories during eight consecutive years (2007–2014), we describe the magnitude of these movements, their geographic extent, and the phenology of the most abundant species in both spring and fall seasons. The most abundant species were Turkey Vulture *Cathartes aura*, Swainson's Hawk *Buteo swainsoni*, Broad-winged Hawk *Buteo platypterus*, Wood Stork *Mycteria americana*, American White Pelican *Pelecanus erythrothynchos*, Franklin's Gull *Leucophaeus pipixcan*, and American Kestrel *Falco sparverius*. In spring, the seasonal average magnitude of migration was over 28,000 birds, while in autumn the average was over one million. The aggregated seasonal phenologies recorded illustrate a variety of migration patterns. The inter-annual variation is lower in autumn than in spring. Migrating raptors and other soaring birds did not seem to use any topographical feature as a leading line for their movements in spring, while in autumn they did. We estimated the main axis of spring flights to run along a SE–NW vector, while autumn migration follows a WNW–ESE general trajectory. Our results place the isthmus as one of the five most important sites in the world for raptors and soaring migrants. Sustaining annual migration counts at these sites is of high importance to track substantial portions (> 90%) of the global population of Turkey Vulture and Swainson's Hawk, as well as over 10% of the global population of Broad-winged Hawk. Autumn migration counts have the potential for long-term population monitoring.

Resumen

Presentamos resultados de la primer investigación sobre la dinámica espacial y temporal de aves rapaces y otras aves planeadoras grandes en el Istmo de Tehuantepec, México. Utilizando conteos sistemáticos de la migración en múltiples localidades en los estados sureños de Oaxaca y Chiapas, así como observaciones de sus trayectorias de vuelo durante ocho años consecutivos (2007–2014), describimos la magnitud de estos movimientos, su distribución geográfica y la fenología de las especies más abundantes registradas en primavera y otoño. Las especies más abundantes fueron *Cathartes aura*, *Buteo swainsoni*, *Buteo platypterus*, *Mycteria americana*, *Pelecanus erythrothynchos*, *Leucophaeus pipixcan* y *Falco sparverius*. En primavera, la magnitud promedio de la migración 2007-2014 fue de más de 28,000 aves; mientras que en otoño, de más de un millón. Las fenologías estacionales agregadas registradas ilustran varios patrones de migración. Las rapaces migratorias y otras aves planeadoras parecen no utilizar atributo topográfico alguno como línea guía en primavera, mientras que en otoño sí. Estimamos que el eje principal de los vuelos migratorios de primavera se alinea a un vector SE–NO, mientras que en otoño sigue una trayectoria general ONO–ESE. Nuestro trabajo ubica al istmo como uno de los cinco sitios más importantes del mundo para el paso de aves rapaces y planeadoras. Mantener conteos anuales de la migración en estos sitios es de gran importancia para monitorear grandes proporciones (>90%) de la población global de *Cathartes aura* y *Buteo swainsoni*, así como más del 10% de la población global de *Buteo platypterus*. Los conteos de la migración durante el otoño tienen el potencial de contribuir al monitoreo de poblaciones a largo plazo.

Introduction

A very large number of North American raptors, wading birds, and other large, thermal-soaring migrants fly twice a year between their breeding and non-breeding ranges along the Gulf of Mexico coastal plain, the lowlands of the Isthmus of Tehuantepec, and the Pacific Coast of Chiapas and Central America (Zalles and Bildstein 2000). This route, a defined pathway of abundant thermal convection with lateral limits set by large water bodies and mountain systems, was named the Mesoamerican Land Corridor by Bildstein and Zalles (2001), and has sparsely been studied from raptor migration monitoring stations set along this migration route. Several investigations have documented large numbers of migrating raptors along this corridor at several localities in Mexico (Ruelas *et al.* 2000), Guatemala (Montejo and Ruelas 1997), El Salvador (Pérez *et al.* 2013), Nicaragua (Arrengi and McCrary 2004, McCrary and Young 2008), Costa Rica (Hidalgo *et al.* 1995, Bildstein and Saborio 2000, Porras-Peñaranda *et al.* 2004), Panama (Batista *et al.* 2005), and Colombia (Bayly *et al.* 2014). This flyway is considered one of the most important corridors for migrating raptors in the world (Ruelas *et al.* 2009).

From the well-described geographic bottleneck in Veracruz, Mexico (Ruelas *et al.* 2000), migrants follow a southbound trajectory into the Isthmus of Tehuantepec. This flyway branches into two different routes, one of them crossing onto the Pacific slope across the Isthmus itself, used primarily by Turkey Vultures *Cathartes aura*, Swainson's Hawks *Buteo swainsoni*, Wood Storks *Mycteria americana*, American White Pelicans *Pelecanus erythrorhynchos*, and Franklin's Gulls *Leucophaeus pipixcan*, and a second route followed by Broad-winged Hawks *Buteo platypterus* and Mississippi Kites *Ictinia mississippiensis* into the heartland of Chiapas and Guatemala (Bildstein and Zalles 2001). American Kestrel *Falco sparverius*, a numerically prominent migrant, has been recorded abundantly along both routes. Within the isthmus region, the only locality with any published reports is Tonalá, Chiapas, about 500 km SE of Veracruz (Tilly *et al.* 1990).

The Isthmus of Tehuantepec is the narrowest part of Mexico, delimited on its northern boundary by the Gulf of Mexico and on the south by the Pacific Ocean. The isthmus is a land bridge that birds are obliged to follow in order to avoid crossing large bodies of water. The topography of the isthmus is well known, with explorations and detailed cartography dating back to the early 1800s for its potential to connect the Gulf and the Pacific (Von Humboldt 1811, Hermersdorf 1862, Binford 1989).

At the heart of the Isthmus lies a gap of lowlands known as Paso de Chivela (244 m above sea level) inserted within the Sierra de Tolistoque (or Sierra Atravesada), a low-elevation ridgeline of a maximum elevation of nearly 400 m that follows an east–west axis. This ridgeline is connected at its eastern end to the Sierras Orientales, a portion of the Sierra Madre del Sur, and to the west with the Sierras del Sur de Chiapas, part of the of the Cordillera Centroamericana (Gallo-Gómez 2009). At the isthmus region, the maximum elevation of the latter two ridges reaches heights above 2,800 m.

This area has been the subject of some studies of bird migration, motivated by the development of wind-energy facilities at the southern end of the isthmus, near the Pacific coast (Cabrera-Cruz *et al.* 2013, Villegas-Patraca *et al.* 2014, Cabrera-Cruz and Villegas Patraca 2016). These studies, however, had different foci, and do not contain detailed descriptions of the general patterns of migration through this area.

This paper presents the first detailed study of the spring and autumn migration of seven species of diurnal raptors and other large, thermal-soaring birds across the Isthmus of Tehuantepec, Mexico. Our aims are to quantify the magnitude of their migration and to identify the geographic extent of their flights relative to regional physiography. We also describe the seasonal patterns of these migrations and use data from a single long-term locality to document the phenology of the most abundant species.

Methods

Study area

We collected data from 11 migration monitoring stations to study the spring and autumn passage of raptors and large soaring migrants in the Pacific coastal plain of the Isthmus of Tehuantepec, Oaxaca, and one station in the coastal plain at the municipality of Tonalá, Chiapas, Mexico (Fig. 1).

The Oaxaca sites were distributed in the municipalities of Juchitán, Unión Hidalgo, Santo Domingo Ingenio, Asunción Ixtaltepec, and El Espinal (the names and coordinates of each site can be consulted in Table 1 and Figure 2). All of the Oaxaca sites are located within one of the

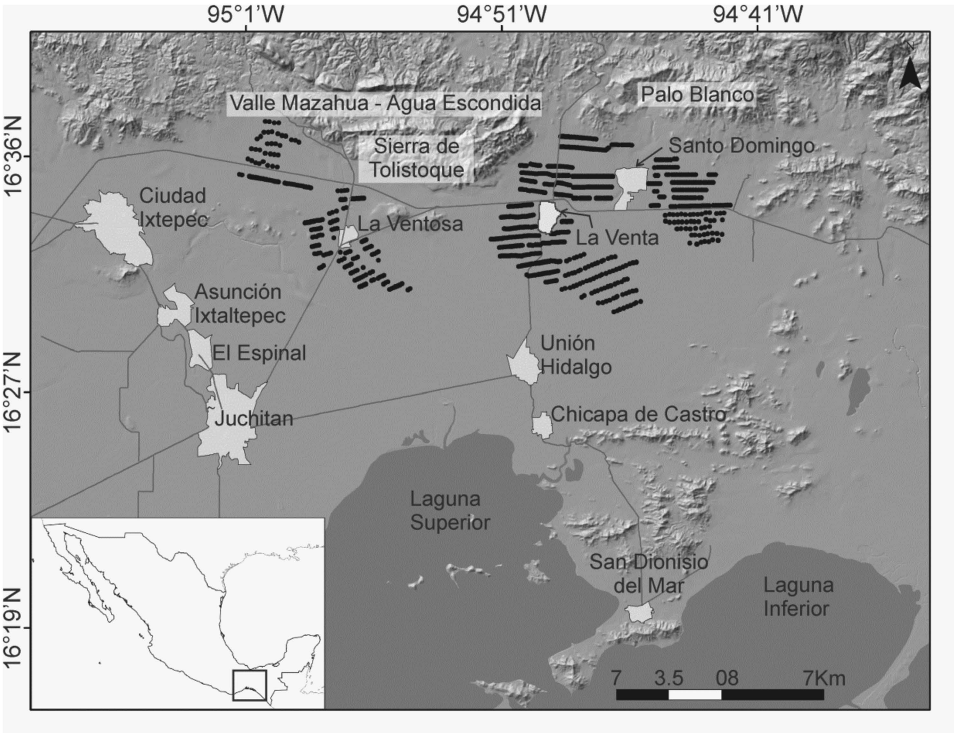

Figure 1. Location of the southern Isthmus of Tehuantepec, Oaxaca, Mexico. The names of topographic features listed in the text are framed; the names of towns and water bodies listed in bold typeface. The location of wind-energy generation facilities is illustrated with black points. Not in this map: the Tonalá, Chiapas site (see coordinates in Table 1).

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Table 1. Localities, sampling effort, and magnitude of migration at the Isthmus of Tehuantepec, Mexico.

Locality	Seasons of observation	Duration of observations	Seasonal count	Ranked abundance of species
Alesco				
16°27′30.71″N	S 2012	01 Apr–14 May (44 d)	26,093	FRGU, TUVU, WOST, AWPE, SWHA, BWHA, AMKE
94°53′35.55″W	F 2011	29 Sep–05 Nov (38 d)	186,107	TUVU, SWHA, WOST, BWHA, AWPE, AMKE
Bii Nee Stipa				
16°33′39.62″N	S 2013–2014	01 Apr–30 Apr (24 d)	12,986	FRGU, TUVU, AMKE, BWHA
94°58′23.29″W	F 2012–2014	10 Oct–06 Nov (23 d)	32,672	TUVU, SWHA, BWHA, AWPE, WOST, AMKE
Espinal				
16°30′20.03″N	F 2010	29 Oct–03 Nov (6 d)	764	TUVU, SWHA, AMKE, BWHA
94°58′50.83″W				
La Venta II				
16°35′45.99″N	S 2007–2014	26 Mar–17 May (40 d)	32,672	FRGU, TUVU, SWHA, AMKE, WOST, BWHA
94°48′21.76″W	F 2007–2014	13 Sep–12 Nov (55 d)	1,187,515	TUVU, SWHA, BWHA, WOST, AWPE, AMKE, FRGU
La Venta III				
16°34′56.19″N	S 2013–2014	01 Apr–30 Apr (27 d)	8,353	FRGU, TUVU, SWHA, BWHA, AMKE, AWPE, WOST
94°43′53.28″W	F 2012 – 2014	03 Oct–07 Nov (29 d)	313,188	TUVU, SWHA, BWHA, WOST, AWPE, AMKE
La Ventosa				
16°34′4.10″N	S 2013–2014	01 Apr–30 Apr (24 d)	13,264	FRGU, TUVU, AMKE, BWHA, SWHA
94°57′22.26″W	F 2012–2014	03 Oct–05 Nov (23 d)	11,715	TUVU, SWHA, AWPE, WOST, BWHA, AMKE
Oaxaca I				
16°33′33.53″N	S 2011, 2013	26 Mar–02 May (39 d)	7,109	FRGU, TUVU, SWHA, AMKE, WOST, AWPE, BWHA
94°43′14.26″W	F 2013	01 Oct–09 Nov (39 d)	63,351	TUVU, SWHA, BWHA, AWPE, WOST, AMKE
Peñoles				
16°36′2.53″N	F 2012	21 Sep–10 Nov (51 d)	46,956	TUVU, SWHA, BWHA, WOST, AWPE, AMKE
95°2′21.35″W				
Santa María				
16°13′15.41″N	F 2010	21 Oct–26 Oct (6 d)	7,285	TUVU, BWHA, AWPE, WOST, AMKE, SWHA
94°51′24.15″W				
Santo Domingo				
16°31′56.71″N	S 2013–2014	05 Apr–15 May (41 d)	4,722	FRGU, TUVU, SWHA, AMKE, WOST, BWHA
94°46′25.80″W	F 2014	22 Sep–09 Nov (49 d)	36,732	TUVU, WOST, AWPE, SWHA, BWHA, AMKE
Tonalá				
16°05′14.21″N	S 1992, 1997	31 Mar–13 Apr (14 d)	237,903	TUVU, SWHA, BWHA, FRGU, WOST, AMKE, AWPE
93°45′23.00″W				

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Table 1. Continued.

Locality	Seasons of observation	Duration of observations	Seasonal count	Ranked abundance of species
Unión Fenosa				
16°26′42.74″N	S 2011	18 Mar–05 May (49 d)	17,200	FRGU, TUVU, WOST, SWHA, AWPE, BWHA, AMKE
94°57′0.29″W	F 2010	23 Sep–31 Oct (35 d)	109,322	TUVU, SWHA, BWHA, WOST, AWPE, AMKE

Codes and abbreviations for the headers of this table: Seasons of observation: F=Fall, S=Spring; Duration of observations, start and end date (day/month), in parenthesis is the total or mean number of observation days; Seasonal count: combined total of all the species listed in the following column; Ranked abundance of species: Most to least abundant, TUVU = Turkey Vulture *Cathartes aura*, SWHA = Swainson's Hawk *Buteo swainsoni*, FRGU = Franklin's Gull *Leucophaeus pipixcan*, BWHA = Broad-winged Hawk *Buteo platypterus*, WOST = Wood Stork *Mycteria americana*, AWPE = American White Pelican *Pelecanus erythrorhynchos*, and AMKE = American Kestrel *Falco sparverius*.

areas with the highest potential for wind-energy production in Mexico (Elliott *et al.* 2003, Alemán-Nava *et al.* 2014), recently experiencing a substantial development of infrastructure. All of our study sites are located at elevations that range from 0 to 60 m. We consider these sites provide a good insight of the width of the migration front that raptors and other large, soaring birds are hypothesised to follow in the southern portion of the Isthmus.

Sampling design

We collected systematic data on the species composition, magnitude, and geographic and temporal extent of soaring bird migration during eight spring and eight autumn migration seasons (2007–2014) from the La Venta II wind-energy facility. Observations from this site took place from mid-September to mid-November, covering the peak of Turkey Vulture and Swainson's Hawk migration as reported for the Veracruz River of Raptors Project (Ruelas *et al.* 2000, Ruelas 2007). Simultaneously (in most years) we operated a series of other monitoring stations from different sites surrounding La Venta II; the duration of field seasons and the localities themselves were, however, uneven every season. We used data from these sites to supplement the observations from our main site (the number of field sampling days, seasons, and years for each site, are shown in Table 1).

Field data collection

We followed the standard data collection protocol of the Hawk Migration Association of North America (Kerlinger 1989, HMANA 2016). Our field technicians collected hourly weather (wind speed and direction, precipitation, cloud cover, cloud type), flight-recording conditions (visibility, number of observers, minutes of observation per hour), and migrant count totals. Identifications were made using 8 and 10× binoculars, Kowa TSN-661 20–60× telescopes, and field guides, mainly Howell and Webb (1995) and Sibley (2000). Because most of our efforts were centred on identifying, counting or estimating the numerous migrating raptors and soaring bird flocks and their flight trajectories, we collected very few data on age, sex, and colour morphs of the individuals observed. During our daily observations, we staffed each site with 1–2 lead observers and 1–2 assistants; the number of technicians varied at each count station according to flight intensity. Because tracking migration in areas with a large volume of migration is a complicated field task, we ensured that our lead field technicians had spent at least two years as trainees in this or other sites.

Individual counts of migrants were usually impossible due to the large volume of the migration. Instead, migrants observed were estimated as precisely as possible. Most birds

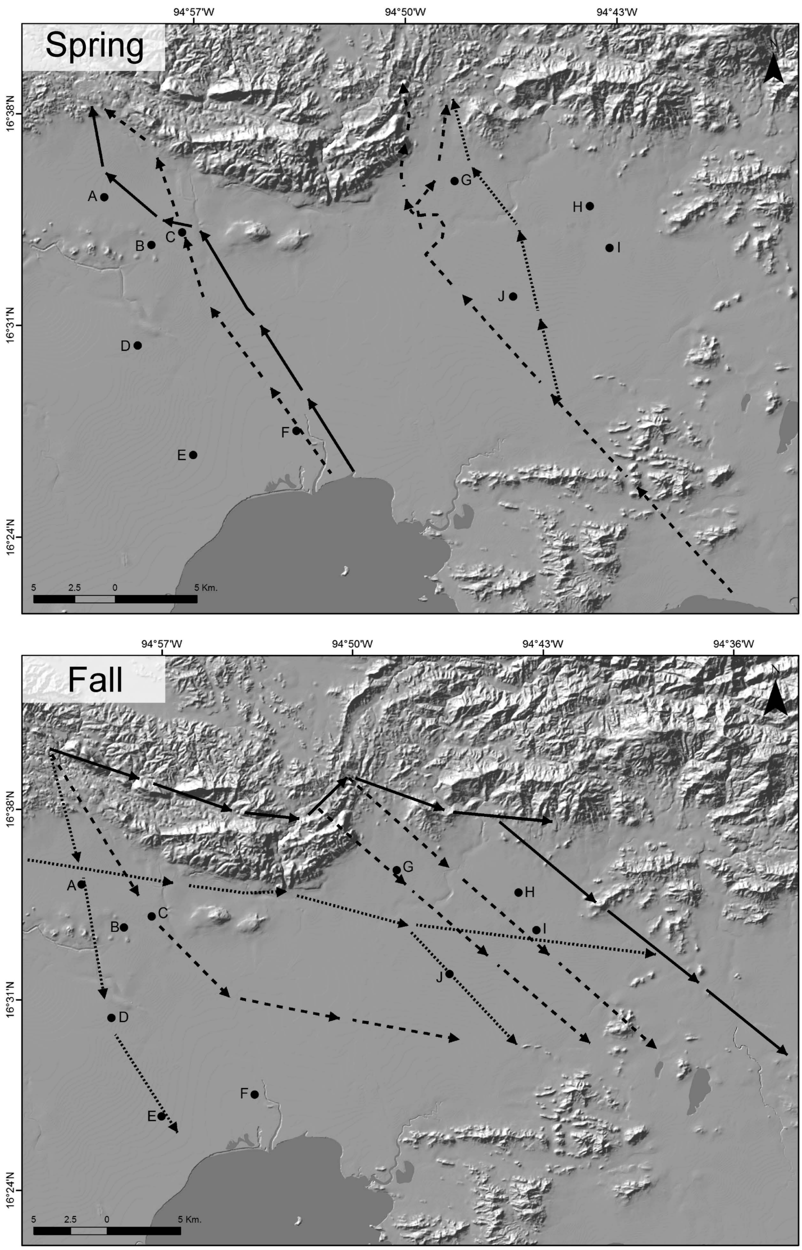

Figure 2. Migration paths followed by raptors and other large soaring birds in the coastal plain of the Isthmus of Tehuantepec, Mexico, obtained from eight years of spring and fall observations. Solid lines depict the most heavily used flyways, thick dotted lines less heavily used, and finely dotted the least used.

occurred in large flocks that used the thermal convection of the atmosphere for cross-country flights (Pennycuick 1998). These counts and estimations were made once the thermal-climbing period had finished and birds were in their straight-line gliding flights. Our field teams

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directly counted the number of birds when quantities were low (e.g. a few tens) and made estimations when numbers were large. Teams estimated the number of birds with the help of a hand tally-counter by counting a small group of birds (e.g. 10 individuals), and extrapolating the approximate area occupied by these 10 birds to the rest of the flock. The most used multiples in these estimations were 3, 5, 10, and 50 individuals. This method has been applied consistently over the years (e.g. Villegas-Patraca *et al.* 2014), and we consider that our methods produce conservative estimates.

Magnitude of migration and phenological descriptions

We used data only from our most systematically sampled site (La Venta II) to describe the phenology of the migration of the most abundant soaring species recorded there and its variation between years. For our phenological descriptions, we created aggregated seasonal timing charts by plotting the mean percentage of each year's total migration observed for each four-day period. We use this percentage to normalise these counts and make the graphs visually comparable across species as well as to make them independent of yearly count total.

Flight trajectories

The paths followed by migrants were irregularly used both within and among seasons, particularly during autumn (Malpica-Topete 2008, Gallo-Gómez 2009). Our technicians plotted the flight trajectories most frequently used by flocks of soaring birds engaged in migratory activity on each monitoring station and season on a map. Each map was printed in colour, depicting the roads, topography, localities (i.e. close towns, if any), location of wind turbines, and wind-power facility limits. These features worked as landmarks, useful for the technicians to accurately map the passage of birds.

Malpica-Topete (2008) recorded and analysed the spatial distribution of autumn flight trajectories of migrating raptors in the vicinity of La Venta II, following those hand-plotted maps, showing that most of the flocks flew to the south-east after leaving the Sierra de Tolistoque ridgeline and passing close to the north-eastern corner of the wind farm boundaries. Her results were in agreement with those of Villegas-Patraca *et al.* (2014), who tracked raptor migration with a marine radar unit, showing that the hand-plotting method is capable of reflecting the spatial displacement of flocks of migrating raptors with a high degree of accuracy. Observers recorded only flight trajectories that were used by migrating soaring birds. Plotted trajectories were arranged by order of magnitude, with continuous lines depicting the most heavily used pathways and dotted lines for those with less transit.

Results

Magnitude of migration in La Venta II

Seven species of soaring migrants accounted for 98.7% of all the birds recorded. Our counts of these most abundant species from the single site that has been studied systematically yielded an average of 28,651 individuals in spring and 1,030,108 in autumn (a > 36-fold difference between seasons; Table 2).

Spring flights were overwhelmingly dominated by Franklin's Gull and Turkey Vulture, with very small, almost incidental, numbers of the remaining species. In autumn, the number of individuals per species followed a more typical ranked-abundance pattern, with two species dominating these flights (Turkey Vulture and Swainson's Hawk) and the remaining species successively reducing their quantities significantly. However, the volume of the less-represented species in autumn still rivals that of the most abundant species in spring, e.g. the two least abundant species in autumn, Franklin's Gull and American Kestrel, each with a seasonal average of

Table 2. Spring and fall counts (2007–2014) of raptors and other large soaring migrants observed from La Venta II at the Isthmus of Tehuantepec, Mexico.

	Spring			Fall		
Species	Mean (SD)	Min	Max	Mean (SD)	Min	Max
Cathartes aura	1,682 ± 1,332	352	4,528	748,839 ± 565,450	198,427	2,103,992
Buteo swainsoni	49 ± 54	3	166	265,177 ± 275,301	7,422	905,579
Buteo platypterus	7 ± 5	3	18	12,998 ± 1,014	1,331	34,683
Mycteria americana	84 ± 106	3	316	1,555 ± 1,306	205	4,088
Pelecanus erythrorhynchos	30 ± 14	16	55	1,283 ± 988	220	3,556
Leucophaeus pipixcan	26,758 ± 1,896	1,896	73,509	152 ± 148	3	300
Falco sparverius	41 ± 2	2	215	104 ± 38	43	189

a few hundred individuals, would rank them as the third and fourth most abundant species, respectively, in spring (Table 2).

Spring and fall geographic distribution

The main axis of spring flights was estimated to run along a SE–NW vector (Figure 2). The Laguna Superior-Laguna Inferior coastal lagoon complex and the shoreline of the Pacific set the southern limits followed by these migrants. When overlaid on a digital elevation model, our observations indicate spring flights do not seem to be associated with topographic leading lines. In spring, migrants fly over open spaces and seem to look for mountain passes between both mountain systems (the Sierra de Tolistoque and the Chimalapas Mountains, as depicted in the thin and medium lines of Figure 2). Migrants seem to avoid the Sierras Orientales (part of the Sierra Madre del Sur in the western boundary of our study area). Our perception of spring geographic distribution has a bias towards what we observed in Franklin's Gull, the most abundant migrant of this season (93.4% of the mean abundance during spring migration). The differences in abundance in autumn was less contrasting: the three most abundant species, Turkey Vulture, Swainson's Hawk, and Broad-winged Hawk, ranged from tens to hundreds of thousands, distributing this perceived bias more evenly (Table 2).

Autumn axis of flight in turn follows a WNW–ESE general trajectory. During this season, flights are clearly associated with the topography of the Sierra de Tolistoque and the southern reaches of the Chimalapas Mountains (solid lines) along the southern boundaries of these mountain ranges (Figure 2). The course of migrants in autumn seems to largely follow the foothills of the Sierra de Tolistoque, particularly a narrow valley that runs parallel to the coastal plain that we call here Valle Mazahua-Agua Escondida, and the foothills of the Chimalapas Mountains to the east. Fewer individuals were observed to cross the open landscape of the coastal plain towards the Pacific.

Phenology

The aggregated (mean) seasonal phenologies recorded illustrate a variety of migration patterns (Figure 3). Although many of them are largely variable, as shown by the breadth of their confidence intervals, all of the variation occurs within relatively fixed temporal windows (Figure 3).

Turkey Vulture The spring migration of this species shows a platykurtic pattern (the flattest among all species recorded and the longest migration season) with a modest peak migration in late April. The migration of this bird begins in mid-March and ends approximately in mid-May. In autumn, the migration has a more abrupt (leptokurtic) process, beginning at the end of September and ending in early November, with a clearly marked peak migration in late October.

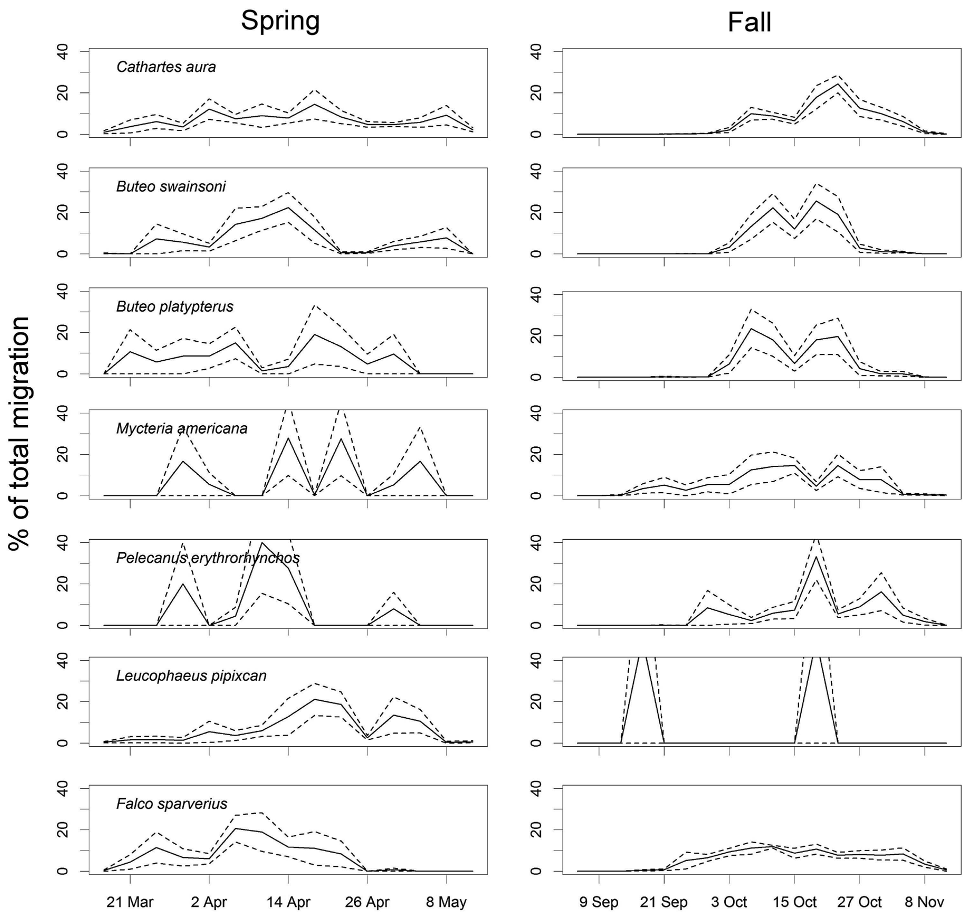

Figure 3. Migration phenology of the most abundant raptors and other large soaring birds at the Isthmus of Tehuantepec, Mexico, based on records from our La Venta II observation site. Data were collected during eight spring and eight fall seasons (2007–2014). Solid line = mean proportion of the total seasonal migration observed per four-day period; dashed lines = 95% confidence intervals.

In both seasons, the inter-annual variation of the volume of migration is low when compared to other species.

Swainson's Hawk. The spring migration of this species begins in late March and extends through mid-May, with a peak migration in mid-April. The aggregated seasonal phenology of spring migration shows a pattern of three pulses, with a marked "depression" in late April (Figure 3). Fall migrations have the shortest duration of all species, beginning at the end of September and extending into late October, with a bimodal appearance and a marked peak migration in mid-October.

Broad-winged Hawk. The migration of this hawk, the least abundant migrant in spring, shows a bimodal pattern in both seasons. In spring, its migration starts in mid-March and extends into early May, with the two apparent peaks separated by a period with very few migrants in mid-April. Autumn migration has a more leptokurtic pattern and a shorter duration, with two apparent peaks (both in October, one in the early part of the month and one at the end of it) and large inter-annual variation as illustrated by broad 95% confidence intervals.

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Wood Stork. This bird's spring migration, one of the least abundant, extends over a season that starts in late March and extends through early May. Because of its low abundance, a seasonal pattern of migration is difficult to discern, with four pulses apparent in its aggregated seasonal phenology. Autumn Wood Storks have the longest migration season among all species covered, with a platykurtic pattern that begins in mid-September and extends into early November. Its aggregated phenology shows a clear depression in late October.

American White Pelican. Its spring migration, with very few individuals, shows a noisy migration pattern, with high inter-annual variation and three pulses, that extends from late March into early May. In autumn, this bird starts its migration in late September and ends in early November. Autumn migration shows a moderate inter-annual variation, three apparent pulses, and an abrupt peak in mid-October.

Franklin's Gull. The most abundant spring migrant, whose seasonality extends for a long period between mid-March and early May. This gull, with a moderate inter-annual variation in migration, shows an apparent bimodal pattern with a peak in mid-April and another one in early May. With only three records of this species in autumn, this is the second-to-least abundant migrant. All observations have been collected in mid-September and mid-October and do not show a discernible pattern.

American Kestrel. The spring migration of this small falcon extends through a moderately long season that begins in mid-March and ends in late April. Its leptokurtic pattern shows a peak in early April and large inter-annual variation. This is the species with the most consistent migration in terms of quantity and phenology, with comparable patterns between the two seasons. In autumn, its migration is the most platykurtic and the one with the least inter-annual variation, beginning in mid-September and ending in early November.

Discussion

The Isthmus of Tehuantepec compared to other sites

A very large number of raptors and large soaring birds traverse the Isthmus of Tehuantepec during their spring and fall migrations. Our estimations of the magnitude of migration from the La Venta II site place the Isthmus of Tehuantepec among the five most important localities for migrating raptors and large soaring birds in the world, after migration monitoring sites in Veracruz, Costa Rica and Panama (Goodrich and Smith 2008, Ruelas *et al.* 2009). Globally, the La Venta II site is one of the two most important sites for Turkey Vultures and Swainson's Hawks (Goodrich and Smith 2008). When comparing the counts of individual species to those from other important localities in the North American continent, the average and high counts of both Turkey Vultures and Swainson's Hawks are second to the Veracruz River of Raptors Project and comparable to those of Talamanca, Costa Rica (Porras-Peñaranda *et al.* 2004, Goodrich and Smith 2008, Ruelas *et al.* 2009).

La Venta II is also very important for Broad-winged Hawks, Wood Storks, and American White Pelicans. This site is fourth after Veracruz, Costa Rica and Panama for the Broad-winged Hawk (Goodrich and Smith 2008), and no data are available to compare out counts of the remaining species in Table 2, but we suspect they also rank high among key migration sites in the continent as their seasonal counts are high when compared to North American population estimates (Rich *et al.* 2004).

Counts at La Venta II are sample a very large proportion of the world's total population of these species: up to 90% of the global populations of Turkey Vulture and Swainson's Hawks, and over 10% of the global population of the Broad-winged Hawk as estimated by Rich *et al.* (2004), Blancher *et al.* (2007) and Ruelas *et al.* (2010). Consistent migration counts at this site, therefore, are critical to understand population trends of these species and provide a strong argument in support of North American raptor migration monitoring programmes such as the Raptor Population Index Project (Bildstein *et al.* 2008, Ruelas 2009). Other broad scale monitoring initiatives, such as the Breeding

Bird Survey or the Christmas Bird Count, do not provide adequate coverage for non-passerine species (Dunn *et al.* 2005). Migration counts are, for the species treated in this manuscript, the single alternative or one of the few, to track their populations (Hussell and Ruelas 2008).

Large seasonal differences in migration counts are typical of migration monitoring sites (Goodrich and Smith 2008). The difference between our spring and fall migration counts is very striking, considering the flight corridor is geographically well-defined and alternative flight paths in the broader area of the isthmus are not known. Fieldwork dates are also appropriate to sample large portions of the migration of most species covered in this study. Many explanations of the difference between spring and autumn flights at other migration monitoring sites have been given, the most extended and supported with empirical evidence (and the one we concur with) is the fact that spring migration environmental conditions are more conducive to a more geographically dispersed flight, and therefore more complicated to track from fixed field sites (Bildstein 2006).

The inter-annual variation of counts in La Venta II is also worth highlighting. Even though the ranked abundance pattern of each species remains relatively constant (the most abundant, intermediate, and least abundant species recorded per season are roughly the same each year), the seasonal counts of all the species recorded are highly variable (Table 2). In eight spring and eight fall seasons, we have recorded differences that range from 3-fold to over 120-fold depending on the species. In this case, some of the inter-annual abundance per species suggest the migration in this whole region is much noisier, hence subject to stronger effects of other sources of variation, than most other tropical sites we have information from (e.g. Porras-Peñaranda *et al.* 2004, McCrary and Young 2008). Inter-annual variation in migration counts, however, is much lower for all species in autumn (Table 2), particularly for Turkey Vulture, Broad-winged Hawk, Wood Stork, and American White Pelican, the species with the highest potential population-level monitoring.

Our data also document the conservation significance of this flyway. It supports the inclusion of the region as an Important Bird Area (BirdLife International 2016a), updating and providing more detailed information about the migration of raptors and other soaring birds through the region. The Important Bird Areas Programme (BirdLife International 2016b) set criteria for global IBAs as follows: category Global A4 (Congregations), for sites with more than 1% of the global population of a given species, and > 20,000 individuals for waterbirds. These numbers are far exceeded by the three most common species in autumn (Table 2).

The Convention on Migratory Species (Galbraith *et al.* 2014), in turn, has identified the general area (Meso-American Corridor), as a global priority, and identifies the international legal framework and instruments, for the protection of sites that meet their criteria of international importance, such as the Isthmus of Tehuantepec.

Migration routes

Our data support the general route of the Mesoamerican corridor hypothesised by Bildstein and Zalles (2001), who suggested that spring migrating Turkey Vultures and Swainson's Hawks follow the Pacific slope flyway before crossing to the Gulf of Mexico slope at the Isthmus of Tehuantepec. However, our spring counts of these species were very low when compared with those in autumn, suggesting that the proportion of spring migrants that follow the coast along the Pacific slope is lower during this season and that a much larger proportion of migrants that cross into the Gulf of Mexico must do so following a different (farther inland) route (e.g. Bryan *et al.* 2008). This is not by any means uncommon, as broad differences in spring and autumn migration routes have been documented in many raptor (e.g. Leshem and Yom-Tov 1996) and non-raptor species (Tøttrup *et al.* 2012, La Sorte *et al.* 2016). Some authors suggest that birds have not only different routes, migration ecologies, and energy-saving strategies, but different aims for each of these two seasonal movements, such as early return migration in spring to improve reproductive success (Berthold 2001) or find high-quality winter territories to optimize non-breeding season survivorship (Newton 2010).

The specific routes followed by migrants in spring and autumn are different as well. Spring migrants in our study area seemed to follow trajectories that correspond less to physiographic features than those of autumn. In Veracruz, the reason for a broader spring migration front has been hypothesised to be a response to a much higher availability of thermal convection that enables soaring birds to migrate over a much broader thermal pathway that the one available in autumn (Ruelas 2007). The boreal 'spring' is, in reality, the dry season at the Isthmus of Tehuantepec, the period of the year with the highest daytime temperatures and hence much more abundant thermal convection (García 2004). Soaring migrants respond accordingly, with higher flight heights and more dispersed migration fronts (Bildstein 2006).

Autumn migration routes follow leading lines more closely. It is possible that the lower availability of thermal convection during the boreal 'autumn' (the rainy season at the isthmus) reduces the migration front of migrants forcing them to fly over the relatively few areas with robust thermal convection. The specific routes visually estimated at our observation sites follow a general 'WNW–ESE' (about 112-degree) axis compared to the 143.9-degree orientation found in the same localities using a marine radar (Villegas-Patraca *et al.* 2014).

Seasonal phenologies

Bildstein (2006), and Goodrich and Smith (2008), have summarised the phenology of migration in North American raptors and explored the correlates between phenology and migration ecology traits for different species. For example, Bildstein (2006) has found that species of obligate ('total') migrants that have longer distances between their breeding and non-breeding ranges migrate south earlier in autumn and arrive later in the spring as a consequence of those longer distances.

The patterns observed at the isthmus correspond to this generality. Autumn migration timing of the two species with the earliest migration are Broad-winged and Swainson's Hawks, which indeed have the longest migration distances. The latitudinal difference between the centroids of the Broad-winged Hawk's breeding and non-breeding ranges is about 45 degrees of latitude (Goodrich *et al.* 1996), whereas the breeding-non-breeding latitudinal difference for the Swainson's Hawk is about 85 degrees (England *et al.* 1997). We do not have information of the specific breeding and wintering range for the populations of American White Pelicans, Wood Storks, and Turkey Vultures, but a close examination of their distribution maps reveals much shorter migration distances than those of the two hawks (Kirk and Mossman 1998, Coulter *et al.* 1999, Knopf 2004).

Spring migrants with noticeable early spring migrations are American White Pelican and American Kestrel, which also have migration distances shorter than many of the remaining species, and late migrants such as Turkey Vultures have comparatively longer migration distances (Kirk and Mossman 1998, Smallwood and Bird 2002, Knopf 2004).

Another important demographic feature that can be quantified in studies of migration phenologies is the difference between sexes, age classes, and populations from different geographical areas (e.g. Stotz and Goodrich 1989, DeLong and Hoffman 1999, Smith *et al.* 2001). However, such data are very difficult to track in localities with a high migratory volume and were not recorded during this investigation.

Many of our migration phenologies (Figure 3), particularly those in spring, most certainly reflect small sample sizes and other data-related noise rather than demographic parameters. The more 'robust' phenologies plotted with our autumn data show, in at least three cases (Broad-winged and Swainson's Hawks, and Wood Storks), bimodal patterns that could be attributed to differences in migration timing of populations, migration timing between years or differences between sex and age classes. The aim of our study, the data collection protocol in use, and the large volume of the migration recorded at the isthmus made it impossible for us to collect data to address this interesting question. The seasonal phenologies of the seven species examined in this paper generally correspond to those reported in Veracruz (Ruelas 2007).

The data provided by our investigation places the Isthmus of Tehuantepec alongside the most important migration sites in the world, particularly for Turkey Vultures, Swainson's, and Broad-winged Hawks (Zalles and Bildstein 2000). It provides additional support for the designation of the isthmus as an Important Bird Area (BirdLife International 2016a). Our observations of specific trajectories chosen by soaring migrants while crossing the isthmus provides an insight into the role of topography in defining migratory pathways, and could serve as guidance for decision-makers of the booming wind-power generation industry in the region and potentially reducing the negative impacts of this industry on migratory birds (Villegas-Patraca *et al.* 2014). This an area of research whose importance warrants further work.

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SERGIO A. CABRERA-CRUZ**

Instituto de Ecología, A.C., Unidad de Servicios Profesionales Altamente Especializados, Coatepec, Veracruz, Mexico 91520 and University of Delaware, Department of Entomology and Wildlife Ecology, Newark, DE 19716, USA.

ERNESTO RUELAS INZUNZA*,**

Universidad Veracruzana, Instituto de Biotecnología y Ecología Aplicada, Xalapa, Veracruz, Mexico 91090.

JUAN A. CERVANTES-PASQUALLI**, TERESO HERNÁNDEZ-MORALES, RAFAEL VILLEGAS-PATRACA*

Instituto de Ecología, A.C., Unidad de Servicios Profesionales Altamente Especializados, Coatepec, Veracruz, Mexico 91520.

**Authors for correspondence; e-mail: rafael.villegas@inecol.mx and ruelas.uv@gmail.com*

***These authors contributed equally to this work; the authorship order was decided by playing the rock-paper-scissors hand game*

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